https://doi.org/10.35662/unine-thesis-3026

Social learning in wild sooty mangabey vocal communication

PhD thesis submitted to the Faculty of Science

Institute of Biology

University of Neuchâtel

For the degree of Doctor of Philosophy

By

José Julián León Ortega

Dissertation committee:

Prof Klaus Zuberbühler, University of Neuchâtel, Thesis director

Prof Redouan Bshary, University of Neuchâtel, Internal examiner

Prof Carel van Schaik, University of Zurich, External examiner

Defended on the 17th of January, 2023

Université de Neuchâtel
Faculté des sciences

Rue Emile-Argand 11
CH-2000 Neuchâtel
doctorat.sciences@unine.ch

IMPRIMATUR POUR THESE DE DOCTORAT

La Faculté des sciences de l'Université de Neuchâtel autorise l'impression de la présente thèse soutenue par

Monsieur José Juliàn León Ortega

Titre :

"Social learning in wild sooty mangabey vocal communication"

sur le rapport des membres du jury composé comme suit:

- Prof. Klaus Zuberbühler, directeur de thèse, Université de Neuchâtel, Suisse
- Prof. Redouan Bshary, Université de Neuchâtel, Suisse
- Prof. Carel van Shaik, Université de Zürich

Neuchâtel, le 2 mars 2023

Le Doyen, Prof. R. Bshary

Dedication

To Sebastian Ramírez and Pablo Stevenson for their life in the forest

Acknowledgements

This document is written in the singular first person but it is the result of the work and effort of many people, all of them have my most sincere gratitude.

First of all, I would like to thank Professor Klaus Zuberbühler for giving me this incredible opportunity. I am grateful for all the support you provided me during this experience and the freedom you gave me to conduct this research. I also appreciate the trust you put in me to manage the Taï Monkey Project during my time on the field. Before starting my PhD, I admired you for your research, now I also respect you for the person you are.

I would like to thank Professors Redouan Bshary and Carel van Schaik for accepting to be part of my thesis committee as internal and external examiners, respectively. I also thank Doctor Catherine Crockford for participating in two thesis chapters as a coauthor.

Thank you to all funders of this research, including the Swiss National Science Foundation and the Swiss National Centre of Competence in Research (NCCR) Evolving Language. I thank the Centre Suisse de Recherches Scientifiques (CSRS), the Ministère de la Recherche Scientifique, the Ministère de l'Agriculture et des Ressources Animales and the Office Ivoirien des Parcs et Réserves (OIPR) of Côte d'Ivoire for support and permission to work in the Taï National Park.

I collected data at the Taï Monkey Project (TMP) run by Professors Klaus Zuberbühler and Scott McGraw. The TMP –and this thesis– would not exist without the skilled, wonderful employees of the Taï Monkey Project and their caring families, Ferdinand Belé, Frederic Gnépa, Bertin Dioré, Ernest Kamy, Noel, Paterson Kalo and Landri Belé have my eternal gratitude and a big place in my heart. They welcomed me into their communities, villages, and families with incredible kindness and generosity. I also thank Doctor Anderson Bitty for his logistic support in Côte d'Ivoire. This thesis also was possible due to the help of amazing field assistants, all the days I spent in the field with Çağla Önsal, Valentina Pezzoli and Constance Thiriau would remain in my memory. I also want to thank Maxence Decellieres and Clementine Bodin whom I collaborated on interesting primatology studies during my time in the Taï forest. The TMP is one of the best field projects in the world, only because of the effort of all the people involved in it.

I am grateful to Doctors Catherine Crockford and Roman Wittig and the Taï Chimpanzee Project (TCP) and its staff for support in the field.

Back at the university, Alba, Alice, Emilie, Marion, Yaelle and all other lab members, thank you for so many good memories, lunch, parties and interesting discussions. Adwait, you were a great labmate, I was really happy when we met again in Konstanz and I hope it happens again. I would like to thank Andrea B., who helped me survive all the administrative paperwork on my arrival at Neuchâtel. I also appreciate the assistance and kindness from the Biology Secretary and administration team of the University. Outside the primate UniNe world, I thank all the friends who have supported me in Neuchâtel, especially Carlitos, Rocio, Patricio, Alfonso, Florian, Sandra, Sara, Tiago, Luis, Mónica, Rutinha, Otti and Geoffrey. I will never forget your friendship. Alida and Auriane, I have a special place for you in my heart, your friendship gave me many laughs and a home when I was far from Colombia, you have no idea how grateful I am to you for that and so more. Alida, your family also has been so kind to me, I am in debt to all of you. In this adventure, I was lucky enough to get two lifetime friends: Miguel, your infinite curiosity and your ability to spot beauty in the simplest things always reminded me of the nice side of science and life. I hope we continue having great conversations and football afternoons and nights. Un abrazo, compita. Melissa, the Titi monkey queen, I cannot even start to count the number of times we have been happy together. Since you adopted me for my first European Christmas, I have enjoyed our friendship so much. I love you guys. I also want to thank Diana, Manuel, Nathalia and the rest of the LEBTYP diaspora in Europe. It is because of all of you people, and others that I did not have space to mention, that I learned to love my time in Neuchâtel.

I thank Ari, Claudio, Martina, Hannah, Danielle, Katrin, Sarah, Sara and Cini for the time I spent in Konstanz, and I hope to see you again and share more laughs when I return to Germany. I thank Dayana M. for her kind understanding, efforts and loving company. I also thank Carolina S. for her writing, love, patience and support.

Finally, my parents, grandparents, family and friends have always encouraged me with love throughout my life choices. Their love and patience keep making me a better person every day. Andrea, bruja, there are no words to describe how grateful I am to you. I was able to go through this part of my life because of you, this PhD was not possible without your love and support. All of you have my most sincere love and gratitude.

Summary

Elucidating the origin of language is considered one of the hardest problems in science. There is considerable support for the idea that the basic components of human cognition, including the language faculty, did not emerge de novo, but have deep roots in the primate lineage. Although much is known about how humans acquire language, and even how birds acquire song, a largely open question is how non-human primates acquire their communicative competence. Comparative research can help us this gap of knowledge undermines our understanding of how deep these evolutionary roots are.

Here, I conducted a set of field experiments with free-ranging sooty mangabeys, a primate species occurring in Taï National Park, Côte d'Ivoire, to shed light on how non-human primates acquire their communicative capacities. First, I combined direct behavioural observations with playback experiments to study the development of con- and heterospecific alarm calls recognition in sooty mangabeys. I found that communicative competence was acquired during the juvenile stage, with alarm call comprehension learning preceding appropriate vocal usage and with no clear difference in learning of con- and heterospecific signals. I also found that, during early stages of life, social referencing, a proactive form of social learning, was key in the acquisition of competent alarm call behaviour.

In a second experiment, I provided one of the few systematic, direct, empirical tests under natural conditions of Seyfarth & Cheney's influential developmental model –the idea that primates learn to communicate by undergoing a cognitive pruning process. Using models of dangerous vipers and not-venomous colubrid snakes, I showed that young juveniles perceived all snakes as dangerous, frequently engaged in social referencing and indiscriminately alarm called, whereas adults responded faster to vipers than colubrids but never alarm called to the latter, unlike juveniles. These results empirically demonstrate that snake predator learning in sooty mangabeys starts with over-generalisation followed by subsequent refinement via social learning.

In a third experiment, I assessed the capacity of sooty mangabeys to socially learn predator knowledge from alarm calls. During individual presentations, I exposed subjects to a novel, chimeric predator model with both snake- and leopard-like visual features in conjunction with playbacks of conspecifics' leopard and snake alarms. I found that the subjects' response patterns to the predator model corresponded to the meaning of the alarm calls they heard during the first encounter, suggesting that they classed the model as either belonging to the snake or leopard category. Nearly 2 years later, I exposed a third of the same individuals to the same predator model for a second assessment and found that subjects continued to show the same anti-predator response, demonstrating long-term semantic memory from one single experience.

In conclusion, non-human primates learn to communicate by a cognitive pruning process that fine-tunes anti-predator and alarm call behaviour. Primate vocal learning is governed by an underlying cognitive development, which departs from innate, over-generalising responses to basic animal classes, followed by subsequent refinement driven by social learning. This social learning process starts during their early stages of life and is refined as the animals mature, and equally shapes the interpretation of alarm calls from their own and other species. Overall, this work made progress with an important scientific problem, that is, how primates acquire the ability to socially learn to communicate, by observing and interacting with others, a core component of the human language faculty.

Keywords:

Language evolution, Primates, Vocal communication, Alarm calls, Social learning, Sooty mangabeys, *Cercocebus atys*.

Résumé

Élucider l'origine du langage est considéré comme l'un des problèmes les plus difficiles de la science. Il existe un soutien considérable à l'idée que les composants de base de la cognition humaine, y compris la faculté de langage, ne sont pas apparus de novo, mais ont des racines profondes dans la lignée des primates. Bien que l'on en sache beaucoup sur la façon dont les humains acquièrent le langage, et même sur l’acquisition du chant des oiseaux, une question restant largement ouverte est de savoir comment les primates non humains acquièrent leur compétence communicative. La recherche comparative s’avère être d’une grande aide pour palier à ce manque de connaissances sur la compréhension de la profondeur de ces racines évolutives.

Ici, j'ai mené une série d'expériences sur le terrain avec des mangabeys fuligineux en liberté, une espèce de primate présente dans le parc national de Taï, en Côte d'Ivoire, pour éclairer la façon dont les primates non humains acquièrent leur faculté de communication. Tout d'abord, j'ai combiné des observations comportementales directes avec des expériences de lecture pour étudier le développement de la reconnaissance des cris d'alarme con- et hétérospécifiques chez les mangabeys fuligineux. J'ai constaté que la compétence communicative était acquise au stade juvénile, avec un apprentissage de la compréhension des appels d'alarme précédant l'utilisation vocale appropriée et sans différence claire dans l'apprentissage des signaux con- et hétérospécifiques. J'ai également constaté que, durant les premières étapes de la vie, la référence sociale, une forme proactive d'apprentissage social, était essentielle à l'acquisition d'un comportement d'appel d'alarme approprié.

Dans une deuxième expérience, j'ai fourni l'un des rares tests systématiques, directs et empiriques dans des conditions naturelles du modèle de développement influent de Seyfarth et Cheney : l'idée que les primates apprennent à communiquer par processus d'élagage cognitif. En utilisant des modèles de vipères dangereuses et de serpents colubridés non venimeux, j'ai montré que les jeunes juvéniles percevaient tous les serpents comme dangereux, étaient fréquemment engagés dans des références sociales et lançaient des appels d'alarme sans discernement. Par opposition, les adultes répondaient plus rapidement aux vipères que les colubridés et ne faisaient jamais d'appel d'alarme à ces derniers, contrairement aux juvéniles. Ces résultats démontrent empiriquement que l'apprentissage de la prédation de serpents chez les mangabeys fuligineux commence par une surgénéralisation avant d'être suivie d'un raffinement ultérieur par apprentissage social.

Dans une troisième expérience, j'ai évalué la capacité des mangabeys fuligineux à apprendre socialement des connaissances sur les prédateurs à partir de cris d'alarme. Par l'utilisation de présentations individuelles, j'ai exposé des sujets à un nouveau modèle de prédateur chimérique avec des caractéristiques visuelles de serpent et de léopard en conjonction avec des lectures d'alarmes de léopard et de serpent de congénères. J'ai trouvé que les schémas de réponse des sujets au modèle prédateur correspondaient à la signification des appels d'alarme qu'ils avaient entendus lors de la première rencontre. Cela suggère qu'ils classaient le modèle comme appartenant à la catégorie serpent ou léopard. Près de deux ans plus tard, j'ai exposé un tiers des mêmes individus au même modèle de prédateur pour une deuxième évaluation et j'ai constaté que les sujets continuaient à montrer la même réponse anti-prédateur, démontrant une mémoire sémantique à long terme à partir d'une seule expérience.

En conclusion, les primates non humains apprennent à communiquer par un processus d'élagage cognitif qui affine le comportement anti-prédateur et d'appel d'alarme. L'apprentissage vocal des primates est régi par un développement cognitif sous-jacent, qui s'écarte des réponses innées et trop généralisatrices aux classes animales de base, suivi d'un raffinement ultérieur entraîné par l'apprentissage social. Ce processus d'apprentissage social commence au cours des premiers stades de vie et s'affine à mesure que les animaux grandissent, et façonne également l'interprétation des appels d'alarme de leur propre et des autres espèces. Dans l'ensemble, ce travail a fait avancer un problème scientifique important, à savoir la façon dont les primates acquièrent la capacité d'apprendre socialement à communiquer, en observant et en interagissant avec les autres, une composante essentielle de la faculté de langage humain.

Mots-clés :

Évolution du langage, Primates, Communication vocale, Cris d'alarme, Apprentissage social, Mangabeys fuligineux, *Cercocebus atys*.

Table of Contents

Chapter 1: General Introduction

1.1 Human language and animal communication

Communication has been defined as a transfer of information between two or more individuals that cause some kind of change in receivers (Tomasello, 2008) - but what is information? Seyfarth et al. (2010) extended Shannon's (1948) definition—a statistical measure of uncertainty—to define it a reduction of uncertainty about the signaller's intentions and likely behaviour in the recipient. All animals communicate, which can include electric, seismic, thermal, chemical, tactile, visual or acoustic cues (Searcy & Nowicki, 2010). Humans also communicate, although it is usually stated that the main form of human communication – language– is unique among all animal communication systems and fundamentally different from it (Chomsky, 2017).

It is certainly true that humans have far greater control over vocal production than many other animal species, especially when compared with non-human primates. One important research question therefore concerns the transition from non-linguistic to linguistic communication and, specifically, what changes occurred in the key components. Recent research increasingly suggests continuity at multiple levels between primate vocal and human linguistic behaviour rather than assuming profoundly different systems (Bergman et al., 2019). Therefore, comparative research on animal vocal communication systems, especially on our closest living relatives–the non-human primates, is promising to clarify the evolutionary history of language.

Despite the marked differences between human language and non-human primate vocal communication systems, comparative methods a powerful tool to identify homologues and to infer hypotheses about how and when human communicative capacities were built on abilities present in the primate lineage (Hauser et al., 2002). The first studies in non-human primate communicative capacities were mainly restricted to human-raised apes and conducted under captive conditions (Hayes, 1951; Kellogg & Kellogg, 1933). Even though these early research efforts made some valuable contributions to the understanding of non-human primate communication, they had limited success and received harsh criticism (Krause & Beran, 2020; Pepperberg, 2017). Most critiques concerned anthropomorphism and low levels of ecological validity inherent to studying captive animals. Studying primate communication and cognition in natural settings is therefore more promising and arguably essential to understand the mechanisms and function of signalling behaviour and the cognitive skills involved in it (Rosati et al., 2022).

For the past decades, significant progress has been made in the understanding of non-human primate communication in natural contexts. Although primate vocal communication appears to be fundamentally different from human speech, some components of language have been identified in different primate species. For instance, primates can use acoustic signals to denote external events (Clarke et al., 2006; Clay & Zuberbühler, 2011; Seyfarth et al., 1980; Zuberbühler, 2003), occasionally in even by meaningful signal combinations (Arnold & Zuberbühler, 2006; Crockford & Boesch, 2005; Leroux & Townsend, 2020; Ouattara et al., 2009). Moreover, different audiences can affect their vocal behaviour in distinct ways (Crockford et al., 2012, 2017; Laporte & Zuberbühler, 2010; Wich & Sterck, 2003), and occasionally there is evidence that they manipulate conspecifics with calls (Wheeler, 2009).

Despite decades of research efforts on a range of primate species, one key feature –acquisition and vocal development – has received relatively little empirical attention (but see Hauser, 1989; Seyfarth & Cheney, 1980, 1986). This is striking if we take into account that there is a large literature on how humans acquire their communicative capacities and skills (Chomsky, 1965; de Boer, 2005; Kuhl, 2000; Luchkina & Waxman, 2021; Mohamad Nor & Rashid, 2018; Seidenberg, 1997).

1.2 How do non-human primates learn to communicate?

Like humans, non-human primates rely on vocal communication as their main mode of communication (Fedurek & Slocombe, 2011), although other modalities also play a role, especially visual and olfactory communication. Particularly great apes perform a variety of gestures that appear very flexible and intentionally produced and some may even be learned (Genty et al., 2009; Liebal & Call, 2012), suggesting more similarities with human language than primate vocal signals (Tomasello, 2008). Thus, to fully understand human language evolution, it is essential to investigate language as a multimodal system (e.g., vocal, gestural and facial signals) (Slocombe et al., 2011). Acknowledging this, in this thesis I focused my research on the vocal communication of non-human primates only.

Conventionally, research in the vocal–auditory domain distinguishes between three processes underlying vocal ontogeny: production, usage and comprehension. Vocal production refers to the selective modification of the structure of existing vocalizations or the production of new calls, vocal usage comprises the uttering of vocalizations in specific contexts, while vocal comprehension encompasses the association of a sound with its source and the understanding of what the sound predicts (Fischer & Hammerschmidt, 2020). It is important to highlight that while these fundamental processes are interconnected and mutually influenced by each other (many vocalizations are produced or used differently depending on the caller's understanding of what the sound 'stands for'), vocal production and usage are mostly focused on the caller, whereas vocal comprehension is focused on the listener.

To date, there is sparse evidence that non-human primates have the capability to learn new vocalizations. In a recent review Lameira (2017) identified around twenty studies that produced evidence for vocal (production) learning in primates, including modification and acquisition of new calls. However, it is clear that at the vocal production level, non-human primates have limited, structurally fixed vocal repertoires, with calls frequently linked to specific contexts and with little acoustic modification during development (Fischer, 2017; Hammerschmidt & Fischer, 2008). This is in contrast to songbirds, parrots, bats, pinnipeds, cetaceans and elephants that are on par with humans in terms of vocal learning abilities (Janik & Slater, 2000; Lattenkamp & Vernes, 2018; Slater, 2006). On the other hand, despite such production constraints, non-human primates have considerable flexibility in call comprehension and usage (Cheney & Seyfarth, 2018). Thus, in primates it is important to distinguish between rare production learning and common usage and comprehension learning (Janik & Slater, 2000).

How do non-human primates learn to produce, use and comprehend their vocalisation? The theoretical framework can be grouped into three, nonexclusive hypotheses, all with varying volume of evidence: communicative competence is hard-wired, self-learned or socially learned.

Initially, vocal communication in non-human primates was thought to be hard-wired and directly governed by affective states (Fischer & Price, 2017): production is innate, reflexive and refers merely to the internal states of the caller. Under this view, call development does not require much environmental or social input. Evidence mainly comes from studies with deaf, acoustically isolated or cross-fostered captive monkeys. For example, studies in infant squirrel monkeys deafened surgically at birth or deaf-born showed that their vocalizations did not differ from the ones produced by hearing animals (Hammerschmidt et al., 2001; Talmage-Riggs et al., 1972; Winter et al., 1973). On the contrary, other deafening experiments reported strong abnormalities in call structure and the persistence of infant-like calls into adulthood in common marmosets (Roupe et al., 2003). Similarly, there is evidence in favour (Eisenberg, 1976; Hammerschmidt et al., 2000, 2001) and against (Newman & Symmes, 1974) the idea that acoustic isolation does not affect primate vocal development. Cross-fostering experiments in Rhesus and Japanese macaques (infants of one species reared with foster mothers of other species) showed that food calls made by cross-fostered infants were dissimilar to those of infants reared by their biological mothers, but similar to normally raised infants of the foster species (Masataka & Fujita, 1989). However, this research has been heavily criticised. As a matter of fact, a follow-up study was unable to replicate these results, possibly due to the acoustic variability and similarity of the calls in both species (Owren et al., 1992). Moreover, since the acoustic features of calls of closely related species are often highly conserved, the idea is that primate utterances are not only innate but evolve along phylogenetic lineages (Meyer et al., 2012; Price et al., 2014; Thinh et al., 2011). However, communicative competence also involves call usage and comprehension, which is unlikely to be hard-wired because environmental conditions vary in time and space, and relevant references are too diverse for any kind of biologically programmed system to evolve (Lima & Dill, 1990).

A second way to acquire communicative competence is through individual learning, whereby an individual acquires a new behaviour or skill via trial-and-error and interaction with the world (ontogenetic ritualization) (Pika et al., 2003). Learning through individual trial-and-error can be very rapid as demonstrated in adult West African green monkeys when exposed to a novel threat, i.e., a remotely operated drone (Wegdell et al., 2019). Individually learned behaviours and signals are more likely to persist if low-cost opportunities are readily available (Thornton & Clutton-Brock, 2011). Studies on the gestural communication of great apes conclude that the majority of gestures are learned via individual learning (reviewed in Pika & Liebal, 2006). On the contrary, individual learning is not effective if mistakes are very costly, e.g., facing a predator, in which case natural selection should favour social learning (see below). Finally, when self-learning occurs, it is not clear what kind of feedback might encourage novel signal-context associations.

A third possibility to acquire and maintain communicative competence is via social learning.

Here, a naive individual obtains information from more experienced ones by observing and interacting with them (Galef & Laland, 2005). This is an advantageous way of learning appropriate responses to specific situations as individual learning implies a trial and error dynamic, and this is often a costly way to learn (Kendal et al., 2005). The typical case in natural situations is that young or inexperienced individuals learn from observing others interacting with the environment, such as what plants to avoid or how to optimize foraging (Galef & Giraldeau, 2001; Rapaport & Brown, 2008), how to interact (both in mating and conflict contexts) with certain group members (Peake & Mcgregor, 2004; White, 2004), or how to recognize a predator (Curio et al., 1978; Griffin, 2004). Despite that non-human primates have traditionally been considered non-vocal learners, currently, there is more and more evidence that juvenile non-human primates learn from adult models how to use vocalizations in contextually appropriate ways (Cheney & Seyfarth, 1990; Deshpande et al., 2022; Lemasson et al., 2011).

Primate alarm calling: production, usage and comprehension

Primate alarm calls have been a useful model to address questions regarding animal cognition and communication. Alarm calls are not only conspicuous signals but also refer to a great extent to external referents, i.e., predators, which make them easier to manipulate experimentally than other calls produced during other contexts, e.g., social interactions (Gill & Bierema, 2013; Townsend & Manser, 2013). Moreover, as predation risk varies in time and space, it is unsurprising that in many species anti-predator behaviour appears to result from a mix of innate species-specific and flexible learned responses (Mery & Burns, 2010). Thus, alarm calls have a key role in the study of flexibility in vocal production, usage and comprehension, and in the acquisition of communicative competence (Zuberbühler, 2007).

The vervet monkey alarm call system —a textbook case of communication in animals— has originally suggested the presence of human-like semantic abilities in monkeys (Seyfarth et al., 1980a, 1980b), although more recent work has challenged this view (Price et al., 2015; Wheeler & Fischer, 2012). Vervet monkeys produce acoustically distinct alarm calls in response to their main predators (leopards, eagles, snakes) and show appropriate antipredator responses when hearing these calls, e.g., rapidly climbing into trees when hearing leopard alarms versus scanning the sky or running for cover when hearing eagle alarms (Seyfarth et al., 1980a). Follow-up research has produced comparable evidence in other primates, suggesting that such abilities are a general feature of primate cognition and, most likely, many other groups of animals (Arnold & Zuberbühler, 2006; Fichtel, 2020; Fichtel & Kappeler, 2002, 2011; Fischer et al., 2001; Fischer & Hammerschmidt, 2001; Kirchhof & Hammerschmidt, 2006; Manser, 2001; Manser et al., 2001; Townsend & Manser, 2013; Zuberbühler, 2003a).

Other important findings from studies on vervet monkey alarm calls concern vocal development. Competence in vocal production, usage and comprehension emerges during the first four years of life (Seyfarth & Cheney, 1986), albeit with differences in flexibility and ontogeny (Seyfarth & Cheney, 2010). Initially, infant vervet monkeys give alarm calls in response to a much wider array of species than adults, although in non-arbitrary ways: leopard alarms are produced to a wide range of terrestrial mammals, eagle alarms to many birds and snake alarms to snake-like objects and reptiles (Seyfarth & Cheney, 1980). Later on, over the course of their development, juveniles then appear to reduce and refine their calling behaviour to the relevant predator species and learn to diversify their responses to different predators. Moreover, when infant vervet monkeys heard alarm calls, they are more likely to respond appropriately if they first looked at more experienced group members (Seyfarth & Cheney, 1986). Similarly, Campbell monkeys pay more attention to calls produced by adults than by immatures (Lemasson et al., 2010). Thus, it seems that during this refinement process not only auditory experience but also social input influences the ontogeny of primates' vocal communication.

The marked contrast between vocal production, usage and comprehension has generated an oddly asymmetrical vocal system of communication in non-human primates: Their vocalizations can be grouped in relatively small repertoires, each linked to a particular general context, with minimal modification in their acoustic features during development, but with an open-ended, highly and voluntarily modifiable, and cognitively rich set of specific meanings (Hammerschmidt & Fischer, 2008; Seyfarth & Cheney, 2010). It is important to note that some more production and usage flexibility has been reported in cases when single vocal units are combined into more complex structures, a relatively new area of research with significant promise (see Girard-Buttoz et al., 2022). However, to what extent infants are born with core knowledge of predator classes (e.g., terrestrial vs aerial) or whether they simply observe others and first overgeneralise is currently unknown. Furthermore, it is still unclear whether communicative competence in the production, usage and comprehension domains emerges either abruptly in response to a single or a small number of key experiences, or gradually over multiple experiences.

Transitions to speech

Humans are unique amongst all primates in their sophisticate control of the vocal apparatus – a necessary evolutionary step towards speech. Research on the vocal abilities in non-human primates is likely to produce insights into the past evolutionary history of this capacity, which must have evolved gradually from preadaptations, some of which probably still visible in the vocal behaviour of modern primates (Bergman et al., 2019; Zuberbühler & Lemasson, 2014). Therefore, it is imperative to conduct systematic studies in ecologically relevant settings to test hypotheses about how non-human primates acquire and develop their communicative competence. Research on vervet monkey vocal communication has already provided key insights, however, it is urgent to extend this line of research to other primate species and enable a truly comparative study of the primate roots of human language.

1.3 Study species

Mangabeys are African catarrhine monkeys belonging to the family *Cercopithecidae*. They are triphyletic and are divided into white-eyelid mangabeys (*Cercocebus*; 6 spp.), crested mangabeys (*Lophocebus*; 6 spp.) and highland mangabeys or kipunji (*Rungwecebus*; 1 spp.) (Davenport et al., 2006; Grubb et al., 2003). Originally, all mangabeys species were considered to be very closely related as part of the genus *Cercocebus*. However, *Cercocebus* species are now understood to be more related to mandrills and drills, while *Lophocebus* and *Rungwecebus* species are more closely related to baboons (Mittermeier et al., 2013). *Cercocebus* species have pink or white eyelids that contrast with the colour of the face and are semiterrestrial, whereas *Lophocebus* and *Rungwecebus* species have black eyelids that do not contrast with the colour of the face and are arboreal (Kingdon, 2015; Mittermeier et al., 2013). Mangabeys of all species are medium-sized monkeys confined to equatorial African forests. Here, I studied the sooty mangabeys, *Cercocebus atys*.

Sooty mangabeys range from Senegal, Guinea-Bissau, Guinea, Sierra Leone and Liberia to the Nzo-Sassandra system in Côte d'Ivoire (Koné et al., 2020). They inhabit primary and secondary forests, gallery forests, swamp forests, mangroves and coastal forests and mountains up to 1,000 m in the western part of the Guinean forest zone. Sooty Mangabeys are predominantly terrestrial monkeys typically found in large multimale, multifemale groups of up to 100 individuals (McGraw & Zuberbühler, 2007). In the Taï National Park, the average population density is estimated to be 4.35 groups/km^2, with a home range of 4–6.5 km^2 per group (Galat and Galat-Luong 1985, McGraw and Zuberbühler 2007). Sooty Mangabeys are considered "vulnerable" by the International Union for Conservation of Nature (IUCN), as their population is estimated to have declined by at least 30% over the past three generations (approx. 27 years). The causes of this decline are intensive hunting and habitat loss and degradation caused by the expansion of commercial and subsistence agriculture.

The species shows a marked sexual dimorphism. Adult males weigh an average 11.0 kg and females 6.2 kg (Oates et al., 1990). Sooty mangabeys are predominantly terrestrial, travelling and foraging on the ground around 76% of their daytime activities (McGraw, 1998). Their diet includes invertebrates, fruit and especially hard seeds and nuts (up to 55% of diet) (McGraw & Zuberbühler, 2007). The nuts of *Sacoglottis gabonensis* trees are the most consumed food every month of the year.

Females are philopatric, exhibit marked swellings during oestrus, with maximally tumescent near ovulation, and typically have a gestation length of ~170 days (Stevenson, 1973). Mating often occurs during the three days preceding maximum swelling. Solitary or small groups of non-resident males are not uncommon and are known to infiltrate resident groups during the breeding season (McGraw & Zuberbühler, 2007). Sooty mangabeys form linear dominance hierarchies within sexes and form coalitions (Range & Noë, 2002).

In the Taï National Park, monkeys usually form temporary mixed-species associations. Sooty Mangabeys intermingle with other primate species (around 60% of time), most often with arboreal Western Red Colobus (*Piliocolobus badius*) and Diana Monkeys (*Cercopithecus diana*) for approximately 5% and 10–15%, respectively, of total observation time (Höner et al., 1997; McGraw & Bshary, 2002; McGraw et al., 2007).

1.4 Vocal communication in sooty mangabeys

I will give a brief summary of sooty mangabey vocal communication in this section. In the following chapters, different features of the sooty mangabey vocal communication and call types are described in further detail within the framework of specific hypotheses. Generally, there are very few studies available on sooty mangabey vocal communication. Range & Fischer (2004) provided the only systematic study of the vocal repertoire, with descriptions of the acoustic structures and the behavioural contexts in which utterances occurred and some acoustical analyses showing individual and contextual differences for the most frequently produced vocalizations. They reported 19 different vocalizations that can be broadly classified as contact, agonistic, copulation or alarm calls.

The most common vocalization is the "grunt", a contact call emitted by adults and juveniles of both sexes in a variety of contexts (e.g., foraging, feeding, moving, resting, social interactions and dominance relations). Grunts are short, low frequency vocalizations given in call bouts. These call bouts show a clear difference in their temporal structure between adult males and females. Males grunt several times in a row with regular short intervals between grunts, while females produce fewer grunts per call bout with inter-call intervals lasting from a few seconds to a few minutes. Despite grunts are frequently produced during foraging they do not convey any information referential to food (Quintero et al., 2022b). "Twitters" are also a frequent call emitted in similar contexts to grunts. Most twitters occur when animals are searching for food and when approaching or grooming other individuals. Twitters are only given by adult females and both sexes of juveniles, and consist of high-pitched calls, which are usually given as long trains of syllables, with each syllable consisting of numerous and irregularly modulated frequency bands. A third important contact call is the "whoop gooble", a loud, low frequency long call emitted only by adult males. It consists of two types of utterances: first, a low-pitched note followed by several seconds of silence and then preceded by a repetitive series of one or two types of longer, more modulated tonal notes. Adult males produce whoop goobles in the mornings before the group descends from the canopy to start daily activities and during intergroup and predator encounters.

"Screams" and "growls" are the most common agonistic calls. Screams are noisy vocalizations produced by all sex-ages classes —but rarely by adult males— in response to aggressions. Growls are uttered by the aggressor in contexts of conflict and they are usually produced in combination with different body gestures such as rapid head turns and eyebrows raise. Other agonistic calls include “grumbles”, “hoos”, “waus” and “intense threat calls”.

Copulation calls are given by adult females during copulations, and occasionally also during defecation, especially during maximally tumescent cycling phase. These calls are composed of different units and present considerable variation in their unit combination and length, containing up to 51 units and lasting up to 10 s. Finally, females appear to have some control over call production as not all copulations are accompanied by calling behaviour.

The last group of calls in the vocal repertoire of sooty mangabeys is the alarm calls. Akin to vervet monkeys’ alarm call system (Seyfarth et al., 1980a), but much less studied, sooty mangabeys produce acoustically different alarm calls in response to their key predators (leopards, eagles and snakes) and show appropriate antipredator responses when hearing these calls: they rapidly climbing into trees when hearing leopard alarms, scanning the sky or run for cover when hearing eagle alarms, and stand bipedally and show vigilance behaviour towards the ground after a snake alarm call. Sooty Mangabey snake alarm calls are particularly interesting as they appear to have evolved as a public good, seem as an active attempt to refer to an external event and show a marked audience effect (Mielke et al., 2019; Quintero et al., 2022a). Recent research on the vervet alarm call system showed that vervet alarm calls are acoustically graded rather than three strongly categorical different alarm call types (Price et al., 2015). If this acoustically graded variation also occurs in sooty mangabey alarm calls is not yet known.

1.5 Study site and groups

Study site

This study took place at the Taï Monkey Project (TMP) in the Taï National Park, located at the west of Côte d’Ivoire (6º20’N to 5º10’N and 4º20’W to 6º50’W). This 330.000 ha of tropical evergreen seasonal lowland forest is considered the last remaining major block of forest in West Africa (McGraw et al., 2007). The forest is inhabited by 11 primates species: two nocturnal: the dwarf galago (*Galago demidovii*) and the Bosman’s potto (*Perodicticus potto*); three Colobinae: the western red colobus (*Colobus badius*), the western black-and-white colobus (*C. polykomos*), and the olive colobus (*C. verus*); three Cercopithecini: the diana monkey (*Cercopithecus diana*), the lesser white-nosed monkey (*C. petaurista*), and the

Campbell's monkey (*C. campbelli*); one Papionini: the sooty mangabey, (*Cercocebus atys*); and one great ape: the West African chimpanzee (*Pan troglodytes verus*). The study site has been described in detail previously by Galat & Galat-Luong (1985) and Boesch & Boesch-Achermann (2000).

Study group

This study was conducted from May to December 2018 and August 2019 to March 2020 with two groups of free-ranging sooty mangabeys in Taï National Park, Côte d'Ivoire. During the study period, the main group size whose size ranged between 74–91 individuals, including 23 adult females (>5 years old), 7 adult males (>7 years old), 6 subadult females (4–5 years old), 6 subadult males (5–7 years old), 9 old juvenile females (3–4 years old), 8 old juvenile males (3–5 years old), 10 young juvenile females (1–2 years old), 12 young juvenile males (1–2 years old) and 10 infants (<1 year old) (McGraw & Zuberbühler, 2007). We also conducted experiments on a non-neighbouring group whose home range was about 4 km Northwest, at the Taï Chimpanzee Project (TCP), which included a similar number and sex ratio of adults and subadults but only half the number of juveniles and of the main study group (Mielke et al., 2019; Wittig, 2018). Both groups were fully habituated to human observers and have been under study for several years.

Sooty mangabey predators

Among the main primate predators in Taï forest, in addition to human hunting, there are leopards (*Panthera pardus*) (Zuberbühler & Jenny, 2002) and crowned eagles (*Stephanoaetus coronatus*) (Shultz & Thomsett, 2007), both ambush predators, that prey substantially on sooty mangabeys. On the other hand, chimpanzees (*Pan troglodytes*) are cooperative pursuit hunters that often prey on monkeys, though Taï chimpanzees hardly ever hunt mangabeys (Boesch & Boesch, 1989; Shultz & Thomsett, 2007). In addition, stationary snakes with sit-and-wait strategies mainly pose danger to primates if approached too closely, but are less of a threat once detected (Mielke et al., 2019; Penner et al., 2008). Specifically, mangabeys sporadically come into contact with large pythons (*Python regius*), which can prey on smaller primates. Moreover, terrestrial primates, such as mangabeys, are particularly vulnerable to accidental snakebites, notably by Gaboon vipers (*Bitis gabonica*) and rhinoceros vipers (*Bitis nasicornis*) (Penner et al., 2008).

Mangabeys, like most primates, show selectively adaptive responses to each predator. Reactions to leopards entail rapidly climbing into the lower forest canopy, followed by mobbing and leopard-specific alarm calls at high rates by some individuals, presumably to drive the predator away (Zuberbühler et al., 1999; Zuberbühler & Jenny, 2002, 2007). For crowned eagles, mangabeys immediately seek cover or monitor the sky to keep visual contact, depending on the eagle's behaviour, again while some individuals give eagle-specific alarm calls at high rates (Shultz & Thomsett, 2007). For chimpanzees, mangabeys adopt a cryptic behaviour and rapidly move away in silence (Zuberbühler et al., 1999). Finally, for pythons and Gaboon and rhinoceros vipers, mangabeys jump aside showing startle responses, followed by standing bipedally and cautiously approaching and scanning the area of the snake (Penner et al., 2008; Range & Fischer, 2004), while some give snake-specific alarm calls that attract other individuals to the site.

1.6 Aims of the thesis

The overall goal of this thesis is to make progress in our understanding of the process by which non-human primates obtain and develop their vocal communicative skills and the role that social learning plays in this process, providing new insights into the development of vocal and cognitive capacities in modern primates and the evolution of human language faculty. To fully understand the development of vocal communication competence, it is necessary to study how and when non-human primate calls become meaningful and start to elicit the correct behavioural responses, a context in which alarm calls are particularly useful.

Here, I conducted a set of observational and experimental studies to provide a comprehensive analysis of the learning mechanisms, ecological aspects and social processes, involved in the usage and comprehension of alarm calls in wild sooty mangabeys, a species whose vocal communication and cognitive capacities have been poorly studied. In doing so, I empirically retested classic (communicative competence acquisition via cognitive pruning, ontogeny of heterospecific alarm call comprehension) and tested novel concepts (acquisition of knowledge via one-trial social learning of alarm calls and long-term retention of socially learned knowledge) proposed to explain non-human primate vocal communication in ecologically relevant settings.

As argued before, sooty mangabeys are an interesting model for vocal social learning research because of their social and behavioural characteristics: (1) they have a diverse vocal repertoire and their alarm call system is similar to the one found in vervet monkeys (Range & Fischer, 2004); (2) young individuals are constantly exposed to model individuals as they live in large groups, to as many as 100 (Galat & Galat-Luong, 1985; McGraw & Zuberbühler, 2007), and exhibit an important degree of social tolerance, with aggressions been typically not severe (Gust, 1994; Gust & Gordon, 1993); (3) they have considerable longevity, up to 18 years in the wild (Harvey & Clutton-Brock, 1985), and slow individual maturity, between 4.5–5 years and 7–8 years, for females and males respectively (Gust et al., 1990), characteristics that provide non-adult individuals enough time and opportunities to socially acquire information related to vocal communication and use it. Moreover, in Taï Forest, mangabeys are exposed to different threats: they are hunted by leopards, crowned eagles and chimpanzees and are also vulnerable to accidental snakebites by vipers. All these dangers differ in their hunting strategies and mangabeys show selectively adaptive responses to each of them, including vocal responses.

Altogether, research on mangabeys could help shed light on how non-human primates acquire their communicative capacities and on the ontogeny of their alarm calling behaviour. Importantly, I will focus on snake and leopard predation (ground predators) because sooty mangabeys are predominantly terrestrial. Predator hunting strategies and dangerousness, threat perception, and habitat structure are among the main drivers of antipredator behaviours evolution, which have shaped the vocal and cognitive abilities of primates (Coss et al., 2007; Seyfarth et al., 1980b; Zuberbühler et al., 1999; Zuberbühler & Jenny, 2002). Thus, the extent of predator-specific responses depends heavily on threat detection, predator type and habitat usage.

Thesis chapters

In a first empirical chapter, I investigated the ontogeny of mangabey specific behavioural responses to their predators. To this end, I combined direct behavioural observations during natural predator encounters with playback experiments to study the development of con- and heterospecific alarm call recognition in mangabeys. Since studies normally address questions of vocal comprehension only with stimuli of the same species, I took an approach closer to the real ecosystem of primates, as I also used sympatric Diana monkey calls to study the development of mangabey alarm calling behaviour. I predicted that juveniles would show lower corresponding response rates to alarm calls, alarm call for a wider variety of stimuli and engage more in social referencing, i.e., looking at other group members when hearing an alarm call, than adults. Moreover, because leopard predation has been linked to the evolution of primates' cognitive flexibility (Zuberbühler & Jenny, 2002), I predicted conspecific leopard alarms being established first in early development. Finally, because primates are unlikely predisposed to respond to alarm calls of unrelated species and because mangabeys probably witness fewer predation events on Diana monkeys than on their own group members —having less opportunities to make specific predator-alarm calls associations, we predicted faster learning of conspecific than heterospecific alarm calls.

Seyfarth & Cheney's alarm call refinement model has become the default of primate vocal development, despite the fact that it has poorly been formally tested directly in natural settings. In a second empirical chapter, I experimentally tested this model by studying the ontogeny of snake antipredator behaviour. In the Taï forest, mangabeys are exposed to more than 50 different snake species. However, only a small number can cause fatal accidents, and previous research has suggested that primates recognise the truly dangerous species (Crockford et al., 2012; Mielke et al., 2019). I used realistic snake models of highly dangerous vipers and not-venomous colubrids to explore age-related snake recognition and antipredator behaviour, including alarm calling. Following Seyfarth & Cheney's learning model, I predicted that young individuals would be less able than adults to recognize viper models as predators and generally less proficient to distinguish between dangerous and not-venomous snake models. If social references and auditory experience are important in the development of snake antipredator behaviours, I predicted that young individuals would engage in more social referencing and be less discriminated in both alarm calling and anti-predator behaviour when exposed to any snake model. Finally, I predicted age-related, gradual changes, with dangerous models being more effective in electing anti-predator behaviour and alarm calling than not-venomous snake models.

In a third empirical chapter, I directly tested how mangabeys learn to classify their predators and the role of social learning during this process. I experimentally tested whether mangabeys could socially learn to categorise a chimera: a visually ambiguous animal model with features of both leopards and vipers. I first examined how subjects from different age groups reacted spontaneously to the chimera, corroborating its ambiguity for appropriate classification. I then exposed naïve subjects simultaneously to the chimera and playbacks of snake or leopard alarm calls. If subjects attended to others' alarm calls to categorise the novel predator, I predicted that they should use this information in future encounters with the chimera and communicate it subsequently to others. Finally, I also conducted retest trials 2 years after the first experiments to test whether any learned categorisation of the chimeric models was retained. If long-term retention of socially learned predator categorisation occurs, subjects should continue to categorise the chimera based on the playbacks they heard during their first exposures to the models.

In the final chapter, I provide a synthesis of the results and conclusions of all experiments and connect my findings with the current theory on how primates acquire vocal communicative competence. I also highlight the importance of conducting research in vocal communication of historically less studied primate species, such as sooty mangabeys. Moreover, I examine how social learning shapes primate vocal communication and compare it to the development of human speech. Finally, I discuss the flaws and strengths of the studies here presented and consider the potential of innovative field experiments using novel approaches in future research to provide new insights into our understanding of the evolution of human language.

1.7 References

Abdai, J., Uccheddu, S., Gácsi, M., & Miklósi, Á. (2022). Exploring the advantages of using artificial agents to investigate animacy perception in cats and dogs. *Bioinspiration & Biomimetics*, *17*(6). https://doi.org/10.1088/1748-3190/ac93d9

Abrams, P. A. (2001). Predator-Prey Interactions. In C. W. Fox, D. A. Roff, & D. J. Fairbairn (Eds.), *Evolutionary Ecology: Concepts and Case Studies* (p. 0). Oxford University Press. https://doi.org/10.1093/oso/9780195131543.003.0028

Adams, D. B., & Kitchen, D. M. (2020). Model vs. playback experiments: The impact of sensory mode on predator-specific escape responses in saki monkeys. *Ethology*, *126*(5), 563–575. https://doi.org/https://doi.org/10.1111/eth.13008

Altmann, J. (1974). Observational Study of Behavior: Sampling Methods. *Behaviour*, *49*(3/4), 227–267. http://www.jstor.org/stable/4533591

Amici, F., Aureli, F., & Call, J. (2010). Monkeys and apes: are their cognitive skills really so different? *American Journal of Physical Anthropology*, *143*(2), 188–197. https://doi.org/10.1002/ajpa.21305

Araya-Salas, M., & Wright, T. (2013). Open-ended song learning in a hummingbird. *Biology Letters*, *9*(5), 20130625. https://doi.org/10.1098/rsbl.2013.0625

Arnold, K., Pohlner, Y., & Zuberbühler, K. (2008). A forest monkey's alarm call series to predator models. *Behavioral Ecology and Sociobiology*, *62*(4), 549–559. https://doi.org/10.1007/s00265-007-0479-y

Arnold, K., & Zuberbühler, K. (2006). Semantic combinations in primate calls. *Nature*, *441*(7091), 303.

Audacity Team. (2020). *Audacity: Free Audio Editor and Recorder* (2.2.2).

Baldwin, D. A., & Moses, L. J. (1996). The Ontogeny of Social Information Gathering. *Child Development*, *67*(5), 1915–1939. https://doi.org/10.2307/1131601

Barros, M., Boere, V., Mello, E. L., & Tomaz, C. (2002). Reactions to Potential Predators in Captive-Born Marmosets (Callithrix penicillata). *International Journal of Primatology*, *23*(2), 443–454. https://doi.org/10.1023/A:1013899931878

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software; Vol 1, Issue 1 (2015)* . https://doi.org/10.18637/jss.v067.i01

Bergman, T. J., Beehner, J. C., Painter, M. C., & Gustison, M. L. (2019). The speech-like properties of nonhuman primate vocalizations. *Animal Behaviour*, *151*, 229–237. https://doi.org/https://doi.org/10.1016/j.anbehav.2019.02.015

Bidner, L. R. (2014). Primates on the Menu: Direct and Indirect Effects of Predation on Primate Communities. *International Journal of Primatology*, *35*(6), 1164–1177. https://doi.org/10.1007/s10764-014-9797-x

Boesch, C., & Boesch-Achermann, H. (2000). *The chimpanzees of the Taï forest : behavioural ecology and evolution*. Oxford : Oxford university press. http://lib.ugent.be/catalog/rug01:000534901

Boesch, C., & Boesch, H. (1989). Hunting behavior of wild chimpanzees in the Taï National Park. *American Journal of Physical Anthropology*, *78*(4), 547–573. https://doi.org/https://doi.org/10.1002/ajpa.1330780410

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., & White, J.-S. S. (2009). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution*, *24*(3), 127–135. https://doi.org/10.1016/j.tree.2008.10.008

Borrow, N. (2014). *Field Guide to Birds of Western Africa*. Bloomsbury Publishing.

Bradbury, J. W., & Balsby, T. J. S. (2016). The functions of vocal learning in parrots. *Behavioral Ecology and Sociobiology*, *70*(3), 293–312. https://doi.org/10.1007/s00265-016-2068-4

Brodbeck, D. R., Burack, O. R., & Shettleworth, S. J. (1992). One-trial associative memory in black-capped chickadees. *Journal of Experimental Psychology: Animal Behavior Processes*, *18*, 12–21. https://doi.org/10.1037/0097-7403.18.1.12

Brumm, H., Voss, K., Köllmer, I., & Todt, D. (2004). Acoustic communication in noise: regulation of call characteristics in a New World monkey. *The Journal of Experimental Biology*, *207*(Pt 3), 443–448. https://doi.org/10.1242/jeb.00768

Bshary, R., & Noë, R. (1997). Red colobus and Diana monkeys provide mutual protection against predators. *Animal Behaviour*, *54*(6), 1461–1474. https://doi.org/https://doi.org/10.1006/anbe.1997.0553

Carlson, N. V, Kelly, E. M., & Couzin, I. (2020). Individual vocal recognition across taxa: a review of the literature and a look into the future. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *375*(1802), 20190479. https://doi.org/10.1098/rstb.2019.0479

Cäsar, C., & Zuberbühler, K. (2012). Referential alarm calling behaviour in New World primates. *Current Zoology*, *58*(5), 680–697. https://doi.org/10.1093/czoolo/58.5.680

Castro, N. A., & Snowdon, C. T. (2000). Development of Vocal Responses in Infant Cotton-Top Tamarins. *Behaviour*, *137*(5), 629–646. http://www.jstor.org/stable/4535727

Center for Conservation Bioacoustics. (2014). Raven Pro: Interactive Sound Analysis Software. In *Ithaca, NY: The Cornell Lab of Ornithology.* (1.5).

Cheney, D. L., & Seyfarth, R. M. (1985). Social and non-social knowledge in vervet monkeys. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences*, *308*(1135), 187–201. https://doi.org/10.1098/rstb.1985.0019

Cheney, D, & Seyfarth, R. (2018). Flexible usage and social function in primate vocalizations. *Proceedings of the National Academy of Sciences*, *115*(9), 1974–1979. https://doi.org/10.1073/pnas.1717572115

Cheney, DL, & Seyfarth, R. (1990). How monkeys see the world: Inside the mind of another species. In *How monkeys see the world: Inside the mind of another species.* University of Chicago Press.

Chippaux, J.-P. (2006). *Les serpents d'Afrique occidentale et centrale*. IRD éditions.

Chomsky, N. (1965). *Aspects of the Theory of Syntax*. MIT press.

Chomsky, N. (2017). Language architecture and its import for evolution. *Neuroscience & Biobehavioral Reviews*, *81*, 295–300. https://doi.org/https://doi.org/10.1016/j.neubiorev.2017.01.053

Chouinard-Thuly, L., Gierszewski, S., Rosenthal, G. G., Reader, S. M., Rieucau, G., Woo, K. L., Gerlai, R., Tedore, C., Ingley, S. J., Stowers, J. R., Frommen, J. G., Dolins, F. L., & Witte, K. (2017). Technical and conceptual considerations for using animated stimuli in studies of animal behavior. *Current Zoology*, *63*(1), 5–19. https://doi.org/10.1093/cz/zow104

Chow, C. P., Mitchell, J. F., & Miller, C. T. (2015). Vocal turn-taking in a non-human primate is learned during ontogeny. *Proceedings. Biological Sciences*, *282*(1807), 20150069. https://doi.org/10.1098/rspb.2015.0069

Clark, E. (2003). *First language acquisition*. Cambridge University Press.

Clarke, E., Reichard, U. H., & Zuberbühler, K. (2006). The syntax and meaning of wild gibbon songs. *PloS One*, *1*(1), e73.

Clay, Z., & Zuberbühler, K. (2011). Bonobos Extract Meaning from Call Sequences. *PLoS ONE*, *6*(4), e18786. https://doi.org/10.1371/journal.pone.0018786

Cook, M., & Mineka, S. (1990). Selective associations in the observational conditioning of fear in rhesus monkeys. *Journal of Experimental Psychology. Animal Behavior Processes*, *16*(4), 372–389.

Coss, R. G., McCowan, B., & Ramakrishnan, U. (2007). Threat-Related Acoustical Differences in Alarm Calls by Wild Bonnet Macaques (Macaca radiata) Elicited by Python and Leopard Models. *Ethology*, *113*(4), 352–367. https://doi.org/https://doi.org/10.1111/j.1439-0310.2007.01336.x

Coss, R. G., & Ramakrishnan, U. (2000). Perceptual Aspects of Leopard Recognition by Wild Bonnet Macaques (Macaca radiata). *Behaviour*, *137*(3), 315–335. http://www.jstor.org/stable/4535708

Coss, R. G., Ramakrishnan, U., & Schank, J. (2005). Recognition of partially concealed leopards by wild bonnet macaques (Macaca radiata): The role of the spotted coat. *Behavioural Processes*, *68*(2), 145–163. https://doi.org/https://doi.org/10.1016/j.beproc.2004.12.004

Crockford, C, & Boesch, C. (2005). Call combinations in wild chimpanzees. *Behaviour*, *142*, 397–421.

Crockford, C, Wittig, R. M., Mundry, R., & Zuberbühler, K. (2012). Wild Chimpanzees Inform Ignorant Group Members of Danger. *Current Biology*, *22*(2), 142–146. https://doi.org/https://doi.org/10.1016/j.cub.2011.11.053

Crockford, C, Wittig, R. M., & Zuberbühler, K. (2015). An intentional vocalization draws others' attention: a playback experiment with wild chimpanzees. *Animal Cognition*, *18*(3), 581–591. https://doi.org/10.1007/s10071-014-0827-z

Crockford, C, Wittig, R. M., & Zuberbühler, K. (2017). Vocalizing in chimpanzees is influenced by social-cognitive processes. *Science Advances*, *3*(11), e1701742. https://doi.org/10.1126/sciadv.1701742

Curio, E. (1976). *The ethology of predation* (Vol. 7). Springer Science & Business Media.

Curio, E., Ernst, U., & Vieth, W. (1978). Cultural Transmission of Enemy Recognition: One Function of Mobbing. *Science*, *202*(4370), 899 LP – 901. https://doi.org/10.1126/science.202.4370.899

Davenport, T. R. B., Stanley, W. T., Sargis, E. J., De Luca, D. W., Mpunga, N. E., Machaga, S. J., & Olson, L. E. (2006). A New Genus of African Monkey, Rungwecebus: Morphology, Ecology, and Molecular Phylogenetics. *Science*, *312*(5778), 1378–1381. https://doi.org/10.1126/science.1125631

de Boer, B. (2005). Evolution of Speech and Its Acquisition. *Adaptive Behavior*, *13*(4), 281–292. https://doi.org/10.1177/105971230501300405

Deshpande, A. (2021). *Social learning and flexibility in vocal communication of wild vervet monkeys* [Université de Neuchâtel]. https://unine.swisscovery.slsp.ch/permalink/41SLSP_UNE/b1j16q/alma991009764729505517%0A

Deshpande, A., Van Boekholt, B., & Zuberbuhler, K. (2022). Preliminary evidence for one-trial social learning of vervet monkey alarm calling. *Royal Society Open Science*, *9*(8), 210560. https://doi.org/10.1098/rsos.210560

Dezecache, G., Crockford, C., & Zuberbühler, K. (2019). The development of communication in alarm contexts in wild chimpanzees. *Behavioral Ecology and Sociobiology*, *73*(8), 104. https://doi.org/10.1007/s00265-019-2716-6

Di Bitetti, M., & Wheeler, B. (2017). The vocal repertoire of the black horned capuchin monkey (Cebus [Sapajus] nigritus): an acoustic and contextual analysis. In M. Kowalewski & L. Oklander (Eds.), *Primatology in Argentina* (Vol. 2, pp. 171–199). Sociedad Argentina para el Estudio de los Mamíferos, Buenos Aires.

Ducheminsky, N., Henzi, S. P., & Barrett, L. (2014). Responses of vervet monkeys in large troops to terrestrial and aerial predator alarm calls. *Behavioral Ecology*, *25*(6), 1474–

1484. https://doi.org/10.1093/beheco/aru151

Edwards, M. C., Ford, C., Hoy, J. M., FitzGibbon, S., & Murray, P. J. (2021). How to train your wildlife: A review of predator avoidance training. *Applied Animal Behaviour Science*, *234*, 105170. https://doi.org/https://doi.org/10.1016/j.applanim.2020.105170

Egnor, S. E. R., & Hauser, M. D. (2004). A paradox in the evolution of primate vocal learning. *Trends in Neurosciences*, *27*(11), 649–654. https://doi.org/https://doi.org/10.1016/j.tins.2004.08.009

Egnor, S. E. R., & Hauser, M. D. (2006). Noise-induced vocal modulation in cotton-top tamarins (Saguinus oedipus). *American Journal of Primatology*, *68*(12), 1183–1190. https://doi.org/10.1002/ajp.20317

Egnor, S. E. R., Iguina, C. G., & Hauser, M. D. (2006). Perturbation of auditory feedback causes systematic perturbation in vocal structure in adult cotton-top tamarins. *The Journal of Experimental Biology*, *209*(Pt 18), 3652–3663. https://doi.org/10.1242/jeb.02420

Eisenberg, J. F. (1976). Communication mechanisms and social integration in the black spider monkey, Ateles fusciceps robustus, and related species. *Smithson. Contrib. to Zool.*, 1–108. https://doi.org/doi:10.5479/si.00810282.213

Elowson, A. M., Snowdon, C. T., & Sweet, C. J. (1992). Ontogeny of trill and J-call vocalizations in the pygmy marmoset, Cebuella pygmaea. *Animal Behaviour*, *43*(5), 703–715. https://doi.org/https://doi.org/10.1016/S0003-3472(05)80195-2

Engqvist, L. (2005). The mistreatment of covariate interaction terms in linear model analyses of behavioural and evolutionary ecology studies. *Animal Behaviour*, *70*(4), 967–971. https://doi.org/https://doi.org/10.1016/j.anbehav.2005.01.016

Ernst, R., & Rödel, M. (2002). A new Atheris species (Serpentes: Viperidae), from Taï National Park, Ivory Coast. *Herpetological Journal*, *12*, 55–61.

Etting, S. F., Isbell, L. A., & Grote, M. N. (2014). Factors increasing snake detection and perceived threat in captive rhesus macaques (Macaca mulatta). *American Journal of Primatology*, *76*(2), 135–145. https://doi.org/10.1002/ajp.22216

Evans, A., & Tomasello, M. (1986). Evidence for social referencing in young chimpanzees (Pan troglodytes). *Folia Primatologica; International Journal of Primatology*, *47*(1), 49–54. https://doi.org/10.1159/000156263

Fedurek, P., & Slocombe, K. E. (2011). Primate vocal communication: a useful tool for understanding human speech and language evolution? *Human Biology*, *83*(2), 153–173. https://doi.org/10.3378/027.083.0202

Fedurek, P., Slocombe, K. E., & Zuberbühler, K. (2015). Chimpanzees communicate to two different audiences during aggressive interactions. *Animal Behaviour*, *110*, 21–28. https://doi.org/https://doi.org/10.1016/j.anbehav.2015.09.010

Feise, R. J. (2002). Do multiple outcome measures require p-value adjustment? *BMC Medical Research Methodology*, *2*, 8. https://doi.org/10.1186/1471-2288-2-8

Fichtel, C. (2004). Reciprocal recognition of sifaka (Propithecus verreauxi verreauxi) and redfronted lemur (Eulemur fulvus rufus) alarm calls. *Animal Cognition*, *7*(1), 45–52. https://doi.org/10.1007/s10071-003-0180-0

Fichtel, C. (2008). Ontogeny of conspecific and heterospecific alarm call recognition in wild Verreaux's sifakas (Propithecus verreauxi verreauxi). *American Journal of Primatology*, *70*(2), 127–135. https://doi.org/https://doi.org/10.1002/ajp.20464

Fichtel, C. (2020). Monkey Alarm Calling: It Ain't all Referential, or is It? *Animal Behavior and Cognition*, *7*, 101–107.

Fichtel, C., & Kappeler, P. M. (2002). Anti-Predator Behavior of Group-Living Malagasy Primates: Mixed Evidence for a Referential Alarm Call System. *Behavioral Ecology and Sociobiology*, *51*(3), 262–275. http://www.jstor.org/stable/4602047

Fichtel, C., & Kappeler, P. M. (2011). Variation in the Meaning of Alarm Calls in Verreaux's and Coquerel's Sifakas (Propithecus verreauxi, P. coquereli). *International Journal of Primatology*, *32*(2), 346–361. https://doi.org/10.1007/s10764-010-9472-9

Fischer, J. (2017). Primate vocal production and the riddle of language evolution. *Psychonomic Bulletin & Review*, *24*(1), 72–78. https://doi.org/10.3758/s13423-016-1076-8

Fischer, J, & Hammerschmidt, K. (2020). Towards a new taxonomy of primate vocal production learning. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *375*(1789), 20190045. https://doi.org/10.1098/rstb.2019.0045

Fischer, J, Metz, M., Cheney, D., & Seyfarth, R. (2001). Baboon responses to graded bark variants. *Animal Behaviour*, *61*(5), 925–931. https://doi.org/https://doi.org/10.1006/anbe.2000.1687

Fischer, J, & Price, T. (2017). Meaning, intention, and inference in primate vocal communication. *Neuroscience & Biobehavioral Reviews*, *82*, 22–31. https://doi.org/https://doi.org/10.1016/j.neubiorev.2016.10.014

Fischer, J. (2020). Nonhuman primate alarm calls then and now. *Animal Behavior and Cognition*, *7*.

Fischer, J. (2021). Primate Vocal Communication and the Evolution of Speech. *Current Directions in Psychological Science*, *30*(1), 55–60. https://doi.org/10.1177/0963721420979580

Fischer, J, Cheney, D. L., & Seyfarth, R. M. (2000). Development of infant baboons' responses to graded bark variants. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *267*(1459), 2317–2321. https://doi.org/10.1098/rspb.2000.1285

Fischer, J, & Hammerschmidt, K. (2001). Functional referents and acoustic similarity revisited: the case of Barbary macaque alarm calls. *Animal Cognition*, *4*(1), 29–35. https://doi.org/10.1007/s100710100093

Fischer, J, Kitchen, D. M., Seyfarth, R. M., & Cheney, D. L. (2004). Baboon loud calls advertise male quality: acoustic features and their relation to rank, age, and exhaustion. *Behavioral Ecology and Sociobiology*, *56*(2), 140–148. https://doi.org/10.1007/s00265-003-0739-4

Foerster, S. (2008). Two incidents of venomous snakebite on juvenile blue and Sykes monkeys (Cercopithecus mitis stuhlmanni and C. m. albogularis). *Primates*, *49*(4), 300–303. https://doi.org/10.1007/s10329-008-0098-x

Friard, O., & Gamba, M. (2016). BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. *Methods in Ecology and Evolution*, *7*(11), 1325–1330. https://doi.org/10.1111/2041-210X.12584

Fröhlich, M., & van Schaik, C. P. (2020). Must all signals be evolved? A proposal for a new classification of communicative acts. *WIREs Cognitive Science*, *11*(4), e1527. https://doi.org/https://doi.org/10.1002/wcs.1527

Fugate, J. M. B., Gouzoules, H., & Nygaard, L. C. (2008). Recognition of rhesus macaque (Macaca mulatta) noisy screams: evidence from conspecifics and human listeners. *American Journal of Primatology*, *70*(6), 594–604. https://doi.org/https://doi.org/10.1002/ajp.20533

Galat, G., & Galat-Luong, A. (1985). La communauté de primates diurnes de la forêt de Taï, Côte-d'Ivoire. *Revue d'écologie (Terre Vie)*, *40*, 3–32.

Galef, B. G., & Giraldeau, L.-A. (2001). Social influences on foraging in vertebrates: causal mechanisms and adaptive functions. *Animal Behaviour*, *61*(1), 3–15. https://doi.org/https://doi.org/10.1006/anbe.2000.1557

Galef, B. G., & Laland, K. N. (2005). Social learning in animals: empirical studies and theoretical models. *Bioscience*, *55*(6), 489–499.

Gamba, M., Friard, O., Riondato, I., Righini, R., Colombo, C., Miaretsoa, L., Torti, V., Nadhurou, B., & Giacoma, C. (2015). Comparative analysis of the vocal repertoire of Eulemur: a dynamic time warping approach. *International Journal of Primatology*, *36*(5), 894–910.

Garcia, J., Kimeldorf, D. J., & Koelling, R. A. (1955). Conditioned aversion to saccharin resulting from exposure to gamma radiation. In *Science* (Vol. 122, pp. 157–158). American Assn for the Advancement of Science. https://doi.org/10.1126/science.122.3179.1089

Gautier-Hion, A., Quris, R., & Gautier, J.-P. (1983). Monospecific vs polyspecific life: A comparative study of foraging and antipredatory tactics in a community of Cercopithecus monkeys. *Behavioral Ecology and Sociobiology*, *12*(4), 325–335. https://doi.org/10.1007/BF00302901

Gelman, A., & Su, Y.-S. (2020). *arm: Data analysis using regression and* *multilevel/hierarchical models* (R package version 1.11-1). https://cran.r-project.org/package=arm

Genovart, M., Negre, N., Tavecchia, G., Bistuer, A., Parpal, L., & Oro, D. (2010). The young, the weak and the sick: evidence of natural selection by predation. *PloS One*, *5*(3), e9774. https://doi.org/10.1371/journal.pone.0009774

Genty, E., Breuer, T., Hobaiter, C., & Byrne, R. W. (2009). Gestural communication of the gorilla (Gorilla gorilla): repertoire, intentionality and possible origins. *Animal Cognition*, *12*(3), 527–546. https://doi.org/10.1007/s10071-009-0213-4

Ghazanfar, A. A., Liao, D. A., & Takahashi, D. Y. (2019). Volition and learning in primate vocal behaviour. *Animal Behaviour*, *151*, 239–247. https://doi.org/https://doi.org/10.1016/j.anbehav.2019.01.021

Gill, S. A., & Bierema, A. M.-K. (2013). On the Meaning of Alarm Calls: A Review of Functional Reference in Avian Alarm Calling. *Ethology*, *119*(6), 449–461. https://doi.org/https://doi.org/10.1111/eth.12097

Girard-Buttoz, C., Zaccarella, E., Bortolato, T., Friederici, A. D., Wittig, R. M., & Crockford, C. (2022). Chimpanzees produce diverse vocal sequences with ordered and recombinatorial properties. *Communications Biology*, *5*(1), 410. https://doi.org/10.1038/s42003-022-03350-8

Goodale, E., Beauchamp, G., Magrath, R. D., Nieh, J. C., & Ruxton, G. D. (2010). Interspecific information transfer influences animal community structure. *Trends in Ecology & Evolution*, *25*(6), 354–361. https://doi.org/10.1016/j.tree.2010.01.002

Goris, R. C. (2011). Infrared Organs of Snakes: An Integral Part of Vision. *Journal of Herpetology*, *45*(1), 2–14. https://doi.org/10.1670/10-238.1

Greene, H. W. (1997). *Snakes: the evolution of mystery in nature*. Univ of California Press.

Greggor, A. L., McIvor, G. E., Clayton, N. S., & Thornton, A. (2022). Wild jackdaws are wary of objects that violate expectations of animacy. *Royal Society Open Science*, *5*(10), 181070. https://doi.org/10.1098/rsos.181070

Griffin, A. (2004). Social learning about predators: a review and prospectus. *Animal Learning*

& Behavior, *32*(1), 131–140. https://doi.org/10.3758/BF03196014

Grubb, P., Butynski, T. M., Oates, J. F., Bearder, S. K., Disotell, T. R., Groves, C. P., & Struhsaker, T. T. (2003). Assessment of the Diversity of African Primates. *International Journal of Primatology*, *24*(6), 1301–1357. https://doi.org/10.1023/B:IJOP.0000005994.86792.b9

Gursky, S. (2003). Predation Experiments on Infant Spectral Tarsiers (Tarsius spectrum). *Folia Primatologica*, *74*(5–6), 272–284. https://doi.org/https://doi.org/10.1159/000073314

Gust, D. A. (1994). A brief report on the social behavior of the crested mangabey (Cercocebus galeritus galeritus) with a comparison to the sooty mangabey (C. torquatus atys). *Primates*, *35*(3), 375–383. https://doi.org/10.1007/BF02382734

Gust, D. A., Busse, C. D., & Gordon, T. P. (1990). Reproductive parameters in the sooty mangabey (Cercocebus torquatus atys). *American Journal of Primatology*, *22*(4), 241–250. https://doi.org/10.1002/ajp.1350220404

Gust, D. A., & Gordon, T. P. (1993). Conflict resolution in sooty mangabeys. *Animal Behaviour*, *46*(4), 685–694. https://doi.org/https://doi.org/10.1006/anbe.1993.1245

Haff, T. M., & Magrath, R. D. (2013). To call or not to call: parents assess the vulnerability of their young before warning them about predators. *Biology Letters*, *9*(6), 20130745. https://doi.org/10.1098/rsbl.2013.0745

Hammerschmidt, K., & Fischer, J. (2008). Constraints in Primate Vocal Production. In *Evolution of Communicative Flexibility*. The MIT Press. https://doi.org/10.7551/mitpress/9780262151214.003.0005

Hammerschmidt, K., Freudenstein, T., & Jürgens, U. (2001). Vocal Development in Squirrel Monkeys. *Behaviour*, *138*(9), 1179–1204. http://www.jstor.org/stable/4535882

Hammerschmidt, K., Newman, J. D., Champoux, M., & Suomi, S. J. (2000). Changes In Rhesus Macaque ‘Coo’ Vocalizations during Early Development. *Ethology*, *106*(10), 873–886. https://doi.org/https://doi.org/10.1046/j.1439-0310.2000.00611.x

Harvey, P. H., & Clutton-Brock, T. H. (1985). Life History Variation in Primates. *Evolution*, *39*(3), 559–581. https://doi.org/10.2307/2408653

Hauser, M. D. (1988). How Infant Vervet Monkeys Learn To Recognize Starling Alarm Calls: the Role of Experience. *Behaviour*, *105*(3–4), 187–201. https://doi.org/https://doi.org/10.1163/156853988X00016

Hauser, M. D. (1989). Ontogenetic changes in the comprehension and production of vervet monkey (Cercopithecus aethiops) vocalizations. *Journal of Comparative Psychology*, *103*(2), 149–158. https://doi.org/10.1037/0735-7036.103.2.149

Hauser, M. D., Chomsky, N., & Fitch, W. T. (2002). The Faculty of Language: What Is It, Who Has It, and How Did It Evolve? *Science*, *298*(5598), 1569–1579. https://doi.org/10.1126/science.298.5598.1569

Hayes, C. (1951). The ape in our house. In *The ape in our house.* Harper.

Headland, T. N., & Greene, H. W. (2011). Hunter–gatherers and other primates as prey, predators, and competitors of snakes. *Proceedings of the National Academy of Sciences*, *108*(52), E1470–E1474. https://doi.org/10.1073/pnas.1115116108

Heyes, C., & Galef Jr, B. (1996). *Social learning in animals: the roots of culture*. Elsevier.

Heymann, E. W., & Buchanan-Smith, H. M. (2000). The behavioural ecology of mixed-species troops of callitrichine primates. *Biological Reviews of the Cambridge Philosophical Society*, *75*(2), 169–190. https://doi.org/10.1017/s0006323199005460

Hollén, L. I., Clutton-Brock, T., & Manser, M. B. (2008). Ontogenetic Changes in Alarm-Call Production and Usage in Meerkats (Suricata suricatta): Adaptations or Constraints? *Behavioral Ecology and Sociobiology*, *62*(5), 821–829. http://www.jstor.org/stable/25511757

Höner, O. P., Leumann, L., & Noë, R. (1997). Dyadic associations of red Colobus and diana monkey groups in the Taï National Park, Ivory Coast. *Primates*, *38*(3), 281–291. https://doi.org/10.1007/BF02381615

Hotchkin, C. F., Parks, S. E., & Weiss, D. J. (2013). Vocal modifications in primates: Effects of noise and behavioral context on vocalization structure. *Proceedings of Meetings on Acoustics. Acoustical Society of America*, *19*. https://doi.org/10.1121/1.4799257

Isbell, L. A. (1994). Predation on primates: Ecological patterns and evolutionary consequences. *Evolutionary Anthropology: Issues, News, and Reviews*, *3*(2), 61–71. https://doi.org/10.1002/evan.1360030207

Isbell, L. A. (2006). Snakes as agents of evolutionary change in primate brains. *Journal of Human Evolution*, *51*(1), 1–35. https://doi.org/https://doi.org/10.1016/j.jhevol.2005.12.012

Isbell, L. A. (2009). *The Fruit, the Tree, and the Serpent*. Harvard University Press. https://doi.org/10.2307/j.ctvjnrvj0

Jaffe, K. . E., & Isbell, L. (2010). The Guenons: Polyspecific associations in sociological perspective. In C. J. Campbell, A. Fuentes, K. C. MacKinnon, S. K. Bearder, & R. Stumpf (Eds.), *Primates in Perspective* (pp. 277–300). Oxford University Press.

Janik, V. M., & Slater, P. J. B. (2000). The different roles of social learning in vocal communication. *Animal Behaviour*, *60*(1), 1–11. https://doi.org/https://doi.org/10.1006/anbe.2000.1410

Janson, C. H., & van Schaik, C. P. (1993). Ecological risk aversion in juvenile primates: slow and steady wins the race. In M. E. Pereira & L. A. Fairbanks (Eds.), *Juvenile primates: life history, development, and behavior* (pp. 57–74). Oxford Univ. Press.

Jeffreys, H. (1939). *The theory of probability* (1st ed.). Oxford University Press.

Johnson, K. E., & Clark, C. J. (2020). Ontogeny of vocal learning in a hummingbird. *Animal Behaviour*, *167*, 139–150. https://doi.org/https://doi.org/10.1016/j.anbehav.2020.07.010

Johnson, K. E., & Clark, C. J. (2022). Costa’s hummingbird has an extended sensitive phase of vocal learning. *Animal Behaviour*, *188*, 75–84. https://doi.org/https://doi.org/10.1016/j.anbehav.2022.04.001

Kaminski, J., Call, J., & Fischer, J. (2004). Word learning in a domestic dog: evidence for “fast mapping”. *Science (New York, N.Y.)*, *304*(5677), 1682–1683. https://doi.org/10.1126/science.1097859

Kawai, N., & He, H. (2016). Breaking Snake Camouflage: Humans Detect Snakes More Accurately than Other Animals under Less Discernible Visual Conditions. *PLOS ONE*, *11*(10), e0164342. https://doi.org/10.1371/journal.pone.0164342

Kawai, N., & Koda, H. (2016). Japanese monkeys (Macaca fuscata) quickly detect snakes but not spiders: Evolutionary origins of fear-relevant animals. In *Journal of Comparative Psychology* (Vol. 130, pp. 299–303). American Psychological Association. https://doi.org/10.1037/com0000032

Keen, S. C., Cole, E. F., Sheehan, M. J., & Sheldon, B. C. (2020). Social learning of acoustic anti-predator cues occurs between wild bird species. *Proceedings of the Royal Society B: Biological Sciences*, *287*(1920), 20192513. https://doi.org/10.1098/rspb.2019.2513

Kelley, J. L., & Magurran, A. E. (2003). Learned predator recognition and antipredator responses in fishes. *Fish and Fisheries*, *4*(3), 216–226. https://doi.org/https://doi.org/10.1046/j.1467-2979.2003.00126.x

Kellogg, W. N., & Kellogg, L. A. (1933). The ape and the child: a study of environmental influence upon early behavior. In *The ape and the child: a study of environmental influence upon early behavior.* Whittlesey House.

Kendal, R. L., Coolen, I., van Bergen, Y., & Laland, K. N. B. T.-A. in the S. of B. (2005). *Trade-Offs in the Adaptive Use of Social and Asocial Learning* (Vol. 35, pp. 333–379). Academic Press. https://doi.org/https://doi.org/10.1016/S0065-3454(05)35008-X

Khamcha, D., & Sukumal, N. (2009). Burmese python (Python molurus) predation on a pig-tailed macaque (Macaca nemestrina) in Khao Yai National Park. *Hamadryad*, *34*, 176–178. https://doi.org/10.13140/2.1.3857.7449

King, S. L., & Janik, V. M. (2013). Bottlenose dolphins can use learned vocal labels to address each other. *Proceedings of the National Academy of Sciences*, *110*(32), 13216–13221. https://doi.org/10.1073/pnas.1304459110

Kingdon, J. (2015). *The Kingdon field guide to African mammals*. Bloomsbury Publishing.

Kirchhof, J., & Hammerschmidt, K. (2006). Functionally Referential Alarm Calls in Tamarins (Saguinus fuscicollis and Saguinus mystax) – Evidence from Playback Experiments. *Ethology*, *112*(4), 346–354. https://doi.org/https://doi.org/10.1111/j.1439-0310.2006.01165.x

Koda, H., Shimooka, Y., & Sugiura, H. (2008). Effects of caller activity and habitat visibility on contact call rate of wild Japanese macaques (Macaca fuscata). *American Journal of Primatology*, *70*(11), 1055–1063. https://doi.org/10.1002/ajp.20597

Koné, I., McGraw, S., Gonedelé Bi, S., & Barrie, A. (2020). *Cercocebus atys*. The IUCN Red List of Threatened Species 2020: E.T136933A92248451. https://dx.doi.org/10.2305/IUCN.UK.2020-2.RLTS.T136933A92248451.en

Krause, M. A., & Beran, M. J. (2020). Words matter: Reflections on language projects with chimpanzees and their implications. *American Journal of Primatology*, *82*(10), e23187. https://doi.org/https://doi.org/10.1002/ajp.23187

Kuhl, P. K. (2000). A new view of language acquisition. *Proceedings of the National Academy of Sciences of the United States of America*, *97*(22), 11850–11857. https://doi.org/10.1073/pnas.97.22.11850

Lameira, A. R. (2017). Bidding evidence for primate vocal learning and the cultural substrates for speech evolution. *Neuroscience & Biobehavioral Reviews*, *83*, 429–439. https://doi.org/https://doi.org/10.1016/j.neubiorev.2017.09.021

Laporte, M. N. C., & Zuberbühler, K. (2010). Vocal greeting behaviour in wild chimpanzee females. *Animal Behaviour*, *80*(3), 467–473. https://doi.org/https://doi.org/10.1016/j.anbehav.2010.06.005

Lattenkamp, E. Z., & Vernes, S. C. (2018). Vocal learning: a language-relevant trait in need of a broad cross-species approach. *Current Opinion in Behavioral Sciences*, *21*, 209–215. https://doi.org/https://doi.org/10.1016/j.cobeha.2018.04.007

Lattenkamp, E. Z., Vernes, S. C., & Wiegrebe, L. (2018). Volitional control of social vocalisations and vocal usage learning in bats. *Journal of Experimental Biology*, *221*(14), jeb180729. https://doi.org/10.1242/jeb.180729

Lemasson, A., Gandon, E., & Hausberger, M. (2010). Attention to elders' voice in non-human primates. *Biology Letters*, *6*(3), 328. https://doi.org/10.1098/rsbl.2009.0875

Lemasson, A., Ouattara, K., Petit, E. J., & Zuberbühler, K. (2011). Social learning of vocal structure in a nonhuman primate? *BMC Evolutionary Biology*, *11*(1), 362. https://doi.org/10.1186/1471-2148-11-362

León, J., Thiriau, C., Bodin, C., Crockford, C., & Zuberbühler, K. (2022). Acquisition of predator knowledge from alarm calls via one-trial social learning in monkeys. *IScience*, *25*, 104853. https://doi.org/https://doi.org/10.1016/j.isci.2022.104853

León, J., Thiriau, C., Crockford, C., & Zuberbühler, K. (2022). *https://osf.io/y2gvc/*.

Leroux, M., & Townsend, S. W. (2020). Call combinations in great apes and the evolution of syntax. *Animal Behavior and Cognition*, *7*(2), 131–139.

Li, J., Smithwick, Q., & Chu, D. (2022). Holobricks: modular coarse integral holographic displays. *Light: Science & Applications*, *11*(1), 57. https://doi.org/10.1038/s41377-022-00742-7

Liebal, K., & Call, J. (2012). The origins of non-human primates' manual gestures. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *367*(1585), 118–128. https://doi.org/10.1098/rstb.2011.0044

Liebal, K., Waller, B. M., Burrows, A. M., & Slocombe, K. E. (2014). Primate communication: A multimodal approach. In *Primate communication: A multimodal approach.* Cambridge University Press.

Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, *68*(4), 619–640. https://doi.org/10.1139/z90-092

Luchkina, E., & Waxman, S. (2021). Acquiring verbal reference: The interplay of cognitive, linguistic, and general learning capacities. *Infant Behavior and Development*, *65*, 101624. https://doi.org/https://doi.org/10.1016/j.infbeh.2021.101624

Magrath, R. D., Haff, T. M., Fallow, P. M., & Radford, A. N. (2015). Eavesdropping on heterospecific alarm calls: from mechanisms to consequences. *Biological Reviews*, *90*(2), 560–586. https://doi.org/https://doi.org/10.1111/brv.12122

Manser, M. B. (2001). The acoustic structure of suricates' alarm calls varies with predator type and the level of response urgency. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *268*(1483), 2315–2324. https://doi.org/10.1098/rspb.2001.1773

Manser, M. B., Bell, M. B., & Fletcher, L. B. (2001). The information that receivers extract from alarm calls in suricates. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *268*(1484), 2485–2491. https://doi.org/10.1098/rspb.2001.1772

Masataka, N., & Fujita, K. (1989). Vocal Learning of Japanese and Rhesus Monkeys. *Behaviour*, *109*(3–4), 191–199. https://doi.org/https://doi.org/10.1163/156853989X00222

McCowan, B., Franceschini, N. V, & Vicino, G. A. (2001). Age differences and developmental trends in alarm peep responses by squirrel monkeys (Saimiri sciureus). *American Journal of Primatology*, *53*(1), 19–31. https://doi.org/https://doi.org/10.1002/1098-2345(200101)53:1<19::AID-AJP2>3.0.CO;2-#

McCullagh, P., & Nelder, J. A. (1989). *Generalized linear models* (Second). Chapman & Hall/CRC.

McGraw, W. (1998). Comparative locomotion and habitat use of six monkeys in the Tai Forest, Ivory Coast. *American Journal of Physical Anthropology*, *105*(4), 493–510. https://doi.org/https://doi.org/10.1002/(SICI)1096-8644(199804)105:4<493::AID-AJPA7>3.0.CO;2-P

McGraw, W., & Bshary, R. (2002). Association of Terrestrial Mangabeys (Cercocebus atys) with Arboreal Monkeys: Experimental Evidence for the Effects of Reduced Ground Predator Pressure on Habitat Use. *International Journal of Primatology*, *23*(2), 311–325. https://doi.org/10.1023/A:1013883528244

McGraw, W. S., Zuberbühler, K., & Noë, R. (2007). *Monkeys of the Taï Forest: an African primate community* (Vol. 51). Cambridge University Press.

McGraw, W., & Zuberbühler, K. (2007). The monkeys of the Taï forest: an introduction. In Klaus Zuberbühler, R. Noë, & W. S. McGraw (Eds.), *Monkeys of the Taï Forest: An African Primate Community* (pp. 1–48). Cambridge University Press. https://doi.org/DOI: 10.1017/CBO9780511542121.002

McGraw, W., Zuberbühler, K., & Noë, R. (2007). *Monkeys of the Tai Forest*. Cambridge University Press. https://doi.org/10.1017/CBO9780511542121

Meno, W., Coss, R. G., & Perry, S. (2013a). Development of Snake-Directed Antipredator

Behavior by Wild White-faced Capuchin Monkeys: I. Snake-Species Discrimination. *American Journal of Primatology*, *75*(3), 281–291. https://doi.org/https://doi.org/10.1002/ajp.22106

Meno, W., Coss, R. G., & Perry, S. (2013b). Development of Snake-Directed Antipredator Behavior by Wild White-Faced Capuchin Monkeys: II. Influence of the Social Environment. *American Journal of Primatology*, *75*(3), 292–300. https://doi.org/https://doi.org/10.1002/ajp.22109

Mery, F., & Burns, J. G. (2010). Behavioural plasticity: an interaction between evolution and experience. *Evolutionary Ecology*, *24*(3), 571–583. https://doi.org/10.1007/s10682-009-9336-y

Meyer, D., Hodges, J. K., Rinaldi, D., Wijaya, A., Roos, C., & Hammerschmidt, K. (2012). Acoustic structure of male loud-calls support molecular phylogeny of Sumatran and Javanese leaf monkeys (genus Presbytis). *BMC Evolutionary Biology*, *12*(1), 16.

Mielke, A., Crockford, C., & Wittig, R. M. (2019). Snake alarm calls as a public good in sooty mangabeys. *Animal Behaviour*, *158*, 201–209. https://doi.org/https://doi.org/10.1016/j.anbehav.2019.10.001

Mielke, A., & Zuberbühler, K. (2013). A method for automated individual, species and call type recognition in free-ranging animals. *Animal Behaviour*, *86*(2), 475–482. https://doi.org/https://doi.org/10.1016/j.anbehav.2013.04.017

Mineka, S. (1992). *Evolutionary Memories, Emotional Processing, and the Emotional Disorders* (D. L. B. T.-P. of L. and M. Medin (ed.); Vol. 28, pp. 161–206). Academic Press. https://doi.org/https://doi.org/10.1016/S0079-7421(08)60490-9

Mineka, S., & Cook, M. (1988). Social learning and the acquisition of snake fear in monkeys. In *Social learning: Psychological and biological perspectives.* (pp. 51–73). Lawrence Erlbaum Associates, Inc.

Mineka, S., & Cook, M. (1993). Mechanisms involved in the observational conditioning of fear. In *Journal of Experimental Psychology: General* (Vol. 122, Issue 1, pp. 23–38). American Psychological Association. https://doi.org/10.1037/0096-3445.122.1.23

Mittermeier, R., Wilson, D., & Rylands, A. B. (2013). *Handbook of the Mammals of the World: 3. Primates*. Lynx Edicions. https://books.google.com.co/books?id=P0-rMQEACAAJ

Mohamad Nor, N., & Rashid, R. A. (2018). A review of theoretical perspectives on language learning and acquisition. *Kasetsart Journal of Social Sciences*, *39*(1), 161–167. https://doi.org/https://doi.org/10.1016/j.kjss.2017.12.012

Mohr, T., Van de Waal, E., Zuberbühler, K., & Mercier, S. (2022). *https://osf.io/mjywg/.*

Morse, D. H. (1977). Feeding Behavior and Predator Avoidance in Heterospecific Groups. *BioScience*, *27*(5), 332–339. https://doi.org/10.2307/1297632

Munn, C. A. (1986). Birds that 'cry wolf.' *Nature*, *319*(6049), 143–145. https://doi.org/10.1038/319143a0

Newman, J. D., & Symmes, D. (1974). Vocal pathology in socially deprived monkeys. *Developmental Psychobiology*, *7*(4), 351–358. https://doi.org/https://doi.org/10.1002/dev.420070412

Oates, J. F., Whitesides, G. H., Davies, A. G., Waterman, P. G., Green, S. M., Dasilva, G. L., & Mole, S. (1990). Determinants of Variation in Tropical Forest Primate Biomass: New Evidence from West Africa. *Ecology*, *71*(1), 328–343. https://doi.org/10.2307/1940272

Oda, R. (1998). The responses of Verreaux's sifakas to anti-predator alarm calls given by sympatric ring-tailed lemurs. *Folia Primatologica; International Journal of Primatology*, *69*(6), 357–360. https://doi.org/10.1159/000021651

Oda, R., & Masataka, N. (1996). Interspecific Responses of Ringtailed Lemurs to Playback of Antipredator Alarm Calls Given by Verreaux's Sifakas. *Ethology*, *102*(3), 441–453. https://doi.org/https://doi.org/10.1111/j.1439-0310.1996.tb01138.x

Öhman, A. (2009). Of snakes and faces: An evolutionary perspective on the psychology of fear. *Scandinavian Journal of Psychology*, *50*(6), 543–552. https://doi.org/https://doi.org/10.1111/j.1467-9450.2009.00784.x

Ohman, A., & Mineka, S. (2001). Fears, phobias, and preparedness: toward an evolved module of fear and fear learning. *Psychological Review*, *108*(3), 483–522. https://doi.org/10.1037/0033-295x.108.3.483

Oliveira, L. C., & Dietz, J. M. (2011). Predation risk and the interspecific association of two Brazilian Atlantic forest primates in Cabruca agroforest. *American Journal of Primatology*, *73*(9), 852–860. https://doi.org/10.1002/ajp.20952

Olsson, A., & Phelps, E. A. (2007). Social learning of fear. *Nature Neuroscience*, *10*(9), 1095–1102. https://doi.org/10.1038/nn1968

Ouattara, K., Lemasson, A., & Zuberbühler, K. (2009a). Anti-predator strategies of free-ranging Campbell's monkeys. *Behaviour*, *146*(12), 1687–1708. https://doi.org/10.1163/000579509X12469533725585

Ouattara, K., Lemasson, A., & Zuberbühler, K. (2009b). Campbell's monkeys concatenate vocalizations into context-specific call sequences. In *PNAS Proceedings of the National Academy of Sciences of the United States of America* (Vol. 106, Issue 51, pp. 22026–22031). National Academy of Sciences. https://doi.org/10.1073/pnas.0908118106

Owren, M. J., Dieter, J. A., Seyfarth, R. M., & Cheney, D. L. (1992). "Food" Calls Produced by Adult Female Rhesus (Macaca mulatta) and Japanese (M. fuscata) Macaques, Their Normally-Raised Offspring, and Offspring Cross-Fostered between Species. *Behaviour*, *120*(3/4), 218–231. http://www.jstor.org/stable/4535009

Owren, M. J., Dieter, J. A., Seyfarth, R. M., & Cheney, D. L. (1993). Vocalizations of rhesus (Macaca mulatta) and Japanese (M. Fuscata) macaques cross-fostered between species show evidence of only limited modification. *Developmental Psychobiology*, *26*(7), 389–406. https://doi.org/https://doi.org/10.1002/dev.420260703

Owren, M. J., & Rendall, D. (1997). *An Affect-Conditioning Model of Nonhuman Primate Vocal Signaling BT - Communication* (D. H. Owings, M. D. Beecher, & N. S. Thompson (eds.); pp. 299–346). Springer US. https://doi.org/10.1007/978-1-4899-1745-4_10

Owren, M. J., & Rendall, D. (2001). Sound on the rebound: Bringing form and function back to the forefront in understanding nonhuman primate vocal signaling. *Evolutionary Anthropology: Issues, News, and Reviews*, *10*(2), 58–71. https://doi.org/https://doi.org/10.1002/evan.1014

Peake, T. M., & Mcgregor, P. K. (2004). Information and aggression in fishes. *Animal Learning & Behavior*, *32*(1), 114–121. https://doi.org/10.3758/BF03196012

Penner, J., Fruteau, C., Range, F., & Rodel, M. (2008). Finding a needle in a haystack: new methods of locating and working with rhinoceros vipers (Bitis rhinoceros). *Herpetological Review*, *39*(3), 310.

Pepperberg, I. M. (2010). Vocal learning in Grey parrots: A brief review of perception, production, and cross-species comparisons. *Brain and Language*, *115*(1), 81–91. https://doi.org/https://doi.org/10.1016/j.bandl.2009.11.002

Pepperberg, I. M. (2017). Animal language studies: What happened? *Psychonomic Bulletin & Review*, *24*(1), 181–185. https://doi.org/10.3758/s13423-016-1101-y

Perry, S., Panger, M., Rose, L. M., Baker, M., Gros-Louis, J., Jack, K., Mackinnon, K. C., Manson, J., Fedigan, L., & Pyle, K. (2003). Traditions in wild white-faced capuchin monkeys. In *The Biology of Traditions* (pp. 391–425). Cambridge University Press. https://doi.org/10.1017/CBO9780511584022.015

Pessoa, D. M. A., Maia, R., de Albuquerque Ajuz, R. C., De Moraes, P. Z. P. M. R., Spyrides, M. H. C., & Pessoa, V. F. (2014). The adaptive value of primate color vision for predator detection. *American Journal of Primatology*, *76*(8), 721–729. https://doi.org/10.1002/ajp.22264

Pika, S., & Liebal, K. (2006). Differences and similarties between the natural gestural communication of the great apes and human children. In *The Evolution of Language* (pp. 267–274). WORLD SCIENTIFIC. https://doi.org/doi:10.1142/9789812774262_0034

Pika, S., Liebal, K., & Tomasello, M. (2003). Gestural communication in young gorillas (Gorilla gorilla): gestural repertoire, learning, and use. *American Journal of Primatology*, *60*(3), 95–111. https://doi.org/10.1002/ajp.10097

Poole, J. H., Tyack, P. L., Stoeger-Horwath, A. S., & Watwood, S. (2005). Elephants are capable of vocal learning. *Nature*, *434*(7032), 455–456. https://doi.org/10.1038/434455a

Potvin, D. A., Ratnayake, C. P., Radford, A. N., & Magrath, R. D. (2018). Birds Learn Socially to Recognize Heterospecific Alarm Calls by Acoustic Association. *Current Biology*, *28*(16), 2632-2637.e4. https://doi.org/https://doi.org/10.1016/j.cub.2018.06.013

Pozzi, L., Gamba, M., & Giacoma, C. (2013). Artificial Neural Networks: A New Tool for

Studying Lemur Vocal Communication. In J. Masters, M. Gamba, & F. Génin (Eds.), *Leaping Ahead: Advances in Prosimian Biology* (pp. 305–313). Springer New York. https://doi.org/10.1007/978-1-4614-4511-1_34

Pozzi, L., Hodgson, J. A., Burrell, A. S., Sterner, K. N., Raaum, R. L., & Disotell, T. R. (2014). Primate phylogenetic relationships and divergence dates inferred from complete mitochondrial genomes. *Molecular Phylogenetics and Evolution*, *75*, 165–183. https://doi.org/10.1016/j.ympev.2014.02.023

Price, T., Ndiaye, O., Hammerschmidt, K., & Fischer, J. (2014). Limited geographic variation in the acoustic structure of and responses to adult male alarm barks of African green monkeys. *Behavioral Ecology and Sociobiology*, *68*(5), 815–825. https://doi.org/10.1007/s00265-014-1694-y

Price, T., Wadewitz, P., Cheney, D., Seyfarth, R., Hammerschmidt, K., & Fischer, J. (2015). Vervets revisited: A quantitative analysis of alarm call structure and context specificity. *Scientific Reports*, *5*, 13220. https://doi.org/10.1038/srep13220

Quam, R. M., Ramsier, M. A., Fay, R. R., & Popper, A. N. (2017). *Primate hearing and communication*. Springer.

Quintero, F., Touitou, S., Magris, M., & Zuberbühler, K. (2022a). An audience effect in sooty mangabey alarm calling. *Front Psychol*, *13*. https://doi.org/10.3389/fpsyg.2022.816744

Quintero, F., Touitou, S., Magris, M., & Zuberbühler, K. (2022b). The Evolution of Food Calls: Vocal Behaviour of Sooty Mangabeys in the Presence of Food . In *Frontiers in Psychology* (Vol. 13). https://www.frontiersin.org/articles/10.3389/fpsyg.2022.897318

R Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

Ramakrishnan, U., & Coss, R. G. (2000). Recognition of heterospecific alarm vocalization by Bonnet Macaques (Macaca radiata). In *Journal of Comparative Psychology* (Vol. 114, Issue 1, pp. 3–12). American Psychological Association. https://doi.org/10.1037/0735-7036.114.1.3

Ramakrishnan, U., Coss, R. G., Schank, J., Dharawat, A., & Kim, S. (2005). Snake Species

Discrimination by Wild Bonnet Macaques (Macaca radiata). *Ethology*, *111*(4), 337–356. https://doi.org/10.1111/j.1439-0310.2004.01063.x

Range, F., & Fischer, J. (2004). Vocal Repertoire of Sooty Mangabeys (Cercocebus torquatus atys) in the Tai National Park. *Ethology*, *110*(4), 301–321. https://doi.org/10.1111/j.1439-0310.2004.00973.x

Range, F., & Noë, R. (2002). Familiarity and dominance relations among female sooty mangabeys in the Taï National Park. *American Journal of Primatology*, *56*(3), 137–153. https://doi.org/https://doi.org/10.1002/ajp.1070

Rapaport, L. G., & Brown, G. R. (2008). Social influences on foraging behavior in young nonhuman primates: Learning what, where, and how to eat. *Evolutionary Anthropology: Issues, News, and Reviews*, *17*(4), 189–201. https://doi.org/https://doi.org/10.1002/evan.20180

Rendall, D., Owren, M. J., & Ryan, M. J. (2009). What do animal signals mean? *Animal Behaviour*, *78*(2), 233–240. https://doi.org/https://doi.org/10.1016/j.anbehav.2009.06.007

Rescorla, L. A. (1980). Overextension in early language development. *Journal of Child Language*, *7*(2), 321–335. https://doi.org/DOI: 10.1017/S0305000900002658

Rescorla, R. A., & Wagner, A. (1972). A theory of Pavlovian conditioning: Variations in the effectiveness of reinforcement and nonreinforcement. In A. Black & P. W (Eds.), *Classical Conditioning II: Current Research and Theory: Vol. Vol. 2* (pp. 64–69). Appleton-Century-Crofts.

Ridgway, S., Carder, D., Jeffries, M., & Todd, M. (2012). Spontaneous human speech mimicry by a cetacean. *Current Biology*, *22*(20), R860–R861. https://doi.org/10.1016/j.cub.2012.08.044

Rödel, M., & Mahsberg, D. (2000). Vorläufige Liste der Schlangen des Taï-Nationalparks / Elfenbeinküste und angrenzender Gebiete. *Salamandra*, *36*, 25–38.

Romano, D., Donati, E., Benelli, G., & Stefanini, C. (2019). A review on animal–robot interaction: from bio-hybrid organisms to mixed societies. *Biological Cybernetics*, *113*(3), 201–225. https://doi.org/10.1007/s00422-018-0787-5

Rosati, A. G., Machanda, Z. P., & Slocombe, K. E. (2022). Cognition in the wild: understanding animal thought in its natural context. *Current Opinion in Behavioral Sciences*, *47*, 101210. https://doi.org/https://doi.org/10.1016/j.cobeha.2022.101210

Roupe, S., Pistorio, A., & Wang, X. (2003). Vocal plasticity induced by auditory deprivation in the common marmoset. *Program No. 627.7 2003 Abstract Viewer and Itinerary Planner. Society for Neuroscience Online*.

Schel, A. M., Machanda, Z., Townsend, S. W., Zuberbühler, K., & Slocombe, K. E. (2013). Chimpanzee food calls are directed at specific individuals. *Animal Behaviour*, *86*(5), 955–965. https://doi.org/https://doi.org/10.1016/j.anbehav.2013.08.013

Schel, A. M., Townsend, S. W., Machanda, Z., Zuberbühler, K., & Slocombe, K. E. (2013). Chimpanzee Alarm Call Production Meets Key Criteria for Intentionality. *PLOS ONE*, *8*(10), e76674. https://doi.org/10.1371/journal.pone.0076674

Schel, A. M., & Zuberbühler, K. (2009). Responses to leopards are independent of experience in Guereza colobus monkeys. *Behaviour*, *146*(12), 1709–1737. https://doi.org/https://doi.org/10.1163/000579509X12483520922007

Schrago, C. G., & Russo, C. A. M. (2003). Timing the Origin of New World Monkeys. *Molecular Biology and Evolution*, *20*(10), 1620–1625. https://doi.org/10.1093/molbev/msg172

Schuppli, C., Meulman, E. J. M., Forss, S. I. F., Aprilinayati, F., van Noordwijk, M. A., & van Schaik, C. P. (2016). Observational social learning and socially induced practice of routine skills in immature wild orang-utans. *Animal Behaviour*, *119*, 87–98. https://doi.org/https://doi.org/10.1016/j.anbehav.2016.06.014

Searcy, W. A., & Nowicki, S. (2010). The Evolution of Animal Communication: Reliability and Deception in Signaling Systems. In *Reliability and Deception in Signaling Systems*. Princeton University Press. https://doi.org/doi:10.1515/9781400835720

Seidenberg, M. S. (1997). Language Acquisition and Use: Learning and Applying Probabilistic Constraints. *Science*, *275*(5306), 1599–1603.

https://doi.org/10.1126/science.275.5306.1599

Seiler, M., Schwitzer, C., Gamba, M., & Holderied, M. W. (2013). Interspecific Semantic Alarm Call Recognition in the Solitary Sahamalaza Sportive Lemur, Lepilemur sahamalazensis. *PLoS ONE*, *8*(6), e67397. https://doi.org/10.1371/journal.pone.0067397

Seppänen, J.-T., Forsman, J. T., Mönkkönen, M., & Thomson, R. L. (2007). Social information use is a process across time, space, and ecology, reaching heterospecifics. *Ecology*, *88*(7), 1622–1633. https://doi.org/10.1890/06-1757.1

Seyfarth, R. M., & Cheney, D. L. (1980). The Ontogeny of Vervet Monkey Alarm Calling Behavior: A Preliminary Report. *Zeitschrift Für Tierpsychologie*, *54*(1), 37–56. https://doi.org/10.1111/j.1439-0310.1980.tb01062.x

Seyfarth, R. M., & Cheney, D. L. (1986). Vocal development in vervet monkeys. *Animal Behaviour*, *34*(6), 1640–1658. https://doi.org/https://doi.org/10.1016/S0003-3472(86)80252-4

Seyfarth, R. M., & Cheney, D. L. (1997). Some general features of vocal development in nonhuman primates. In C. T. Snowdon & M. Hausberger (Eds.), *Social Influences on Vocal Development* (pp. 249–273). Cambridge University Press. https://doi.org/DOI: 10.1017/CBO9780511758843.013

Seyfarth, R. M., Cheney, D. L., & Marler, P. (1980). Vervet monkey alarm calls: semantic communication in a free-ranging primate. *Animal Behaviour*, *28*(4), 1070–1094.

Seyfarth, R, & Cheney, D. (2010). Production, usage, and comprehension in animal vocalizations. *Brain and Language*, *115*(1), 92–100. https://doi.org/https://doi.org/10.1016/j.bandl.2009.10.003

Seyfarth, R, Cheney, D., Bergman, T., Fischer, J., Zuberbühler, K., & Hammerschmidt, K. (2010). The central importance of information in studies of animal communication. *Animal Behaviour*, *80*(1), 3–8. https://doi.org/https://doi.org/10.1016/j.anbehav.2010.04.012

Seyfarth, R, Cheney, D., & Marler, P. (1980). Monkey responses to three different alarm calls: evidence of predator classification and semantic communication. *Science*, *210*(4471), 801–803.

Seyfarth, R, & Cheney, D. (1990). The assessment by vervet monkeys of their own and another species' alarm calls. *Animal Behaviour*, *40*(4), 754–764. https://doi.org/https://doi.org/10.1016/S0003-3472(05)80704-3

Shannon, C. E. (1948). A Mathematical Theory of Communication. *Bell System Technical Journal*, *27*(3), 379–423. https://doi.org/https://doi.org/10.1002/j.1538-7305.1948.tb01338.x

Sheldon, B. C., Kruuk, L. E. B., & Alberts, S. C. (2022). The expanding value of long-term studies of individuals in the wild. *Nature Ecology & Evolution*. https://doi.org/10.1038/s41559-022-01940-7

Shibasaki, M., & Kawai, N. (2009). Rapid detection of snakes by Japanese monkeys (Macaca fuscata): An evolutionarily predisposed visual system. In *Journal of Comparative Psychology* (Vol. 123, pp. 131–135). American Psychological Association. https://doi.org/10.1037/a0015095

Shultz, S, & Thomsett, S. (2007). Interactions between African crowned eagles and their prey community. In Klaus Zuberbühler, R. Noë, & W. S. McGraw (Eds.), *Monkeys of the Taï Forest: An African Primate Community* (pp. 171–193). Cambridge University Press. https://doi.org/DOI: 10.1017/CBO9780511542121.008

Shultz, S, Noë, R., McGraw, W. S., & Dunbar, R. I. M. (2004). A community-level evaluation of the impact of prey behavioural and ecological characteristics on predator diet composition. *Proceedings. Biological Sciences*, *271*(1540), 725–732. https://doi.org/10.1098/rspb.2003.2626

Simmons, J. P., Nelson, L. D., & Simonsohn, U. (2011). False-Positive Psychology: Undisclosed Flexibility in Data Collection and Analysis Allows Presenting Anything as Significant. *Psychological Science*, *22*(11), 1359–1366. https://doi.org/10.1177/0956797611417632

Slater, P. J. B. (2006). *Animal Communication: Vocal Learning* (K. B. T.-E. of L. & L. (Second E. Brown (ed.); pp. 291–294). Elsevier. https://doi.org/https://doi.org/10.1016/B0-08-044854-2/00824-5

Slocombe, K E, & Zuberbühler, K. (2005). Functionally Referential Communication in a Chimpanzee. *Current Biology*, *15*(19), 1779–1784. https://doi.org/https://doi.org/10.1016/j.cub.2005.08.068

Slocombe, K E, & Zuberbühler, K. (2007). Chimpanzees modify recruitment screams as a function of audience composition. *Proceedings of the National Academy of Sciences*, *104*(43), 17228 LP – 17233. https://doi.org/10.1073/pnas.0706741104

Slocombe, K. E., Waller, B. M., & Liebal, K. (2011). The language void: the need for multimodality in primate communication research. *Animal Behaviour*, *81*(5), 919–924. https://doi.org/https://doi.org/10.1016/j.anbehav.2011.02.002

Smid, S. C., McNeish, D., Miočević, M., & van de Schoot, R. (2020). Bayesian Versus Frequentist Estimation for Structural Equation Models in Small Sample Contexts: A Systematic Review. *Structural Equation Modeling: A Multidisciplinary Journal*, *27*(1), 131–161. https://doi.org/10.1080/10705511.2019.1577140

Snowdon, C. T. B. T.-A. in the S. of B. (2009). Chapter 7 Plasticity of Communication in Nonhuman Primates. In *Advances in the Study of Behavior* (Vol. 40, pp. 239–276). Academic Press. https://doi.org/https://doi.org/10.1016/S0065-3454(09)40007-X

Stansbury, A. L., & Janik, V. M. (2019). Formant Modification through Vocal Production Learning in Gray Seals. *Current Biology*, *29*(13), 2244-2249.e4. https://doi.org/10.1016/j.cub.2019.05.071

Stauffer, R. L., Walker, A., Ryder, O. A., Lyons-Weiler, M., & Hedges, S. B. (2001). Human and Ape Molecular Clocks and Constraints on Paleontological Hypotheses. *Journal of Heredity*, *92*(6), 469–474. https://doi.org/10.1093/jhered/92.6.469

Stensland, E., Angerbjörn, A., & Berggren, P. (2003). Mixed species groups in mammals. *Mammal Review*, *33*(3-4), 205–223. https://doi.org/https://doi.org/10.1046/j.1365-2907.2003.00022.x

Stephan, C., & Zuberbühler, K. (2008). Predation increases acoustic complexity in primate alarm calls. *Biology Letters*, *4*(6), 641–644. https://doi.org/10.1098/rsbl.2008.0488

Stephan, C., & Zuberbühler, K. (2014). Predation affects alarm call usage in female Diana monkeys (Cercopithecus diana diana). *Behavioral Ecology and Sociobiology*, *68*(2), 321–331. https://doi.org/10.1007/s00265-013-1647-x

Stephan, C., & Zuberbühler, K. (2021). *Alarm Calling and Kinship BT - Encyclopedia of Evolutionary Psychological Science* (T. K. Shackelford & V. A. Weekes-Shackelford (eds.); pp. 163–171). Springer International Publishing. https://doi.org/10.1007/978-3-319-19650-3_1512

Stevenson, M. (1973). Notes on pregnancy in the Sooty mangabey Cercocebus atys. *International Zoo Yearbook*, *13*(1), 134–135. https://doi.org/https://doi.org/10.1111/j.1748-1090.1973.tb02126.x

Stoeger, A. S., Mietchen, D., Oh, S., de Silva, S., Herbst, C. T., Kwon, S., & Fitch, W. T. (2012). An Asian Elephant Imitates Human Speech. *Current Biology*, *22*(22), 2144–2148. https://doi.org/10.1016/j.cub.2012.09.022

Struhsaker, T. T. (1967). Ecology of Vervet Monkeys (Cercopithecus Aethiops) in The Masai-Amboseli Game Reserve, Kenya. *Ecology*, *48*(6), 891–904. https://doi.org/https://doi.org/10.2307/1934531

Sugiura, H. (1998). Matching of acoustic features during the vocal exchange of coo calls by Japanese macaques. *Animal Behaviour*, *55*(3), 673–687. https://doi.org/https://doi.org/10.1006/anbe.1997.0602

Takahashi, D. Y., Liao, D. A., & Ghazanfar, A. A. (2017). Vocal Learning via Social Reinforcement by Infant Marmoset Monkeys. *Current Biology*, *27*(12), 1844-1852.e6. https://doi.org/10.1016/j.cub.2017.05.004

Talmage-Riggs, G., Winter, P., Ploog, D., & Mayer, W. (1972). Effect of deafening on the vocal behavior of the squirrel monkey (Saimiri sciureus). *Folia Primatologica; International Journal of Primatology*, *17*(5), 404–420. https://doi.org/10.1159/000155458

Team, J. (2020). *JASP (Version 0.14.1)*. https://jasp-stats.org/

Thinh, V. N., Hallam, C., Roos, C., & Hammerschmidt, K. (2011). Concordance between vocal and genetic diversity in crested gibbons. *BMC Evolutionary Biology*, *11*(1), 36.

https://doi.org/10.1186/1471-2148-11-36

Thornton, A., & Clutton-Brock, T. (2011). Social learning and the development of individual and group behaviour in mammal societies. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*(1567), 978–987. https://doi.org/10.1098/rstb.2010.0312

Tomasello, M. (2010). *Why we cooperate*. Boston Review Books.

Tomasello, M, & Call, J. (1994). Social cognition of monkeys and apes. *American Journal of Physical Anthropology*, *37*(S19), 273–305. https://doi.org/https://doi.org/10.1002/ajpa.1330370610

Tomasello, M. (2008). *Origins of Human Communication*. MIT press.

Townsend, S. W., & Manser, M. B. (2013). Functionally Referential Communication in Mammals: The Past, Present and the Future. *Ethology*, *119*(1), 1–11. https://doi.org/https://doi.org/10.1111/eth.12015

Trape, J.-F., Trape, S., & Chirio, L. (2012). *Lézards, crocodiles et tortues d'Afrique occidentale et du Sahara*. IRD éditions.

Urbani, B. (2017). Humans as Primate Predators. In *The International Encyclopedia of Primatology* (pp. 1–3). https://doi.org/https://doi.org/10.1002/9781119179313.wbprim0258

Valente, D., De Gregorio, C., Torti, V., Miaretsoa, L., Friard, O., Randrianarison, R. M., Giacoma, C., & Gamba, M. (2019). Finding Meanings in Low Dimensional Structures: Stochastic Neighbor Embedding Applied to the Analysis of Indri indri Vocal Repertoire. *Animals : An Open Access Journal from MDPI*, *9*(5). https://doi.org/10.3390/ani9050243

van Doorn, J., van den Bergh, D., Böhm, U., Dablander, F., Derks, K., Draws, T., Etz, A., Evans, N. J., Gronau, Q. F., Haaf, J. M., Hinne, M., Kucharský, Š., Ly, A., Marsman, M., Matzke, D., Gupta, A. R. K. N., Sarafoglou, A., Stefan, A., Voelkel, J. G., & Wagenmakers, E.-J. (2021). The JASP guidelines for conducting and reporting a Bayesian analysis. *Psychonomic Bulletin & Review*, *28*(3), 813–826. https://doi.org/10.3758/s13423-020-01798-5 van Schaik, C. P., van Noordwijk, M. A., Warsono, B., & Sutriono, E. (1983). Party size and early detection of predators in sumatran forest primates. *Primates*, *24*(2), 211–221. https://doi.org/10.1007/BF02381083

Vernes, S. C., & Wilkinson, G. S. (2020). Behaviour, biology and evolution of vocal learning in bats. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *375*(1789), 20190061. https://doi.org/10.1098/rstb.2019.0061

Verzani, J. (2004). *Using R for introductory statistics* (1st ed.). Chapman and Hall/CRC. https://doi.org/https://doi.org/10.4324/9780203499894

Wadewitz, P., Hammerschmidt, K., Battaglia, D., Witt, A., Wolf, F., & Fischer, J. (2015). Characterizing vocal repertoires - Hard vs. Soft classification approaches. *PLoS ONE*, *10*(4). https://doi.org/10.1371/journal.pone.0125785

Watson, S. K., Townsend, S. W., Schel, A. M., Wilke, C., Wallace, E. K., Cheng, L., West, V., & Slocombe, K. E. (2015). Vocal Learning in the Functionally Referential Food Grunts of Chimpanzees. *Current Biology*, *25*(4), 495–499. https://doi.org/https://doi.org/10.1016/j.cub.2014.12.032

Wegdell, F., Hammerschmidt, K., & Fischer, J. (2019). Conserved alarm calls but rapid auditory learning in monkey responses to novel flying objects. *Nature Ecology & Evolution*, *3*(7), 1039–1042. https://doi.org/10.1038/s41559-019-0903-5

Weiss, L., Brandl, P., & Frynta, D. (2015). Fear reactions to snakes in naïve mouse lemurs and pig-tailed macaques. *Primates*, *56*(3), 279–284. https://doi.org/10.1007/s10329-015-0473-3

Wheeler, B. C. (2009). Monkeys crying wolf? Tufted capuchin monkeys use anti-predator calls to usurp resources from conspecifics. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1669), 3013–3018. https://doi.org/10.1098/rspb.2009.0544

Wheeler, B. C., Fahy, M., & Tiddi, B. (2019). Experimental evidence for heterospecific alarm signal recognition via associative learning in wild capuchin monkeys. *Animal Cognition*, *22*(5), 687–695. https://doi.org/10.1007/s10071-019-01264-3

Wheeler, B. C., & Fischer, J. (2012). Functionally referential signals: A promising paradigm whose time has passed. *Evolutionary Anthropology: Issues, News, and Reviews*, *21*(5), 195–205. https://doi.org/https://doi.org/10.1002/evan.21319

Wheeler, B. C., & Hammerschmidt, K. (2013). Proximate factors underpinning receiver responses to deceptive false alarm calls in wild tufted capuchin monkeys: is it counterdeception? *American Journal of Primatology*, *75*(7), 715–725. https://doi.org/10.1002/ajp.22097

White, D. J. (2004). Influences of social learning on mate-choice decisions. *Animal Learning & Behavior*, *32*(1), 105–113. https://doi.org/10.3758/BF03196011

Whiten, A., & van de Waal, E. (2018). The pervasive role of social learning in primate lifetime development. *Behavioral Ecology and Sociobiology*, *72*(5), 80. https://doi.org/10.1007/s00265-018-2489-3

Whitesides, G. H. (1989). Interspecific associations of Diana monkeys, Cercopithecus diana, in Sierra Leone, West Africa: biological significance or chance? *Animal Behaviour*, *37*, 760–776. https://doi.org/https://doi.org/10.1016/0003-3472(89)90062-6

Wich, S. A., & Sterck, E. H. M. (2003). Possible audience effect in Thomas langurs (Primates; Presbytis thomasi): an experimental study on male loud calls in response to a tiger model. *American Journal of Primatology*, *60*(4), 155–159. https://doi.org/10.1002/ajp.10102

Winter, P., Handley, P., Ploog, D., & Schott, D. (1973). Ontogeny of squirrel monkey calls under normal conditions and under acoustic isolation. *Behaviour*, *47*(3), 230–239. https://doi.org/10.1163/156853973x00085

Wittig, R. M. (2018). 40 years of research at the Taï Chimpanzee Project. *Pan Africa News*, *25*(2), 16–18.

Wrangham, R. W., & Cheney, D. L. (1985). Predation rates and social-structure in primates. *American Journal of Primatology*, *8*(4), 372.

Zhang, Y. S., & Ghazanfar, A. A. (2018). Vocal development through morphological computation. *PLOS Biology*, *16*(2), e2003933. https://doi.org/10.1371/journal.pbio.2003933

Zuberbühler, K. (2000a). Interspecies semantic communication in two forest primates.

Proceedings of the Royal Society of London. Series B: Biological Sciences, *267*(1444), 713–718. https://doi.org/10.1098/rspb.2000.1061

Zuberbühler, K. (2000b). Causal cognition in a non-human primate: field playback experiments with Diana monkeys. *Cognition*, *76*(3), 195–207. https://doi.org/10.1016/s0010-0277(00)00079-2

Zuberbühler, K. (2001). Predator-specific alarm calls in Campbell's monkeys, Cercopithecus campbelli. *Behavioral Ecology and Sociobiology*, *50*(5), 414–422.

Zuberbühler, K. (2003a). Natural semanticity in wild primates. In *Animal social complexity: Intelligence, culture, and individualized societies.* (pp. 362–367). Harvard University Press.

Zuberbühler, K. (2003b). Referential signaling in non-human primates: Cognitive precursors and limitations for the evolution of language. In *Advances in the study of behavior, Vol 33.* (pp. 265–307). Elsevier Academic Press. https://doi.org/10.1016/S0065-3454(03)33006-2

Zuberbühler, K. (2007). Monkey alarm calls. In Klaus Zuberbühler, R. Noë, & W. S. McGraw (Eds.), *Monkeys of the Taï Forest: An African Primate Community* (pp. 194–220). Cambridge University Press. https://doi.org/DOI: 10.1017/CBO9780511542121.009

Zuberbühler, K, & Jenny, D. (2002). Leopard predation and primate evolution. *Journal of Human Evolution*, *43*(6), 873–886. https://doi.org/https://doi.org/10.1006/jhev.2002.0605

Zuberbühler, K, & Jenny, D. (2007). Interaction between leopard and monkeys. In Klaus Zuberbühler, R. Noë, & W. S. McGraw (Eds.), *Monkeys of the Taï Forest: An African Primate Community* (pp. 133–154). Cambridge University Press. https://doi.org/DOI: 10.1017/CBO9780511542121.006

Zuberbühler, K, Jenny, D., & Bshary, R. (1999). The Predator Deterrence Function of Primate Alarm Calls. *Ethology*, *105*(6), 477–490. https://doi.org/10.1046/j.1439-0310.1999.00396.x

Zuberbühler, K, Noë, R., & Seyfarth, R. M. (1997). Diana monkey long-distance calls:

messages for conspecifics and predators. *Animal Behaviour*, *53*(3), 589–604.

Zuberbühler, K. (2000). Causal knowledge of predators' behaviour in wild Diana monkeys. *Animal Behaviour*, *59*(1), 209–220. https://doi.org/https://doi.org/10.1006/anbe.1999.1296

Zuberbühler, K. (2009). Survivor Signals: The Biology and Psychology of Animal Alarm Calling. *Advances in the Study of Behavior*, *40*, 277–322. https://doi.org/https://doi.org/10.1016/S0065-3454(09)40008-1

Zuberbühler, K, & Lemasson, A. (2014). *Primate Communication: Meaning from Strings of Calls BT - Language and Recursion* (F. Lowenthal & L. Lefebvre (eds.); pp. 115–125). Springer New York. https://doi.org/10.1007/978-1-4614-9414-0_9

Zuberbühler, K, León, J., Deshpande, A., & Quintero, F. (2022). Socially scripted vocal learning in primates. *Current Opinion in Behavioral Sciences*, *46*, 101153. https://doi.org/https://doi.org/10.1016/j.cobeha.2022.101153

Chapter 2: Comprehension of own and other species' alarm calls in sooty mangabey vocal development

Julián León[1, 2,*], Constance Thiriau[2], Catherine Crockford[3,4] and Klaus Zuberbühler[1, 2,5]

[1]Institute of Biology, University of Neuchâtel, 2000 Neuchâtel, Switzerland.

[2]Taï Monkey Project, Centre Suisse de Recherches Scientifiques, 01 BP1303 Abidjan 01, Cote d'Ivoire.

[3]Taï Chimpanzee Project, Centre Suisse de Recherches Scientifiques, 01 BP1303 Abidjan 01, Cote d'Ivoire.

[4]Institute of Cognitive Sciences Marc Jeannerod, CNRS, 69330, Lyon, France

[5]School of Psychology and Neuroscience, University of St. Andrews, KY16 9JP Saint Andrews, Scotland (UK).

(Manuscript in press in Behavioral Ecology and Sociobiology)

2.1 Abstract

Primates understand the meaning of their own and other species' alarm calls, but little is known about how they acquire such knowledge. Here, we combined direct behavioural observations with playback experiments to investigate two key processes underlying vocal development: comprehension and usage. Specifically, we studied the development of con- and heterospecific alarm call recognition in free-ranging sooty mangabeys, *Cercocebus atys*, across three age groups: young juveniles (1–2y), old juveniles (3–4y) and adults (>5y). We observed that, during natural predator encounters, juveniles alarm called to a significantly wider range of species than adults, with evidence of refinement during the first four years of life. In the experiments, we exposed subjects to leopard, eagle and snake alarm calls given by other group members or sympatric Diana monkeys. We found that young juveniles' locomotor and vocal responses were least appropriate and that they engaged in more social referencing (look at adults when hearing an alarm call) than older individuals, suggesting that vocal competence is obtained via social learning. In conclusion, our results suggest that alarm call comprehension is socially learned during the juvenile stage, with comprehension preceding appropriate usage but no difference between learning their own or other species' alarm calls.

2.2 Keywords:

Vocal communication, Primates vocalizations, Heterospecific communication, Predation, Alarm calls, Playback experiments

2.3 Introduction

Research in primate communication continues to contribute to theories of speech and language evolution, with growing evidence of a continuum of abilities between human and non-human primates, especially in terms of comprehension (Bergman et al., 2019; Crockford et al., 2017; Fischer, 2017, 2021; Fischer & Price, 2017; Ghazanfar et al., 2019; Liebal et al., 2014; Quam et al., 2017; Slocombe & Zuberbühler, 2005; Stensland et al., 2003; Watson et al., 2015; Zuberbühler, 2003). Yet, key differences remain, particularly in terms of vocal production, which is surprisingly limited in non-human primates, but also in vocal usage, with many utterances fixed to specific biological functions (Cheney & Seyfarth, 2018; see Hammerschmidt & Fischer, 2008 for review). Some flexibility in production and usage has been reported in cases when single vocal units are combined into more complex structures, a relatively novel line of research with considerable potential (see Girard-Buttoz et al., 2022).

Alarm calls have traditionally played a key role in studies of flexibility in vocal production, usage and comprehension (Zuberbühler, 2007). Pioneering work on vervet monkey (*Cercopithecus aethiops*) alarm calls has originally suggested human-like semantic abilities (Seyfarth et al., 1980a, 1980b), although more recent work has challenged this view (Price et al., 2015; Wheeler & Fischer, 2012). Vervet monkeys produce acoustically distinct alarm calls in response to their key predators (leopards, eagles, snakes) and show appropriate antipredator responses when hearing these calls, e.g., rapidly climbing into trees when hearing leopard alarms versus scanning the sky or running for cover when hearing eagle alarms (Seyfarth et al., 1980a). Follow-up research has produced comparable evidence in other primates, suggesting that such abilities are a general feature of primate cognition and, most likely, many other groups of animals (Arnold & Zuberbühler, 2006; Fichtel, 2020; Fichtel & Kappeler, 2002, 2011; Fischer et al., 2001; Fischer & Hammerschmidt, 2001; Kirchhof & Hammerschmidt, 2006; Manser, 2001; Manser et al., 2001; Townsend & Manser, 2013; Zuberbühler, 2003a).

How do primates learn the meaning of their calls? The literature on acquisition and development of non-human primate communication is comparably limited, mainly because it is difficult to continuously monitor animals under field conditions with development likely to be affected by key life experiences (Chow et al., 2015; Egnor & Hauser, 2004; Elowson et al., 1992; Hauser, 1989; Owren et al., 1993). Classic research on vervet monkeys suggests that full competence in vocal comprehension, usage and production occurs during the first four years of life (Seyfarth & Cheney, 1986), albeit with differences in flexibility (Seyfarth & Cheney, 2010; Wegdell et al., 2019). One remarkable finding is that infant vervet monkeys give alarm calls in response to a much wider array of species than adults, although in non-arbitrary ways: leopard alarms are produced to a wide range of terrestrial mammals, eagle alarms to many flying objects (including falling leaves) and snake alarms to any snake-like objects and reptiles (Seyfarth & Cheney, 1980). Over the course of their development, youngsters then appear to reduce and refine their calling behaviour to the relevant predator species. Whether infants are born with core knowledge of predator classes (e.g., aerial vs terrestrial) or whether they simply observe others and first overgeneralise is currently unknown. It also remains unclear whether communicative competence in the main domains (production, usage, comprehension) emerges either gradually over multiple experiences or suddenly in response to one or a few key experiences.

Regarding comprehension and subsequent use, there is good experimental evidence that learning can be rapid requiring only a small number of experiences. For example, when exposed to a remotely operated drone, an unfamiliar potential aerial threat, green monkeys produced alarm calls that were similar to the aerial alarm calls of closely related East African vervet monkeys (Wegdell et al., 2019). After a few such exposures, the sound of the drone was already sufficient for subjects to respond appropriately, i.e., by immediately scanning the sky and running for cover. Two further studies involving potentially dangerous terrestrial threats have also provided evidence for rapid, one-trial social learning in monkeys (Deshpande et al 2022; Leon et al 2022). There is also evidence for more gradual learning, mainly supported by older observational studies (Castro & Snowdon, 2000: *Saguinus oedipus*; Fichtel, 2008: *Propithecus verreauxi verreauxi*; Fischer et al., 2000: *Papio cynocephalus ursinus*; McCowan et al., 2001: *Saimiri sciureus*; Ramakrishnan & Coss, 2000: *Macaca radiata*), although it is often unknown what sorts of experiences individuals have had throughout their early lives.

Whatever the mechanism, social learning is likely to be of key importance during acquisition. In a recent study, when infant vervet monkeys heard alarm calls, they were more likely to respond appropriately if they first looked at more experienced group members (Mohr et al., submitted; Seyfarth & Cheney, 1986), a form of social referencing (Baldwin & Moses, 1996; Evans & Tomasello, 1986). Moreover, research on immature wild orangutans has shown that observational social learning by peering is a critical component of the acquisition of learned subsistence skills like feeding and nest-building (Schuppli et al., 2016).

Another important but often overlooked factor in ontogenetic studies of primate communication is that, under natural conditions, animals do not just interact with members of their own species, but usually operate in a network of associated species, with sometimes shared predators. This leads to opportunities for mutually beneficial antipredator efforts, especially if there are discrepancies in the abilities to detect predators (Goodale et al., 2010; Seppänen et al., 2007), but also for learning by eavesdropping on other species' alarm calling. For example, arboreal species that forage in the upper canopy may be better at detecting aerial predators than species exploiting the lower vegetation (Gautier-Hion et al., 1983; Morse, 1977; Munn, 1986). Many species, and particularly forest primates, exploit this fact by forming mixed-species associations, a behavioural strategy that reduces predation risk (Bshary & Noë, 1997; Heymann & Buchanan-Smith, 2000; Oliveira & Dietz, 2011; Stensland et al., 2003; Whitesides, 1989). Alarm calling may play a key role in mediating the benefits of such mixed species associations. Primates respond well and appropriately to the alarm calls of other species (Di Bitetti & Wheeler, 2017; Ramakrishnan & Coss, 2000; Wheeler & Hammerschmidt, 2013), regardless of taxonomic groups (Hauser, 1988; Seiler et al., 2013; Seyfarth & Cheney, 1990; Zuberbühler, 2000a). For example, both Diana monkeys (*Cercopithecus diana*) and Campbell's monkeys (*C. campbelli*) understand each other's leopard and eagle alarm calls

(Zuberbühler, 2000b, 2001) and similar findings have been reported among prosimians (Fichtel, 2004; Oda, 1998; Oda & Masataka, 1996) and platyrrhines (Wheeler et al., 2019).

Although predation is one of the main selection pressures, learning about predators during actual predation events can be dangerous, which poses the question of how animals can acquire alarm call competence if learning opportunities are costly. Moreover, though vocal production in non-human primates is predominantly innate, vocal usage and comprehension are influenced by learning (Seyfarth & Cheney, 2010). This is even more pertinent for the comprehension of most heterospecific calls because it is unlikely that there is a genetic predisposition for understanding signals of unrelated species. However, there is little research comparing the development of con- and heterospecific alarm call comprehension in non-human primates, so much of these arguments are merely based on general plausibility. Notable exceptions are the studies conducted by Hauser (1988) and Fichtel (2008). In the first one, infant vervet monkeys did not recognize superb starling (*Lamprotornis superbus*) alarm calls at birth but there were individual differences in how fast juveniles learned to respond appropriately as a function of local starling densities (Hauser 1988). Similar findings have also been reported from young Verreaux's sifakas learning red fronted lemur (*Eulemur fulvusrufus*) alarm calls. After only 4 months old, infant sifakas started to discriminate between alarm and non-alarm stimuli (parrot song) and adult-like responses to their own and red fronted lemur alarm calls appeared only after 6–8 months (Fichtel, 2008). Overall, both studies presented evidence that alarm call competence depends on experience, but the details of how and when exactly young primates learn the meaning of other species' alarm calls are unknown.

Here, we investigated the development of con- and heterospecific alarm call recognition in sooty mangabeys (*Cercocebus atys*; hereafter mangabeys), a terrestrial, forest-dwelling, West African monkey. In Taï Forest (Côte d'Ivoire), mangabeys form temporary mixed-species associations with other primate species (around 60% of time), mostly with arboreal Diana monkeys (10–15% of time) (Höner et al., 1997; McGraw & Bshary, 2002; McGraw et al., 2007), with whom they share the same predators (Shultz et al., 2004): leopards (*Panthera pardus*), crowned eagles (*Stephanoaetus coronatus*), chimpanzees (*Pan troglodytes*) (Boesch & Boesch-Achermann, 2000; McGraw et al., 2007) and humans. Encounters with snakes are also common although snakes do not typically prey on mangabeys. Nevertheless, lethal accidental encounters occur, most often with highly venomous Gaboon (*Bitis gabonica*) and rhinoceros vipers (*B. nasicornis*) (Range & Fischer, 2004). Overall estimated predation rates (proportion of population removed per year) by leopards, crowned eagles and chimpanzees are higher for terrestrial than for arboreal Taï forest prey (Shultz & Thomsett, 2007). Moreover, leopard diets are biased towards terrestrial prey, whereas crowned eagle diets do not show a bias towards either terrestrial or arboreal prey (Shultz et al., 2004). Furthermore, the estimated crowned eagle, leopard and chimpanzee predation rates are around 13%, 6% and <1% of the mangabey Taï population, respectively (Shultz et al., 2004).

The different predators differ in their hunting strategies and primates usually show adaptive responses to each predator. Reactions to leopards entail rapidly climbing into the lower forest canopy, followed by mobbing and leopard-specific alarm calls at high rates by some individuals, presumably to drive the predator away (Zuberbühler et al., 1999; Zuberbühler & Jenny, 2002, 2007). For crowned eagles, mangabeys immediately seek cover or monitor the sky to keep visual contact, depending on the eagle's behaviour, again while some individuals give eagle-specific alarm calls at high rates (Shultz & Thomsett, 2007). For stationary snakes, such as Gaboon and rhinoceros vipers, mangabeys jump aside showing startle responses, followed by standing bipedally and cautiously approaching and scanning the area of the snake (Penner et al., 2008; Range & Fischer, 2004), while some give snake-specific alarm calls that attract other individuals to the site. Finally, for chimpanzees, mangabeys adopt a cryptic behaviour and rapidly move away in silence (Zuberbühler et al., 1999). Diana monkeys not only produce acoustically distinct alarm calls in response to leopards and eagles, similar to mangabeys, but they also produce distinct calls for non-predatory disturbances (i.e., falling trees or branches) (Zuberbühler et al., 1997).

We are not aware of any systematic research on the development of con- and heterospecific alarm call comprehension in primates, apart from Hauser (1988) and Fichtel (2008). To address this gap, we combined natural observations with playback experiments to observe the response of mangabeys of three age classes—young juveniles (1–2 years), old juveniles (3–4 years), and adults (>4 years)—to predator-specific alarm calls produced by their own group members or by sympatric Diana monkeys.

Similar to what has already been reported from vervet monkey alarm call development, we predicted that juveniles would show lower response rates to alarm calls and alarm call to a wider variety of stimuli than adults. We also predicted that social referencing, i.e., looking at other group members when hearing an alarm call, would play a key role in alarm call behaviour, especially in young individuals. Moreover, we predicted predator threat to be a major driver of development, with conspecific leopard alarms being established first in early development, because leopard predation has been linked to the evolution of primates' cognitive flexibility (Zuberbühler & Jenny, 2002). Regarding heterospecific alarms, i.e., the alarm calls of Diana monkeys, we predicted that mangabeys would first discriminate predatory (leopard and eagle alarms) from non-predatory threats (falling tree alarms), as seen in other species (Cheney & Seyfarth, 1990; Fichtel, 2008), before learning to discriminate specifically between Diana monkeys' eagle and leopard alarms. Finally, because primates are unlikely predisposed to respond to alarm calls of unrelated species and because mangabeys probably witness fewer predation events on Diana monkeys than on their own group members —having less opportunities to make specific predator-alarm calls associations, we predicted faster learning of conspecific than heterospecific alarm calls.

2.4 Methods

Study site and species

The study was conducted from May to December 2018 and August 2019 to March 2020 with two groups of free-ranging mangabeys in Taï National Park, Côte d'Ivoire. During the study period, we conducted 84 trials on the main group (TCP mangabeys) whose size ranged between 74–91 individuals, including 23 adult females (>5 years old), 7 adult males (>7 years old), 6 subadult females (4–5 years old), 6 subadult males (5–7 years old), 9 old juvenile females (3–4 years old), 8 old juvenile males (3–5 years old), 10 young juvenile females (1–2 years old), 12 young juvenile males (1–2 years old) and 10 infants (<1 years old) (McGraw & Zuberbühler, 2007). We also conducted 28 trials on a non-neighbouring group (TMP mangabeys) whose home range was about 4 km Northwest and which included 62–67 individuals, including 24–26 adults, 9 subadults and 20 juveniles and 9–12 infants (Mielke et al., 2019; Wittig, 2018). Both groups were fully habituated to human observers and have been under study for several years.

Playback Stimuli

Playback stimuli were obtained at the study site by recording alarm calls occurring during encounters with real predators, leopard and snake models and playbacks of leopard growls and eagle shrieks. Recordings were made with a Marantz PMD 661 MKII digital recorder and an MKH 416-P48U3 Sennheiser directional microphone. Sound files were stored and processed as .wav files with 44.1 kHz sampling rate, 16 bits amplitude resolution using Audacity 2.2.2 (Audacity Team, 2020) and Raven 1.4 software (Center for Conservation Bioacoustics, 2014). Recordings were screened for exemplars with low signal-to-noise ratio, absence of signal overlap and recorded at distances from 4–15 m. Playback stimuli were edited such that each consisted of three alarm call sequences with intervals of 5 s silence in between, trying to mimic natural alarm call sequences. We used 43 alarm calls produced by 25 mangabeys for leopards (N=15), crowned eagles (N=14) and vipers (N=14) as conspecific stimuli (Figure S2.1), and 57 alarm calls produced by 21 male Diana monkeys for leopards (N=16), eagles (N=22) and falling trees (N=21) as heterospecific stimuli (Figure S2.2). No stimulus was used in more than two trials. We did not include responses to chimpanzees because monkeys adopt a cryptic behaviour in response to them and chimpanzees rarely prey on mangabeys.

Playback procedures

We conducted a total of 112 playback trials (N=49 conspecific; N=63 heterospecific) on 15 young juveniles, 16 old juveniles and 18 adults (see Table S2.1 and Supplementary online data). Thirty six (N=36) subjects were used in more than one trial (2–4 trials), yet subjects were never tested more than once for each condition. To avoid pseudo-replication, we used vocalizations from different adult individuals as playback stimuli where possible, and never used the same stimulus nor the same call provider twice on a subject. Moreover, for the 10 stimuli that were used twice, we ensured that the same stimulus was not played more than once during the same month to prevent habituation effects. Finally, we excluded nine conspecific trials from analysis (N=2 young and N=5 old juveniles, and N=2 adults) because other monkey species started alarm calling before the subject reacted and three more heterospecific trials were aborted because of a technical failure (N=2 young juveniles and N=1 adult).

Mangabeys commonly hear alarm calls of other group members and Diana monkeys in the study area (Table S2.2), suggesting that two trials per week, one from each species, was well within the monkeys' natural range of experience. For each conspecific trial, we took care to always broadcast a call from a call provider that was in the same social group, but out of sight at the moment of the experiment. Subjects were tested in a randomized but counterbalanced order, and when they were alone or in small parties and engaged in quiet activities (e.g., foraging, resting or auto-grooming).

Two experimenters were needed to carry out a playback trial. Experimenter 1 followed and filmed the focal subject using a Panasonic HC-V500 camera continuously, before (~30 s), during and after the playback (~30 s or as long as possible). Experimenter 2 predicted the subject path and strategically positioned the playback equipment around 5–10m away from the subject, hidden behind buttress roots out of sight of individuals. To emulate natural conditions, the speaker was positioned on the ground or on elevated locations, such as trunks of fallen trees or small hills, during con- and heterospecific trials, respectively. Before each trial, the focal subject was followed for 15min prior to starting the playback to ensure there were no external stimuli modifying his/her behaviour. We proceeded to broadcast the playback stimulus if no alarm calls were produced during the hour before, neither by the any member of the studied group or any other monkey species. Subjects were never more than 2m high during the experiments.

All stimuli were broadcasted using an Apple iPod touch digital player connected to an AER alpha speaker amplifier. We used a Dostmann MS-85 (Dostmann) mini-amplitude level meter to adjust the sound level. Absolute amplitude levels of the different stimuli variated between 95–103 dB(C) and 81–85 dB(C) for mangabey calls produce in response to leopards and eagles, and snakes, respectively, and 99–107 dB(C) for Diana monkey calls, measured at 50 cm from the speaker, to match natural characteristics of the different calls.

Independent variables

For every trial, we noted subject and caller provider identity, caller provider species, alarm call type, using stratum and audience composition within a 10m radius of the subject. We considered a subject to be alone when no other group members were present within that distance. We used BORIS coder (Friard & Gamba, 2016; www.boris.unito.it) to analyse video recordings on a frame-by-frame basis (25 frames s^{-1}) during the first 30 s after model detection.

Behavioural response variables

We first scored the occurrence of predator-specific behavioural responses to leopards, eagles and snakes (Table 2.1). Then, we classified a behavioural response as "appropriate" if it matched the corresponding predator-specific alarm call used as stimulus. For Diana monkey loud calls given to trees the absence of antipredator behaviours was considered as the appropriate response. Additionally, we registered the number and type of calls emitted by the focal individual when vocal responses occurred.

Table 2.1 Definitions and predictions of behavioural responses.

Behavioural response	**Definition**
Leopard antipredator	Subject climbs into a tree, flees and/or emits leopard alarm calls.
Eagle antipredator	Subject looks for cover or runs down trees, constantly scans the sky and/or emits eagle alarm calls.
Snake antipredator	Subject stays and scans the forest floor, approaches and inspects, jumps aside, stands bipedally and/or emits snake alarm calls.
No antipredator response	Subject shows no particular antipredator response and continues engage in his/her activity previous the experiment

To explore whether juveniles copied or looked for clues among other individuals when not knowing how to respond to the stimulus (see Fichtel, 2008; Seyfarth & Cheney, 1986), we also counted the number of subjects that looked at adults as response to the playback experiments as a form of social referencing.

To estimate observer reliability, JL and CT separately blind-coded (65/100) 65% of the trials, resulting in a very good inter-rater reliability (Cohen's kappa for appropriate antipredator behaviour K=0.91 and for social referencing: K=1).

Natural stimuli eliciting alarm calls

We followed the main study group from dawn to dusk and used 20-min focal animal samples (Altmann, 1974) to record detailed behavioural data for all members of the group. We registered 930 focal samples (number of focal samples: adults N=531; subadults N=126; old juveniles N=138, young juveniles N=135). During each focal sample, we recorded data on the stimuli that elicited different types of alarm calls by the focal subject using an all-occurrence sampling. These stimuli were either the antipredator behaviour, usually alarm calls, exhibited by another group member or an heterospecific close by, the sight of a predator or the occurrence of a potential threat. We classified the species (or objects) that elicited alarm calls as confirmed predators (cp): defined as animals that prey on mangabeys; potential predators (pp): defined as animals that prey on species the size of mangabeys but are seldom observed to attack monkeys; confirmed threat (ct): defined as animals that are a lethal threat to mangabeys; potential threat (pt): defined as animals that can potentially pose a threat to mangabeys; non-threating (nt): defined as animals or objects that elicited alarm calls but do not pose a likely threat to mangabeys. Since an individual’s alarm calling is affected by the alarm calls of others, we only analysed data on the first alarm given in any alarming bout. We considered bouts of alarming to be independent after intervals of 15min with no alarm calls. If more than one individual alarmed simultaneously at the start of a bout, all such callers were scored as first callers. The type of alarm call was identified by ear. We chose the first focal subject opportunistically and then sampled all individuals of the same age-sex class before making repeated samples of the same individual. No subsequent samples on the same individual were made less than 1h apart from the previous focal sample.

Statistical analysis

To investigate which factors had an impact on mangabey antipredator behavioural responses, we used a series of Binomial Generalized Linear Mixed Models (Bolker et al., 2009) using R version 4.0.3 (R Core Team, 2020) and the function ‘glmer’ of the package lme4 (Bates et al., 2015). We tested appropriate behavioural response as the response variable in three separate models. The first two models had a con- and a heterospecific approach, respectively, by analysing the response variable against the same set of four fixed effects predictor variables: Playback stimulus (*conspecific model:* leopard, eagle or snake; *heterospecific model:* leopard, eagle, or falling tree), Age (young and old juvenile or adult), Stratum (ground or understory), and Audience (alone or in company). The third model had an interspecific approach and analysed the response variable against a dataset considering only alarm calls shared by both caller species (leopard and eagle alarm calls). For this last model, ‘Caller species’ (sooty mangabey or Diana monkey) was included as an additional fixed factor. ‘Playback stimulus’, ‘Age’ and ‘Caller species’ were our main variables of interest and were considered the test predictors, with ‘Stratum’ and ‘Audience’ considered to be control predictors. Moreover, ‘Subject’ and ‘Caller identity’ were taken as random factors in all models to account for repeated measurements. To check whether the control predictors drove the results (Simmons et al., 2011), we re-ran all the analyses without it. The results were robust. Spatial autocorrelation was tested for each model and when an effect was detected it was corrected in the model. Finally, for all models, we checked for over-dispersion.

To test the significance of the fixed factors and their relations, we used the ‘Anova’ function (car package) in each model to perform a type III or II ANOVA Wald Chi-Square Tests, depending on whether or not there was a significant interaction in the model. Originally, all explanatory variables and interactions involving the test predictors were integrated into the full models. Then, insignificant interactions were removed to simplify the model (Engqvist, 2005). The significance threshold α related to the test predictors was set at 0.05. We then conducted pairwise post hoc comparisons between levels of statistically significant control predictors by computing estimated marginal means for each model, using the ‘emmeans’ function and package. For these comparisons, we included a Tukey honest significant difference adjustment to account for running multiple tests on the same data. We also conducted binomial tests to analyse the vocal response of the subjects during the trials. Because of the low number of alarm calls given as response (N=7), we could not run any further analyses. Finally, we analysed whether juveniles and subadults were less selective in their alarm calling as compared with adults by comparing the observed distributions of immatures alarm calls with the distributions that would have been expected if immatures had produced their alarms exactly like adults did during natural alarm calling events by goodness-of-fit tests. When expected counts were too small, we estimated *P* values using Monte Carlo simulations based on 10,000 permutations of the original data set to properly perform goodness-of-fit tests (option “simulate.p.value=TRUE” in the R chisq.test function) (Verzani, 2004).

2.5 Results

Call usage: vocal responses during natural encounters

During 310 hours of focal animal data, we registered 91 alarm calls in 86 natural predator encounters in which focal subjects were the first individuals to call. In five of those encounters two individuals gave the first alarm calls simultaneously. Encounters with leopards, crowned eagles, dangerous snakes (pythons and vipers: N=45) and potential dangers (civets, genets, dwarf crocodiles, large-sized non-carnivorous mammals; N=23) accounted for 73.3% of the events. The remaining alarm calls were given during 23 encounters with animals and objects that probably were not a threat to them.

We found that alarm calls given for non-threatening stimuli and potential threats decreased with age. After correcting for the number of hours of focal animal data in each age class, young juveniles were the most likely individuals to give first alarm calls (number of first alarm calls per hour: young juveniles: 0.58; old juveniles: 0.37; subadults: 0.45; adults: 0.16). However, young juveniles produced more than half of their alarm calls in response to animals and objects that were unlikely to pose a threat to them (Table 2.2). In contrast, most of the alarm calls produced by subadults and adults were given in response to confirmed predators and threats to mangabeys.

All individuals produced each type of alarm call in non-arbitrary ways. Leopard alarm calls were restricted in response to carnivores and terrestrial mammals, usually of medium to large body size (Table 2.3). Moreover, eagle alarm calls were only given for avian species, while snakes alarm calls were elicited by reptiles, mostly snakes, and animals and objects that resemble the colour or the shape of vipers, i.e., toads and small logs.

However, the number of species classified within these broad categories varied considerably among age classes (Table 2.3). Juveniles gave leopard alarm calls for at least ten different species, whereas adults produced leopard alarm calls to five. In a similar way, juveniles gave snake alarm calls in response to seven different species or objects, whereas adults restricted snake alarm calls to Gaboon and rhinoceros vipers. Overall, we found that juveniles but not subadults were less selective than adults in their alarm call behaviour. When giving alarm calls, juveniles were significantly less likely to restrict alarms to confirmed predators and threats, and significantly more likely to give alarm calls for potential dangers and, in particular, for non-threatening animals (Table 2.2).

Table 2.2 Distribution of alarm calls produced by immatures, compared with the distribution of alarm calls that would have been expected if immatures had distributed their alarm calls as adults did. Expected values are in parentheses.

	N of alarm calls in response to			
	Confirmed dangers	Potential dangers	Unlikely threats	Significance
Young juveniles (N=26)	3 *(20.6)*	7 *(4.5)*	16 *(0.9)*	χ^2=268.8, *P* <0.001
Old juveniles (N=17)	6 *(13.5)*	6 *(2.9)*	5 *(0.6)*	χ^2=40.33, *P* <0.001
Subadults (N=19)	13 *(15.1)*	5 *(3.3)*	1 *(0.7)*	χ^2=1.37, *P* =0.54
Adults (N=29)	23	5	1	–

Table 2.3 Number of times individuals in each age class gave an alarm call for different species and objects during focal follows. Number of hours of focal animal data for each age class are in parentheses. Species are listed by body size in each category (data from: mammals: Kingdon (2015); birds: Borrow (2014); reptiles: Chippaux (2006) and Trape et al. (2012)). Cp: confirmed predator, Pp: potential predator, Ct: confirmed threat, Pt: potential threat, Nt: non-threating.

			N *calling events*			
Scientific name	**Common name**	**Threat**	**Adults (177hr)**	**Subadults (42hr)**	**Old juveniles (46hr)**	**Young juveniles (45hr)**
Leopard alarm call for carnivores						
Panthera pardus	Leopard	Cp	2	1	1	
Civettictis civetta	African civet	Pp	1		1	
Genetta pardina	Genet	Pt	1		2	2
Leopard alarm call for other mammals						
Hylochoerus meinertzhageni	Giant forest hog	Pt		1	1	
Hexaprotodon liberiensis	Pigmy hippopotamus	Pt	1	1		2
Cephalophus jentinki	Jentink's duiker	Pt		1	1	1
Potamochoerus porcus	Red river hog	Pt	1	1		1
Cephalophus dorsalis	Bay duiker	Nt			1	2
Cephalophus niger	Blacked duiker	Nt				1
Cephalophus (undet.)	Unknown duikers	Nt			1	2
Eagle alarm call for birds						
Stephanoaetus coronatus	African crowned eagle	Cp	15	7	3	1
Ceratogymna atrata	Black-casqued hornbill	Nt	1		1	3
Strigidae (undet.)	Unknown small-size owl	Pt				1
Snake alarm call for reptiles, amphibians and vegetation						

Python regius	Python	Cp			1	
Osteolaemus tetraspis	African dwarf crocodile	Pt	1	1	1	
Bitis gabonica / B. rhinoceros	Gaboon viper / Rhinoceros viper	Ct	6	5	1	2
Colubridae (undet.)	Unknown small-size colubrids	Nt			1	4
Sclerophrys (undet.)	Unknown toad	Nt				1
–	Small logs and dry leaves on the ground	Nt		1	1	3

Call usage: vocal responses during experiments

Six (N=6) responded with their own alarm calls to alarm call playbacks in seven (N=7) of 100 trials (7%) (leopard alarms: conspecific 3 of 13; heterospecific 2 of 17; eagle alarms: conspecific: 1 of 12; heterospecific 0 of 21; snake alarms: conspecific: 1 of 15; tree alarms: heterospecific 0 of 22; Supplementary data), always with the correct semantic category of the alarm call they had just heard (Binomial test (0.5): P=0.007). All subjects were adults (N=4 females, N=2 males; Binomial test (0.5): P=0.015) and all were on the ground (Binomial test (0.5): P=0.007). Neither caller species nor audience drove the vocal response of the callers (Binomial test (0.5): Caller Species P=0.226; Audience P=0.226). Finally, the call providers during these trials were always different and did not follow any evident categorization pattern (e.g., sex, ranking pattern).

Call comprehension: non-vocal responses during experiments (conspecific alarms)

In 40 of 49 trials, we were able to code the subjects' antipredator responses to conspecific alarm call playbacks. In the 'conspecific model', we found that the test predictors 'Age' (χ^2_2=7.47, P=0.023) and 'Playback Stimulus' (χ^2_2=6.679, P=0.035) had an influence on the display of appropriate antipredator behavioural responses (Table 2.4a), with adults showing more corresponding specific antipredator behaviours than young juveniles (z=2.733, P=0.017; proportion of subjects mean ± SE: adults 0.92 ± 0.07 vs young juveniles 0.42 ± 0.13; Figure 2.1; Supplementary Videos S2.1 & S2.2). Likewise, conspecific leopard alarm calls elicited more corresponding specific antipredator behaviours than conspecific snakes alarm calls (z=2.568, P=0.027; proportion of subjects mean ± SE: leopard alarm 0.92 ± 0.07 vs snake alarm 0.46 ± 0.13; Figure S2.3).

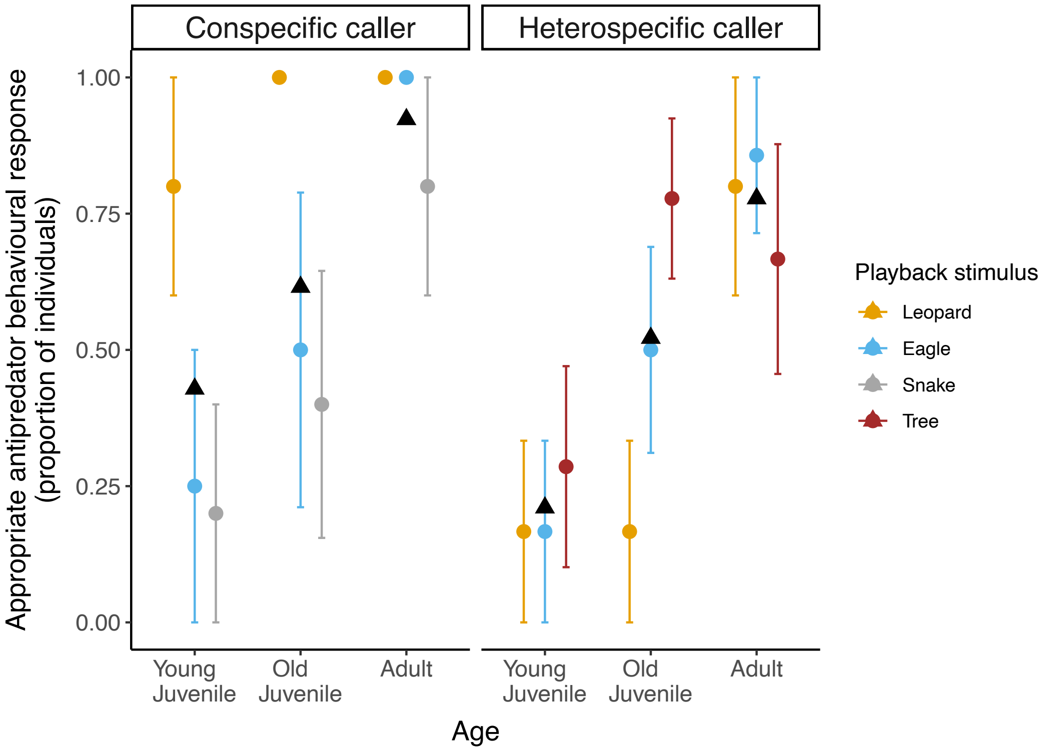

Figure 2.1 Development of con- and heterospecific alarm call behaviour: Proportion of individuals that showed appropriate specific antipredator behavioural responses to con- and heterospecific alarm call playbacks by age. Colour dots indicate mean values ± SE for leopard (yellow), eagle (blue), snake (grey), and tree (brown) playback stimuli. Black triangles indicate mean values for each age group' corresponding response.

Call comprehension: non-vocal responses during experiments (heterospecific alarms)

In 60 of 63 trials, we were able to code subjects' antipredator behavioural response to Diana monkey alarm call playbacks. In the 'heterospecific model', we found that the test predictor 'Age' (χ^2_2=10.68, *P*=0.004) had an influence on the display of appropriate antipredator behavioural responses (Table 2.4b). Pairwise comparisons revealed that adults showed more corresponding specific antipredator behaviours as response to heterospecific alarm calls than young juveniles (*z*=3.268, *P*=0.003; proportion of subjects mean ± SE: adults 0.77 ± 0.1 vs young juveniles 0.21 ± 0.09; Figure 2.1; Supplementary Video S2.3).

Table 2.4 Influence of predictor variables on behavioural responses.

Predictor variable	Estimates	SE	*P**
a. Conspecific model			
Age			**0.023**
Age (old juvenile)	*−2.19*	*1.29*	
Age (young juvenile)	*−4.12*	*1.5*	
Playback stimulus			**0.035**
Playback stimulus (eagle)	*−3.13*	*1.46*	
Playback stimulus (snake)	*−3.87*	*1.5*	
Stratum			0.876
Stratum (understory)	*0.2*	*1.33*	
Audience			0.276
Audience (yes)	*1.19*	*1.09*	
b. Heterospecific model			
Age			**0.004**
Age (old juvenile)	*−1.59*	*0.78*	
Age (young juvenile)	*−2.87*	*0.88*	
Playback stimulus			0.208
Playback stimulus (eagle)	*0.66*	*0.95*	
Playback stimulus (tree)	*1.43*	*0.81*	
Stratum			0.157
Stratum (understory)	*1.13*	*0.8*	
Audience			0.808
Audience (yes)	*−0.16*	*0.68*	
c. Interspecific model			
Caller species			**0.001**
Caller species (Diana monkey)	*−5.02*	*1.56*	
Age			**0.001**
Age (old juvenile)	*−2.98*	*1.05*	
Age (young juvenile)	*−3.92*	*1.1*	
Playback stimulus			**0.02**
Playback stimulus (eagle)	*−3.27*	*1.41*	
Stratum			0.065
Stratum (understory)	*1.89*	*1.03*	
Audience			0.082
Audience (yes)	*1.56*	*0.89*	
Caller species * Playback stimulus			**0.011**
*Caller species (Diana monkey) * Playback stimulus (eagle)*	*4.48*	*1.77*	

() denote the variable level that reflects the estimate when tested against the alternative level:

Eagle and Snake v Leopard, Old and Young juvenile v Adult, Understory v Ground, Audience v Alone, Diana monkey v Sooty Mangabey

*The critical *P* value related to the test predictors was set at 0.05

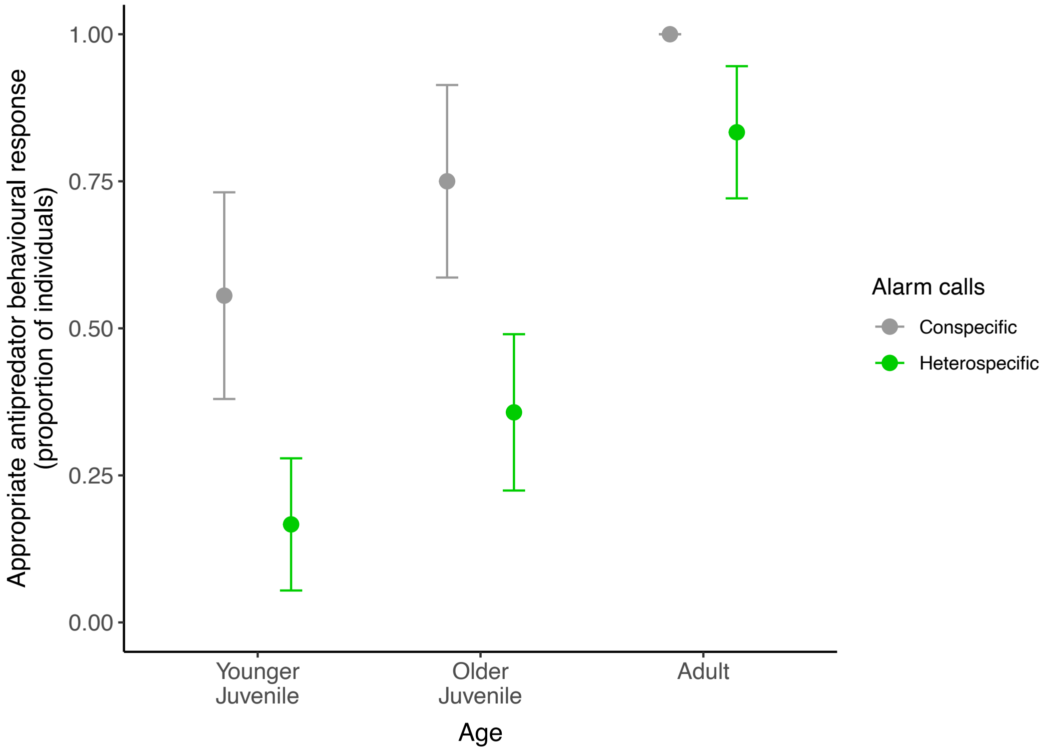

Figure 2.2 Development of con- and heterospecific alarm call behaviour: Proportion of individuals that showed appropriate specific antipredator behavioural responses to leopard and eagle alarm call playbacks from con- and heterospecifics by age. Colour dots indicate mean values ± SE for conspecific (grey), and heterospecific (green) playback stimuli.

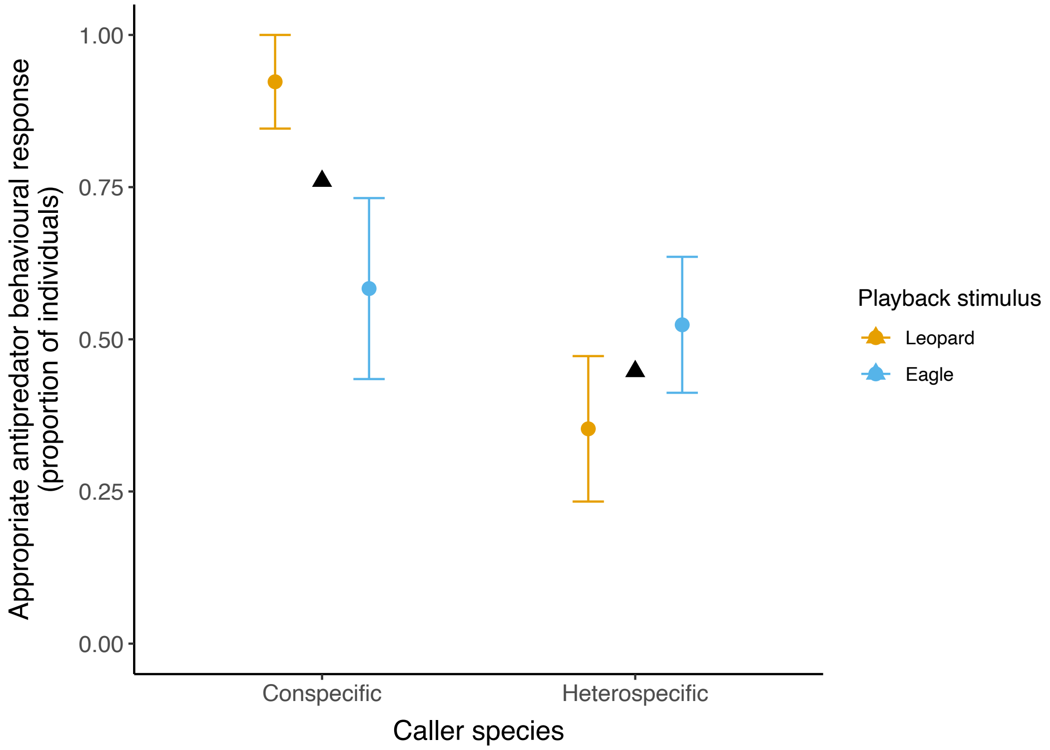

Figure 2.3 Interspecies comparison: Proportion of individuals that showed appropriate specific antipredator behavioural responses to leopard and eagle alarm call playbacks depending on the caller species. Colour dots indicate mean values ± SE for leopard (orange) and eagle (blue) playback stimuli. Black triangles indicate corresponding response mean values to con- and heterospecific alarm calls.

Call comprehension: interspecies comparisons

In the interspecific model, we evaluated subjects' antipredator behavioural responses to mangabeys' and Diana monkeys' leopard and eagle alarm call playbacks (N=63 trials) and found that the test predictor 'Age' (χ^2_2=12.86, *P*=0.001) had an influence on the display of appropriate antipredator behavioural responses (Table 2.4c). Adults showed more corresponding specific antipredator behaviours as response to alarm calls of both species than juveniles (Old juveniles: *z*=2.814, *P*=0.013; proportion of subjects mean ± SE: adults 0.9 ± 0.06 vs old juveniles 0.5 ± 0.11; Young juveniles: *z*=3.544, *P*=0.001; proportion of subjects mean ± SE: adults 0.9 ± 0.06 vs young juveniles 0.33 ± 0.1; Figures 2.1 & 2.2). Moreover, we found a significant interaction between 'Playback stimulus' and 'Caller Species' (χ^2_1=6.381, *P*=0.011) (Table 2.4c). Post hoc tests showed that leopard alarm calls produced by conspecifics elicited more corresponding specific antipredator behaviours than the ones given by heterospecifics in response to both leopards and eagles (Heterospecific leopard alarms: z=3.205, P=0.007; proportion of subjects mean ± SE: conspecific leopard alarms 0.92 ± 0.07 vs heterospecific leopard alarms 0.35 ± 0.12; Heterospecific eagle alarms: z=2.731, P=0.032; proportion of subjects mean ± SE: conspecific leopard alarms 0.92 ± 0.07 vs heterospecific eagle alarms 0.52 ± 0.11; Figure 2.3).

Table 2.5 Number of individuals that showed antipredator behavioural responses with respect to the stimulus heard.

	Antipredator response		
	correct	look at adult	incorrect
Conspecific alarm calls			
Young juveniles (N=14)	6 (42.9%)	6 (42.9%)	2 (14.3%)
Old juveniles (N=13)	8 (61.5%)	4 (30.8%)	1 (7.7%)
Adults (N=13)	12 (92.3%)	0 (0.0%)	1 (7.7%)
Heterospecific alarm calls			
Young juveniles (N=19)	4 (21.1%)	10 (52.6%)	5 (26.3%)
Old juveniles (N=23)	12 (52.2%)	5 (21.7%)	6 (26.1%)
Adults (N=18)	14 (77.8%)	3 (16.7%)	1 (5.5%)

Social referencing

We found that for both con- and heterospecific alarm calls the number of individuals looking toward an adult just after hearing an alarm call decreased with age (Supplementary Video S2.4). When hearing conspecific alarm calls, young and old juveniles looked towards adults in 6 of 14 (42.9%) and 4 of 13 trials (30.8%), respectively, whereas no adult showed this response. Similarly, during heterospecific alarm call trials, young and old juveniles looked towards adults in 10 of 19 (52.6%) and 5 of 23 trials (21.7%), respectively, whereas adults did it in 3 of 18 trials (16.7%; Table 2.5). Because of low sample size, we could not run any further statistical analyses.

2.6 Discussion

Sooty mangabeys show specific behavioural responses, including predator-specific alarm calls, to their predators , but little is known about the development of such behaviour. In this study, we examined the development of alarm call behaviour during natural encounters and in response to experimentally presented conspecific and heterospecific alarm calls. Generally, we found increasing competence with age, both in terms of alarm call comprehension, usage and production. Across conditions, young juveniles (12 to 24 months old) showed the poorest performance and were most likely to engage in social referencing. Old juveniles (24 to 48 months), on the other hand, already showed responses that did not differ significantly from adults, suggesting that the main learning events mainly happen in the first 24 months of their lives. Adults differed from the juveniles insofar as they were particularly sensitive to others' alarm calls and were more likely to respond with corresponding antipredator behaviours, including by responding with their own alarm calls. Mangabeys classified species and objects from the world around them into broad categories since a young age (Table 2.3). However, adults were more selective than juveniles in their alarm calling (Table 2.2). In sum, these results suggest that in mangabeys alarm call comprehension becomes entrenched during the first 2 years of life, while competent alarm call usage does not appear until about 4 years of age, suggesting that comprehension precedes usage and production in the alarm call system of mangabeys.

Across predator types, leopard alarm calls elicited the strongest overall responses in all age classes, while snake alarm calls only prompted mild responses in juveniles in both con- and heterospecific conditions. Alarm call vocal responses, specifically, depended on whether the caller was a con- or heterospecific and the predator reference. Mangabey leopard alarms elicited more corresponding antipredator behaviours than both Diana monkeys' leopard and eagle alarm calls, highlighting the importance of leopard predation pressure in shaping mangabeys' alarm call behaviour. Finally, we also found no clear differences in learning between predatory and non-predatory Diana monkey loud calls nor of con- and heterospecific alarm call signal meaning.

Our findings align with previous work that has shown that—despite some degree of predisposition towards discriminating between predator-specific alarm calls— experience and social input are essential for the development of primate alarm call behaviour (Fichtel, 2008: Sifakas, *Propithecus verreauxi verreauxi*; Fischer et al., 2000: baboons, *Papio cynocephalus ursinus*; McCowan et al., 2001: squirrel monkeys, *Saimiri sciureus*; Hauser, 1988; Seyfarth & Cheney, 1980, 1986: vervet monkeys, *Cercopithecus aethiops*). Learning appears to begin as soon as infants start moving independently at around 6 months. However, our results suggest that the full development of adult-like responses to alarm calls in mangabeys requires at least 2 years, which is longer than what has been reported for other primates (Fichtel, 2008; Fischer et al., 2000; McCowan et al., 2001; Seyfarth & Cheney, 1980, 1986). The fact that we took into account not only social referencing behaviour that emerges early, but also conspicuous locomotor and vocal responses could account for some, but not all, of this discrepancy. Moreover, similar to findings in vervet monkeys (Mohr et al., submitted; Seyfarth & Cheney, 1986), it is likely that social referencing plays an important role in how unexperienced individuals learn to respond to alarm calls. Across conditions, looking towards an adult when hearing an alarm call was the most common response in young juveniles (Table 2.5), suggesting that they were gathering information from more experienced individuals about how to respond to alarm calls. A similar behaviour, social peering, has been validated as an index of observational and social learning in young wild orangutans (Schuppli et al., 2016).

When analysing call usage during natural encounters with predators, we found that juveniles were more reactive and less selective in their calling behaviour, producing alarm calls far more often and to a wider variety of species and objects, than adults. However, this lack of selectivity of stimuli-signal associations was not arbitrary, analogous to young children’s overextension of early use of words (Clark, 2003; Rescorla, 1980). Juveniles produced leopard alarms almost exclusively to carnivores and medium to large body size terrestrial mammals, eagle alarms for birds and snake alarms for reptiles and snake-like animals and objects. Moreover, this broad categorisation appeared to be based not only on stimuli appearance but also on its behaviour and, possibly, its potential to pose a danger to the monkeys. For example, mangabeys, including adults, use leopard alarms as a warning mechanism in response to animals that, due to their body size, could pose a threat to a mangabey when charging or running around aimlessly (e.g., giant forest hogs, pigmy hippopotamus, large-sized duikers, herd of red river hogs) (Table 2.3). Another example of possible categorisation by overextension is the observation of a juvenile giving an eagle alarm after seeing a Dwarf galago (*Galagoides demidovii*) flying nearby (Clémentine Bodin personal communication). These differences in the usage of alarm calls between juveniles and adults may be related to the higher predation risks and lack of experience in dealing with predators of the former (Isbell, 1994; Janson & van Schaik, 1993; Wrangham & Cheney, 1985).

Overall, these results provide evidence that over the course of their first four years of life, mangabeys reduce and refine their alarm calling behaviour to relevant predator species and dangerous contexts. Furthermore, our findings align with the gradual development of alarm call usage in vervet monkeys (Cheney & Seyfarth, 1990; Seyfarth & Cheney, 1986). Thus, while non-primate vocalizations are in many ways fundamentally different from human language and speech, future research should address how limited are the analogies between the ontogeny of alarm call usage in monkeys and the acquisition of communicative competence in young children.

When analysing call usage during playback experiments, we found age and location had an important effect on alarm calling behaviour as only adults that were foraging on the ground alarm called to the playbacks. Although further research is needed, this suggests that costly alarm calling requires general maturational processes, full integration into the group's social and kin networks and parental status (e.g., access to mating partners, survival of socially important individuals and its kin, and enhance likelihood to sire offspring) (Cheney & Seyfarth, 1990; Haff & Magrath, 2013; Quintero et al., 2022; Stephan & Zuberbühler, 2021). Alternatively, and not necessarily mutually exclusive, the small number of vocal responses to the playbacks could indicate that it is the predator-call association, and not alarm calls alone, that elicits strong responses, including alarm call behaviour (Ducheminsky et al., 2014; Owren & Rendall, 2001). The finding that callers were on the ground at the moment of calling was simply a consequence of the mangabeys' terrestrial foraging habits and the fact they could only encounter vipers on the floor of the forest.

As expected, conspecific leopard alarm calls elicited the strongest responses across age classes. Additionally, mangabeys' leopard alarm calls elicited more corresponding antipredator behaviours than both Diana monkeys' leopard and eagle alarm calls (Figure 2.3). In the Taï forest, leopards often prey on mangabeys, probably because these are medium-sized terrestrial monkeys living in large groups, which are easier for the leopards to locate and ambush successfully than other prey (Zuberbühler & Jenny, 2002). During focal follows, we observed that young mangabeys react to most events or signals (e.g., alarm calls) that generate arousal with a default reaction, which includes fleeing by jumping and climbing into the nearest tree, a behaviour that is effective for escaping a leopard attack. Moreover, mangabeys are better sentinels for ground predators than any other monkey species in the Taï forest and can spot a leopard visual model at a distance of up to 40m (McGraw & Bshary, 2002). Furthermore, field experiments have shown that experience with leopards is not required for Guereza colobus monkeys to produce antipredator-specific responses (Schel & Zuberbühler, 2009). Our results suggest that young mangabeys seem to exhibit a predetermined reaction to threats as a hardwired evolutionary adaptation to produce better survival rates during leopard attacks. Overall, the observed patterns of behaviour in response to leopard-related stimuli supports the idea that leopard predation seems to have had a significant effect on primates' cognitive evolution (Zuberbühler & Jenny, 2002).

On the other hand, contrary to conspecific leopard alarm calls, snake alarm calls only prompted strong responses from adults (Figure 2.1). While the predetermined behaviour of juveniles described above is adaptative for a leopard attack, it is likely an overreaction for a viper snake encounter, wherein the predator relies on short distance infrared imaging to detect prey and is not fast-moving over distance (Foerster, 2008; Goris, 2011; Penner et al., 2008). Mangabeys' snake-specific antipredator behaviour appears to be complex: Because of their behavioural ecology and morphology, snakes may be more difficult to detect than other predators (Etting et al., 2014). Additionally, although 50–60 snake species can be found in the Taï forest region (Ernst & Rödel, 2002; Rödel & Mahsberg, 2000), only pythons and Gaboon and rhinoceros vipers elicit antipredator-specific responses from mangabeys. Hence, showing proper snake antipredator behaviours requires not only the recognition of snakes as predatory disturbances but also differentiation between the different snake types to distinguish the dangerous ones. Overall, it appears that the mild responses of juveniles for snake alarm calls are a consequence of mangabeys perceiving vipers as a less threatening and more complex danger than leopards, suggesting that snake antipredator behaviour requires more experience to be fully acquired than responses to other predators.

Our results showed that mangabeys are sensitive to the predator-specific alarm calls of Diana monkeys and respond to them as if the corresponding predator was present (Figure 2.1). However, contrary to our predictions, there was no clear difference in the learning of predatory and non-predatory Diana monkey loud calls. A possible explanation could be found in the acoustic structure of these calls. Although loud calls given to falling trees tend to elicit calls with more syllables compared to leopard loud alarm calls (median number of syllables per call: 7 (range 1–16) vs. 3 (range 1–33), respectively), their general acoustic structure is very similar, which could create certain ambiguity between them (Zuberbühler et al., 1997). Thus, it might be possible that Diana monkeys' tree loud calls could be difficult to distinguish from the loud alarm calls given for leopards and therefore, young individuals may require enough experience to learn how to distinguish them accurately.

Although mangabeys of all age-groups were more likely to respond to conspecific alarm calls than to Diana monkey calls (Figure 2.1), this effect seemed to be driven by the strong responses given to conspecific leopard alarm calls. Indeed, we found no difference in con- and heterospecific signal meaning learning (Figure 2.2). Functional semanticity of alarm calls of both species was acquired during juvenile stage, with adults showing higher response rates to con- and heterospecific alarm calls than both juveniles age classes, who presented considerable variation in their responses. This finding supports the notion that there should exist little genetic predisposition to comprehend heterospecific's alarm calls. Therefore, a similar pattern in the development of comprehension between con- and heterospecific alarm calls might be seen as a sign that that the underlying mechanism in the ontogeny of vocal comprehension is learning rather than simple maturation. Similar development rates of responses to con- and heterospecific alarm calls has also been shown in Verreaux's sifakas —albeit at a much earlier age (6–7 months old) (Fichtel, 2008). Thus, it might be possible that the full appearance of adult-like responses to con- and heterospecific alarm calls in primates is mediated by similar learning process mechanisms, which could have species-specific learning parameters.

Of further interest is the extent to which primates are predisposed from birth to respond to their alarm calls, and how they learn the meaning of their alarm calls. In most primate species alarm calls are short with abrupt onsets and broadband noisy spectra (Rendall et al., 2009). Furthermore, studies on the vocalizations of African green monkeys (*Chlorocebus*) revealed that male barks of closely related species and subspecies are highly conserved in their acoustic structure (Price et al., 2014, 2015). However, mangabeys and Diana monkeys share a most recent common ancestor some 14.1 million years ago and are grouped in different tribes of the subfamily Cercopithecinae (Pozzi et al., 2014). Therefore, it is likely that mangabeys' comprehension of indirect signs, such as Diana monkey alarm calls, requires considerable learning rather than being largely predisposed from birth. On the other hand, morphological computation research in infant common marmosets has demonstrated how changes in body morphology (lung growth) refine vocal usage over time (Zhang & Ghazanfar, 2018). Our results show that the development of alarm call comprehension, usage and production in mangabeys occurs during juvenile stage, which may be simultaneously refined by observing other individuals and through individual experience. In a recent study, we found that mangabeys can acquire predator knowledge from alarm calls by one-trial social learning (León, Thiriau, Bodin, et al., 2022). Rapid individual learning and flexibility in alarm call usage have been also demonstrated in adult West African green monkeys when exposed to a novel threat, i.e., a remotely operated drone (Wegdell et al., 2019). Thus, innate knowledge seems unlikely and the appropriate categorization and response of con- and heterospecific alarm calls could occur through a combination of body maturation and, to a greater extent, social and individual learning.

We have shown that mangabeys' competent alarm call behaviour towards con- and heterospecific signals arises during juvenile stage. However, we did not determinate the exact age at which infants start identifying the different con- and heterospecific alarm call types. This should be addressed in future comparative research to test which socioecology and cognitive features may shape species-specific learning rates. In a recent field experiment on immature chimpanzees, subjects consistently produced alarm calls in response to an unfamiliar but potentially hazardous object, i.e., a large spider model, starting only at 80 months old (Dezecache et al., 2019). The later development of adult-like responses to alarm calls in mangabeys that we found (at least 24 months old) is in between the ages that have been reported for other monkeys and prosimians (6–12 months old) (Fichtel, 2008; Fischer et al., 2000; McCowan et al., 2001; Seyfarth & Cheney, 1980, 1986) and chimpanzees. This suggests that further research on the ontogeny of alarm call comprehension in mangabeys could shed light to the cognitive division between apes and monkeys (Amici et al., 2010; Tomasello, 2010; Tomasello & Call, 1994). Additionally, it would be interesting and informative to conduct an analysis of the acoustic features of the different mangabey alarm calls. Finally, due to the complexity of mangabeys' snake-specific antipredator behaviour, this could be a promising model to explore the ability of primates to socially learn relevant contextual information related to their alarm calls.

In summary, this study provides insights on the developmental process by which young primates comprehend their own and other species' alarm calls and display species-specific antipredator behaviours. Our findings illustrated how call comprehension starts eliciting simple but adaptative escape responses, as individuals simultaneously acquire more experience and receive inputs from other group members and heterospecifics. Eventually, escape responses diversify showing predator specificity. Our findings support the view of an oddly asymmetrical communication system in primates, wherein vocal comprehension, usage, and production exhibit fundamental differences in their flexibility and ontogeny, with vocal comprehension being highly flexible and preceding appropriate vocal usage and vocal production. Examining both conspecific and heterospecific information available to individuals during predator encounters is particularly valuable in shedding light on the development of alarm call behaviour, as primates inhabit ecosystems with multiple sources of information, including non-predatory heterospecifics. The acoustic variation of signals produced in these multi-information environments and additional contextual information, possibly together with learning mechanisms, allows listeners to select appropriate responses to their different predation pressures. While the degree to which natural selection favours social learning or alternative more general learning mechanisms to produce optimal anti-predatory behavioural strategies remains an open question, there is no doubt that the animals' ability to understand the meaning of their own and other species' alarm calls is, to a large extent, a learning process that occurs during their early stages of life and refine throughout their maturation process.

2.7 Acknowledgements

We are grateful to the Centre Suisse de Recherches Scientifiques (CSRS), the Ministère de la Recherche Scientifique, the Ministère de l'Agriculture et des Ressources Animales and the Office Ivoirien des Parcs et Réserves (OIPR) of Côte d'Ivoire for support and permission to conduct research in the Taï National Park. Fieldwork was made possible thanks to Paterson Kalo, Landri Bele and the rest of the Taï Monkey Project (TMP) assistants, to whom we express our gratitude. We thank the Taï Chimpanzee Project (TCP) and its staff for support in the field. We also thank Anderson Bitty for logistic support, Radu Slobodeanu for statistical advice and Alison Ashbury for helpful discussions and comments on the drafts of this manuscript.

2.8 Funding

This work was funded by the Swiss National Science Foundation (Grant numbers 31003A_166458; 310030_185324; 51NF40_180888) (KZ).

2.9 Author Contributions

Conceptualization: JL, KZ; Methodology and experiments: JL, CT; Formal analysis and investigation: JL; Access to the TCP study group: CC; Writing - original draft preparation: JL, CT, KZ; Writing - review and editing: JL, CC, KZ; Funding acquisition: KZ; Supervision: KZ

2.10 Competing interests

The authors declare no competing interests.

2.11 Data and code availability

The datasets generated during and/or analysed during the current study and the R code are available in the OSF repository, https://osf.io/zrgdj/. All supplementary videos have been deposited at OSF and are publicly available at the following link: https://osf.io/hw2r7/?view_only=c5581e1a8e6e4cdba8311ed18871239d. All additional material related to this study may be requested from the corresponding author.

2.12 References

Abdai, J., Uccheddu, S., Gácsi, M., & Miklósi, Á. (2022). Exploring the advantages of using artificial agents to investigate animacy perception in cats and dogs. *Bioinspiration & Biomimetics*, *17*(6). https://doi.org/10.1088/1748-3190/ac93d9

Abrams, P. A. (2001). Predator-Prey Interactions. In C. W. Fox, D. A. Roff, & D. J. Fairbairn (Eds.), *Evolutionary Ecology: Concepts and Case Studies* (p. 0). Oxford University Press.

https://doi.org/10.1093/oso/9780195131543.003.0028

Adams, D. B., & Kitchen, D. M. (2020). Model vs. playback experiments: The impact of sensory mode on predator-specific escape responses in saki monkeys. *Ethology*, *126*(5), 563–575. https://doi.org/https://doi.org/10.1111/eth.13008

Altmann, J. (1974). Observational Study of Behavior: Sampling Methods. *Behaviour*, *49*(3/4), 227–267. http://www.jstor.org/stable/4533591

Amici, F., Aureli, F., & Call, J. (2010). Monkeys and apes: are their cognitive skills really so different? *American Journal of Physical Anthropology*, *143*(2), 188–197. https://doi.org/10.1002/ajpa.21305

Araya-Salas, M., & Wright, T. (2013). Open-ended song learning in a hummingbird. *Biology Letters*, *9*(5), 20130625. https://doi.org/10.1098/rsbl.2013.0625

Arnold, K., Pohlner, Y., & Zuberbühler, K. (2008). A forest monkey's alarm call series to predator models. *Behavioral Ecology and Sociobiology*, *62*(4), 549–559. https://doi.org/10.1007/s00265-007-0479-y

Arnold, K., & Zuberbühler, K. (2006). Semantic combinations in primate calls. *Nature*, *441*(7091), 303.

Audacity Team. (2020). *Audacity: Free Audio Editor and Recorder* (2.2.2).

Baldwin, D. A., & Moses, L. J. (1996). The Ontogeny of Social Information Gathering. *Child Development*, *67*(5), 1915–1939. https://doi.org/10.2307/1131601

Barros, M., Boere, V., Mello, E. L., & Tomaz, C. (2002). Reactions to Potential Predators in Captive-Born Marmosets (Callithrix penicillata). *International Journal of Primatology*, *23*(2), 443–454. https://doi.org/10.1023/A:1013899931878

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software; Vol 1, Issue 1 (2015)* . https://doi.org/10.18637/jss.v067.i01

Bergman, T. J., Beehner, J. C., Painter, M. C., & Gustison, M. L. (2019). The speech-like properties of nonhuman primate vocalizations. *Animal Behaviour*, *151*, 229–237.

https://doi.org/https://doi.org/10.1016/j.anbehav.2019.02.015

Bidner, L. R. (2014). Primates on the Menu: Direct and Indirect Effects of Predation on Primate Communities. *International Journal of Primatology*, *35*(6), 1164–1177. https://doi.org/10.1007/s10764-014-9797-x

Boesch, C., & Boesch-Achermann, H. (2000). *The chimpanzees of the Taï forest : behavioural ecology and evolution*. Oxford : Oxford university press. http://lib.ugent.be/catalog/rug01:000534901

Boesch, C., & Boesch, H. (1989). Hunting behavior of wild chimpanzees in the Taï National Park. *American Journal of Physical Anthropology*, *78*(4), 547–573. https://doi.org/https://doi.org/10.1002/ajpa.1330780410

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., & White, J.-S. S. (2009). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution*, *24*(3), 127–135. https://doi.org/10.1016/j.tree.2008.10.008

Borrow, N. (2014). *Field Guide to Birds of Western Africa*. Bloomsbury Publishing.

Bradbury, J. W., & Balsby, T. J. S. (2016). The functions of vocal learning in parrots. *Behavioral Ecology and Sociobiology*, *70*(3), 293–312. https://doi.org/10.1007/s00265-016-2068-4

Brodbeck, D. R., Burack, O. R., & Shettleworth, S. J. (1992). One-trial associative memory in black-capped chickadees. *Journal of Experimental Psychology: Animal Behavior Processes*, *18*, 12–21. https://doi.org/10.1037/0097-7403.18.1.12

Brumm, H., Voss, K., Köllmer, I., & Todt, D. (2004). Acoustic communication in noise: regulation of call characteristics in a New World monkey. *The Journal of Experimental Biology*, *207*(Pt 3), 443–448. https://doi.org/10.1242/jeb.00768

Bshary, R., & Noë, R. (1997). Red colobus and Diana monkeys provide mutual protection against predators. *Animal Behaviour*, *54*(6), 1461–1474. https://doi.org/https://doi.org/10.1006/anbe.1997.0553

Carlson, N. V, Kelly, E. M., & Couzin, I. (2020). Individual vocal recognition across taxa: a review of the literature and a look into the future. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *375*(1802), 20190479. https://doi.org/10.1098/rstb.2019.0479

Cäsar, C., & Zuberbühler, K. (2012). Referential alarm calling behaviour in New World primates. *Current Zoology*, *58*(5), 680–697. https://doi.org/10.1093/czoolo/58.5.680

Castro, N. A., & Snowdon, C. T. (2000). Development of Vocal Responses in Infant Cotton-Top Tamarins. *Behaviour*, *137*(5), 629–646. http://www.jstor.org/stable/4535727

Center for Conservation Bioacoustics. (2014). Raven Pro: Interactive Sound Analysis Software. In *Ithaca, NY: The Cornell Lab of Ornithology.* (1.5).

Cheney, D. L., & Seyfarth, R. M. (1985). Social and non-social knowledge in vervet monkeys. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences*, *308*(1135), 187–201. https://doi.org/10.1098/rstb.1985.0019

Cheney, D, & Seyfarth, R. (2018). Flexible usage and social function in primate vocalizations. *Proceedings of the National Academy of Sciences*, *115*(9), 1974–1979. https://doi.org/10.1073/pnas.1717572115

Cheney, DL, & Seyfarth, R. (1990). How monkeys see the world: Inside the mind of another species. In *How monkeys see the world: Inside the mind of another species.* University of Chicago Press.

Chippaux, J.-P. (2006). *Les serpents d'Afrique occidentale et centrale*. IRD éditions.

Chomsky, N. (1965). *Aspects of the Theory of Syntax*. MIT press.

Chomsky, N. (2017). Language architecture and its import for evolution. *Neuroscience & Biobehavioral Reviews*, *81*, 295–300. https://doi.org/https://doi.org/10.1016/j.neubiorev.2017.01.053

Chouinard-Thuly, L., Gierszewski, S., Rosenthal, G. G., Reader, S. M., Rieucau, G., Woo, K. L., Gerlai, R., Tedore, C., Ingley, S. J., Stowers, J. R., Frommen, J. G., Dolins, F. L., & Witte, K. (2017). Technical and conceptual considerations for using animated stimuli in studies of animal behavior. *Current Zoology*, *63*(1), 5–19. https://doi.org/10.1093/cz/zow104

Chow, C. P., Mitchell, J. F., & Miller, C. T. (2015). Vocal turn-taking in a non-human primate is learned during ontogeny. *Proceedings. Biological Sciences*, *282*(1807), 20150069. https://doi.org/10.1098/rspb.2015.0069

Clark, E. (2003). *First language acquisition*. Cambridge University Press.

Clarke, E., Reichard, U. H., & Zuberbühler, K. (2006). The syntax and meaning of wild gibbon songs. *PloS One*, *1*(1), e73.

Clay, Z., & Zuberbühler, K. (2011). Bonobos Extract Meaning from Call Sequences. *PLoS ONE*, *6*(4), e18786. https://doi.org/10.1371/journal.pone.0018786

Cook, M., & Mineka, S. (1990). Selective associations in the observational conditioning of fear in rhesus monkeys. *Journal of Experimental Psychology. Animal Behavior Processes*, *16*(4), 372–389.

Coss, R. G., McCowan, B., & Ramakrishnan, U. (2007). Threat-Related Acoustical Differences in Alarm Calls by Wild Bonnet Macaques (Macaca radiata) Elicited by Python and Leopard Models. *Ethology*, *113*(4), 352–367. https://doi.org/https://doi.org/10.1111/j.1439-0310.2007.01336.x

Coss, R. G., & Ramakrishnan, U. (2000). Perceptual Aspects of Leopard Recognition by Wild Bonnet Macaques (Macaca radiata). *Behaviour*, *137*(3), 315–335. http://www.jstor.org/stable/4535708

Coss, R. G., Ramakrishnan, U., & Schank, J. (2005). Recognition of partially concealed leopards by wild bonnet macaques (Macaca radiata): The role of the spotted coat. *Behavioural Processes*, *68*(2), 145–163. https://doi.org/https://doi.org/10.1016/j.beproc.2004.12.004

Crockford, C, & Boesch, C. (2005). Call combinations in wild chimpanzees. *Behaviour*, *142*, 397–421.

Crockford, C, Wittig, R. M., Mundry, R., & Zuberbühler, K. (2012). Wild Chimpanzees Inform Ignorant Group Members of Danger. *Current Biology*, *22*(2), 142–146. https://doi.org/https://doi.org/10.1016/j.cub.2011.11.053

Crockford, C, Wittig, R. M., & Zuberbühler, K. (2015). An intentional vocalization draws others' attention: a playback experiment with wild chimpanzees. *Animal Cognition*, *18*(3), 581–591. https://doi.org/10.1007/s10071-014-0827-z

Crockford, C, Wittig, R. M., & Zuberbühler, K. (2017). Vocalizing in chimpanzees is influenced by social-cognitive processes. *Science Advances*, *3*(11), e1701742. https://doi.org/10.1126/sciadv.1701742

Curio, E. (1976). *The ethology of predation* (Vol. 7). Springer Science & Business Media.

Curio, E., Ernst, U., & Vieth, W. (1978). Cultural Transmission of Enemy Recognition: One Function of Mobbing. *Science*, *202*(4370), 899 LP – 901. https://doi.org/10.1126/science.202.4370.899

Davenport, T. R. B., Stanley, W. T., Sargis, E. J., De Luca, D. W., Mpunga, N. E., Machaga, S. J., & Olson, L. E. (2006). A New Genus of African Monkey, Rungwecebus: Morphology, Ecology, and Molecular Phylogenetics. *Science*, *312*(5778), 1378–1381. https://doi.org/10.1126/science.1125631

de Boer, B. (2005). Evolution of Speech and Its Acquisition. *Adaptive Behavior*, *13*(4), 281–292. https://doi.org/10.1177/105971230501300405

Deshpande, A. (2021). *Social learning and flexibility in vocal communication of wild vervet monkeys* [Université de Neuchâtel]. https://unine.swisscovery.slsp.ch/permalink/41SLSP_UNE/b1j16q/alma991009764729505517%0A

Deshpande, A., Van Boekholt, B., & Zuberbuhler, K. (2022). Preliminary evidence for one-trial social learning of vervet monkey alarm calling. *Royal Society Open Science*, *9*(8), 210560. https://doi.org/10.1098/rsos.210560

Dezecache, G., Crockford, C., & Zuberbühler, K. (2019). The development of communication in alarm contexts in wild chimpanzees. *Behavioral Ecology and Sociobiology*, *73*(8), 104. https://doi.org/10.1007/s00265-019-2716-6

Di Bitetti, M., & Wheeler, B. (2017). The vocal repertoire of the black horned capuchin monkey (Cebus [Sapajus] nigritus): an acoustic and contextual analysis. In M. Kowalewski & L. Oklander (Eds.), *Primatology in Argentina* (Vol. 2, pp. 171–199).

Sociedad Argentina para el Estudio de los Mamíferos, Buenos Aires.

Ducheminsky, N., Henzi, S. P., & Barrett, L. (2014). Responses of vervet monkeys in large troops to terrestrial and aerial predator alarm calls. *Behavioral Ecology*, *25*(6), 1474–1484. https://doi.org/10.1093/beheco/aru151

Edwards, M. C., Ford, C., Hoy, J. M., FitzGibbon, S., & Murray, P. J. (2021). How to train your wildlife: A review of predator avoidance training. *Applied Animal Behaviour Science*, *234*, 105170. https://doi.org/https://doi.org/10.1016/j.applanim.2020.105170

Egnor, S. E. R., & Hauser, M. D. (2004). A paradox in the evolution of primate vocal learning. *Trends in Neurosciences*, *27*(11), 649–654. https://doi.org/https://doi.org/10.1016/j.tins.2004.08.009

Egnor, S. E. R., & Hauser, M. D. (2006). Noise-induced vocal modulation in cotton-top tamarins (Saguinus oedipus). *American Journal of Primatology*, *68*(12), 1183–1190. https://doi.org/10.1002/ajp.20317

Egnor, S. E. R., Iguina, C. G., & Hauser, M. D. (2006). Perturbation of auditory feedback causes systematic perturbation in vocal structure in adult cotton-top tamarins. *The Journal of Experimental Biology*, *209*(Pt 18), 3652–3663. https://doi.org/10.1242/jeb.02420

Eisenberg, J. F. (1976). Communication mechanisms and social integration in the black spider monkey, Ateles fusciceps robustus, and related species. *Smithson. Contrib. to Zool.*, 1–108. https://doi.org/doi:10.5479/si.00810282.213

Elowson, A. M., Snowdon, C. T., & Sweet, C. J. (1992). Ontogeny of trill and J-call vocalizations in the pygmy marmoset, Cebuella pygmaea. *Animal Behaviour*, *43*(5), 703–715. https://doi.org/https://doi.org/10.1016/S0003-3472(05)80195-2

Engqvist, L. (2005). The mistreatment of covariate interaction terms in linear model analyses of behavioural and evolutionary ecology studies. *Animal Behaviour*, *70*(4), 967–971. https://doi.org/https://doi.org/10.1016/j.anbehav.2005.01.016

Ernst, R., & Rödel, M. (2002). A new Atheris species (Serpentes: Viperidae), from Taï National Park, Ivory Coast. *Herpetological Journal*, *12*, 55–61.

Etting, S. F., Isbell, L. A., & Grote, M. N. (2014). Factors increasing snake detection and perceived threat in captive rhesus macaques (Macaca mulatta). *American Journal of Primatology*, *76*(2), 135–145. https://doi.org/10.1002/ajp.22216

Evans, A., & Tomasello, M. (1986). Evidence for social referencing in young chimpanzees (Pan troglodytes). *Folia Primatologica; International Journal of Primatology*, *47*(1), 49–54. https://doi.org/10.1159/000156263

Fedurek, P., & Slocombe, K. E. (2011). Primate vocal communication: a useful tool for understanding human speech and language evolution? *Human Biology*, *83*(2), 153–173. https://doi.org/10.3378/027.083.0202

Fedurek, P., Slocombe, K. E., & Zuberbühler, K. (2015). Chimpanzees communicate to two different audiences during aggressive interactions. *Animal Behaviour*, *110*, 21–28. https://doi.org/https://doi.org/10.1016/j.anbehav.2015.09.010

Feise, R. J. (2002). Do multiple outcome measures require p-value adjustment? *BMC Medical Research Methodology*, *2*, 8. https://doi.org/10.1186/1471-2288-2-8

Fichtel, C. (2004). Reciprocal recognition of sifaka (Propithecus verreauxi verreauxi) and redfronted lemur (Eulemur fulvus rufus) alarm calls. *Animal Cognition*, *7*(1), 45–52. https://doi.org/10.1007/s10071-003-0180-0

Fichtel, C. (2008). Ontogeny of conspecific and heterospecific alarm call recognition in wild Verreaux's sifakas (Propithecus verreauxi verreauxi). *American Journal of Primatology*, *70*(2), 127–135. https://doi.org/https://doi.org/10.1002/ajp.20464

Fichtel, C. (2020). Monkey Alarm Calling: It Ain't all Referential, or is It? *Animal Behavior and Cognition*, *7*, 101–107.

Fichtel, C., & Kappeler, P. M. (2002). Anti-Predator Behavior of Group-Living Malagasy Primates: Mixed Evidence for a Referential Alarm Call System. *Behavioral Ecology and Sociobiology*, *51*(3), 262–275. http://www.jstor.org/stable/4602047

Fichtel, C., & Kappeler, P. M. (2011). Variation in the Meaning of Alarm Calls in Verreaux's and Coquerel's Sifakas (Propithecus verreauxi, P. coquereli). *International Journal of Primatology*, *32*(2), 346–361. https://doi.org/10.1007/s10764-010-9472-9

Fischer, J. (2017). Primate vocal production and the riddle of language evolution. *Psychonomic Bulletin & Review*, *24*(1), 72–78. https://doi.org/10.3758/s13423-016-1076-8

Fischer, J, & Hammerschmidt, K. (2020). Towards a new taxonomy of primate vocal production learning. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *375*(1789), 20190045. https://doi.org/10.1098/rstb.2019.0045

Fischer, J, Metz, M., Cheney, D., & Seyfarth, R. (2001). Baboon responses to graded bark variants. *Animal Behaviour*, *61*(5), 925–931. https://doi.org/https://doi.org/10.1006/anbe.2000.1687

Fischer, J, & Price, T. (2017). Meaning, intention, and inference in primate vocal communication. *Neuroscience & Biobehavioral Reviews*, *82*, 22–31. https://doi.org/https://doi.org/10.1016/j.neubiorev.2016.10.014

Fischer, J. (2020). Nonhuman primate alarm calls then and now. *Animal Behavior and Cognition*, *7*.

Fischer, J. (2021). Primate Vocal Communication and the Evolution of Speech. *Current Directions in Psychological Science*, *30*(1), 55–60. https://doi.org/10.1177/0963721420979580

Fischer, J, Cheney, D. L., & Seyfarth, R. M. (2000). Development of infant baboons' responses to graded bark variants. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *267*(1459), 2317–2321. https://doi.org/10.1098/rspb.2000.1285

Fischer, J, & Hammerschmidt, K. (2001). Functional referents and acoustic similarity revisited: the case of Barbary macaque alarm calls. *Animal Cognition*, *4*(1), 29–35. https://doi.org/10.1007/s100710100093

Fischer, J, Kitchen, D. M., Seyfarth, R. M., & Cheney, D. L. (2004). Baboon loud calls advertise male quality: acoustic features and their relation to rank, age, and exhaustion. *Behavioral Ecology and Sociobiology*, *56*(2), 140–148. https://doi.org/10.1007/s00265-003-0739-4

Foerster, S. (2008). Two incidents of venomous snakebite on juvenile blue and Sykes monkeys (Cercopithecus mitis stuhlmanni and C. m. albogularis). *Primates*, *49*(4), 300–303.

https://doi.org/10.1007/s10329-008-0098-x

Friard, O., & Gamba, M. (2016). BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. *Methods in Ecology and Evolution*, *7*(11), 1325–1330. https://doi.org/10.1111/2041-210X.12584

Fröhlich, M., & van Schaik, C. P. (2020). Must all signals be evolved? A proposal for a new classification of communicative acts. *WIREs Cognitive Science*, *11*(4), e1527. https://doi.org/https://doi.org/10.1002/wcs.1527

Fugate, J. M. B., Gouzoules, H., & Nygaard, L. C. (2008). Recognition of rhesus macaque (Macaca mulatta) noisy screams: evidence from conspecifics and human listeners. *American Journal of Primatology*, *70*(6), 594–604. https://doi.org/https://doi.org/10.1002/ajp.20533

Galat, G., & Galat-Luong, A. (1985). La communauté de primates diurnes de la forêt de Taï, Côte-d'Ivoire. *Revue d'écologie (Terre Vie)*, *40*, 3–32.

Galef, B. G., & Giraldeau, L.-A. (2001). Social influences on foraging in vertebrates: causal mechanisms and adaptive functions. *Animal Behaviour*, *61*(1), 3–15. https://doi.org/https://doi.org/10.1006/anbe.2000.1557

Galef, B. G., & Laland, K. N. (2005). Social learning in animals: empirical studies and theoretical models. *Bioscience*, *55*(6), 489–499.

Gamba, M., Friard, O., Riondato, I., Righini, R., Colombo, C., Miaretsoa, L., Torti, V., Nadhurou, B., & Giacoma, C. (2015). Comparative analysis of the vocal repertoire of Eulemur: a dynamic time warping approach. *International Journal of Primatology*, *36*(5), 894–910.

Garcia, J., Kimeldorf, D. J., & Koelling, R. A. (1955). Conditioned aversion to saccharin resulting from exposure to gamma radiation. In *Science* (Vol. 122, pp. 157–158). American Assn for the Advancement of Science. https://doi.org/10.1126/science.122.3179.1089

Gautier-Hion, A., Quris, R., & Gautier, J.-P. (1983). Monospecific vs polyspecific life: A comparative study of foraging and antipredatory tactics in a community of Cercopithecus monkeys. *Behavioral Ecology and Sociobiology*, *12*(4), 325–335. https://doi.org/10.1007/BF00302901

Gelman, A., & Su, Y.-S. (2020). *arm: Data analysis using regression and multilevel/hierarchical models* (R package version 1.11-1). https://cran.r-project.org/package=arm

Genovart, M., Negre, N., Tavecchia, G., Bistuer, A., Parpal, L., & Oro, D. (2010). The young, the weak and the sick: evidence of natural selection by predation. *PloS One*, *5*(3), e9774. https://doi.org/10.1371/journal.pone.0009774

Genty, E., Breuer, T., Hobaiter, C., & Byrne, R. W. (2009). Gestural communication of the gorilla (Gorilla gorilla): repertoire, intentionality and possible origins. *Animal Cognition*, *12*(3), 527–546. https://doi.org/10.1007/s10071-009-0213-4

Ghazanfar, A. A., Liao, D. A., & Takahashi, D. Y. (2019). Volition and learning in primate vocal behaviour. *Animal Behaviour*, *151*, 239–247. https://doi.org/https://doi.org/10.1016/j.anbehav.2019.01.021

Gill, S. A., & Bierema, A. M.-K. (2013). On the Meaning of Alarm Calls: A Review of Functional Reference in Avian Alarm Calling. *Ethology*, *119*(6), 449–461. https://doi.org/https://doi.org/10.1111/eth.12097

Girard-Buttoz, C., Zaccarella, E., Bortolato, T., Friederici, A. D., Wittig, R. M., & Crockford, C. (2022). Chimpanzees produce diverse vocal sequences with ordered and recombinatorial properties. *Communications Biology*, *5*(1), 410. https://doi.org/10.1038/s42003-022-03350-8

Goodale, E., Beauchamp, G., Magrath, R. D., Nieh, J. C., & Ruxton, G. D. (2010). Interspecific information transfer influences animal community structure. *Trends in Ecology & Evolution*, *25*(6), 354–361. https://doi.org/10.1016/j.tree.2010.01.002

Goris, R. C. (2011). Infrared Organs of Snakes: An Integral Part of Vision. *Journal of Herpetology*, *45*(1), 2–14. https://doi.org/10.1670/10-238.1

Greene, H. W. (1997). *Snakes: the evolution of mystery in nature*. Univ of California Press.

Greggor, A. L., McIvor, G. E., Clayton, N. S., & Thornton, A. (2022). Wild jackdaws are wary of objects that violate expectations of animacy. *Royal Society Open Science*, *5*(10), 181070. https://doi.org/10.1098/rsos.181070

Griffin, A. (2004). Social learning about predators: a review and prospectus. *Animal Learning & Behavior*, *32*(1), 131–140. https://doi.org/10.3758/BF03196014

Grubb, P., Butynski, T. M., Oates, J. F., Bearder, S. K., Disotell, T. R., Groves, C. P., & Struhsaker, T. T. (2003). Assessment of the Diversity of African Primates. *International Journal of Primatology*, *24*(6), 1301–1357. https://doi.org/10.1023/B:IJOP.0000005994.86792.b9

Gursky, S. (2003). Predation Experiments on Infant Spectral Tarsiers (Tarsius spectrum). *Folia Primatologica*, *74*(5–6), 272–284. https://doi.org/https://doi.org/10.1159/000073314

Gust, D. A. (1994). A brief report on the social behavior of the crested mangabey (Cercocebus galeritus galeritus) with a comparison to the sooty mangabey (C. torquatus atys). *Primates*, *35*(3), 375–383. https://doi.org/10.1007/BF02382734

Gust, D. A., Busse, C. D., & Gordon, T. P. (1990). Reproductive parameters in the sooty mangabey (Cercocebus torquatus atys). *American Journal of Primatology*, *22*(4), 241–250. https://doi.org/10.1002/ajp.1350220404

Gust, D. A., & Gordon, T. P. (1993). Conflict resolution in sooty mangabeys. *Animal Behaviour*, *46*(4), 685–694. https://doi.org/https://doi.org/10.1006/anbe.1993.1245

Haff, T. M., & Magrath, R. D. (2013). To call or not to call: parents assess the vulnerability of their young before warning them about predators. *Biology Letters*, *9*(6), 20130745. https://doi.org/10.1098/rsbl.2013.0745

Hammerschmidt, K., & Fischer, J. (2008). Constraints in Primate Vocal Production. In *Evolution of Communicative Flexibility*. The MIT Press. https://doi.org/10.7551/mitpress/9780262151214.003.0005

Hammerschmidt, K., Freudenstein, T., & Jürgens, U. (2001). Vocal Development in Squirrel Monkeys. *Behaviour*, *138*(9), 1179–1204. http://www.jstor.org/stable/4535882

Hammerschmidt, K., Newman, J. D., Champoux, M., & Suomi, S. J. (2000). Changes In Rhesus Macaque 'Coo' Vocalizations during Early Development. *Ethology*, *106*(10), 873–886. https://doi.org/https://doi.org/10.1046/j.1439-0310.2000.00611.x

Harvey, P. H., & Clutton-Brock, T. H. (1985). Life History Variation in Primates. *Evolution*, *39*(3), 559–581. https://doi.org/10.2307/2408653

Hauser, M. D. (1988). How Infant Vervet Monkeys Learn To Recognize Starling Alarm Calls: the Role of Experience. *Behaviour*, *105*(3–4), 187–201. https://doi.org/https://doi.org/10.1163/156853988X00016

Hauser, M. D. (1989). Ontogenetic changes in the comprehension and production of vervet monkey (Cercopithecus aethiops) vocalizations. *Journal of Comparative Psychology*, *103*(2), 149–158. https://doi.org/10.1037/0735-7036.103.2.149

Hauser, M. D., Chomsky, N., & Fitch, W. T. (2002). The Faculty of Language: What Is It, Who Has It, and How Did It Evolve? *Science*, *298*(5598), 1569–1579. https://doi.org/10.1126/science.298.5598.1569

Hayes, C. (1951). The ape in our house. In *The ape in our house.* Harper.

Headland, T. N., & Greene, H. W. (2011). Hunter–gatherers and other primates as prey, predators, and competitors of snakes. *Proceedings of the National Academy of Sciences*, *108*(52), E1470–E1474. https://doi.org/10.1073/pnas.1115116108

Heyes, C., & Galef Jr, B. (1996). *Social learning in animals: the roots of culture*. Elsevier.

Heymann, E. W., & Buchanan-Smith, H. M. (2000). The behavioural ecology of mixed-species troops of callitrichine primates. *Biological Reviews of the Cambridge Philosophical Society*, *75*(2), 169–190. https://doi.org/10.1017/s0006323199005460

Hollén, L. I., Clutton-Brock, T., & Manser, M. B. (2008). Ontogenetic Changes in Alarm-Call Production and Usage in Meerkats (Suricata suricatta): Adaptations or Constraints? *Behavioral Ecology and Sociobiology*, *62*(5), 821–829. http://www.jstor.org/stable/25511757

Höner, O. P., Leumann, L., & Noë, R. (1997). Dyadic associations of red Colobus and diana monkey groups in the Taï National Park, Ivory Coast. *Primates*, *38*(3), 281–291. https://doi.org/10.1007/BF02381615

Hotchkin, C. F., Parks, S. E., & Weiss, D. J. (2013). Vocal modifications in primates: Effects of noise and behavioral context on vocalization structure. *Proceedings of Meetings on Acoustics. Acoustical Society of America*, *19*. https://doi.org/10.1121/1.4799257

Isbell, L. A. (1994). Predation on primates: Ecological patterns and evolutionary consequences. *Evolutionary Anthropology: Issues, News, and Reviews*, *3*(2), 61–71. https://doi.org/10.1002/evan.1360030207

Isbell, L. A. (2006). Snakes as agents of evolutionary change in primate brains. *Journal of Human Evolution*, *51*(1), 1–35. https://doi.org/https://doi.org/10.1016/j.jhevol.2005.12.012

Isbell, L. A. (2009). *The Fruit, the Tree, and the Serpent*. Harvard University Press. https://doi.org/10.2307/j.ctvjnrvj0

Jaffe, K. . E., & Isbell, L. (2010). The Guenons: Polyspecific associations in sociological perspective. In C. J. Campbell, A. Fuentes, K. C. MacKinnon, S. K. Bearder, & R. Stumpf (Eds.), *Primates in Perspective* (pp. 277–300). Oxford University Press.

Janik, V. M., & Slater, P. J. B. (2000). The different roles of social learning in vocal communication. *Animal Behaviour*, *60*(1), 1–11. https://doi.org/https://doi.org/10.1006/anbe.2000.1410

Janson, C. H., & van Schaik, C. P. (1993). Ecological risk aversion in juvenile primates: slow and steady wins the race. In M. E. Pereira & L. A. Fairbanks (Eds.), *Juvenile primates: life history, development, and behavior* (pp. 57–74). Oxford Univ. Press.

Jeffreys, H. (1939). *The theory of probability* (1st ed.). Oxford University Press.

Johnson, K. E., & Clark, C. J. (2020). Ontogeny of vocal learning in a hummingbird. *Animal Behaviour*, *167*, 139–150. https://doi.org/https://doi.org/10.1016/j.anbehav.2020.07.010

Johnson, K. E., & Clark, C. J. (2022). Costa's hummingbird has an extended sensitive phase of vocal learning. *Animal Behaviour*, *188*, 75–84. https://doi.org/https://doi.org/10.1016/j.anbehav.2022.04.001

Kaminski, J., Call, J., & Fischer, J. (2004). Word learning in a domestic dog: evidence for "fast mapping". *Science (New York, N.Y.)*, *304*(5677), 1682–1683.

https://doi.org/10.1126/science.1097859

Kawai, N., & He, H. (2016). Breaking Snake Camouflage: Humans Detect Snakes More Accurately than Other Animals under Less Discernible Visual Conditions. *PLOS ONE*, *11*(10), e0164342. https://doi.org/10.1371/journal.pone.0164342

Kawai, N., & Koda, H. (2016). Japanese monkeys (Macaca fuscata) quickly detect snakes but not spiders: Evolutionary origins of fear-relevant animals. In *Journal of Comparative Psychology* (Vol. 130, pp. 299–303). American Psychological Association. https://doi.org/10.1037/com0000032

Keen, S. C., Cole, E. F., Sheehan, M. J., & Sheldon, B. C. (2020). Social learning of acoustic anti-predator cues occurs between wild bird species. *Proceedings of the Royal Society B: Biological Sciences*, *287*(1920), 20192513. https://doi.org/10.1098/rspb.2019.2513

Kelley, J. L., & Magurran, A. E. (2003). Learned predator recognition and antipredator responses in fishes. *Fish and Fisheries*, *4*(3), 216–226. https://doi.org/https://doi.org/10.1046/j.1467-2979.2003.00126.x

Kellogg, W. N., & Kellogg, L. A. (1933). The ape and the child: a study of environmental influence upon early behavior. In *The ape and the child: a study of environmental influence upon early behavior.* Whittlesey House.

Kendal, R. L., Coolen, I., van Bergen, Y., & Laland, K. N. B. T.-A. in the S. of B. (2005). *Trade-Offs in the Adaptive Use of Social and Asocial Learning* (Vol. 35, pp. 333–379). Academic Press. https://doi.org/https://doi.org/10.1016/S0065-3454(05)35008-X

Khamcha, D., & Sukumal, N. (2009). Burmese python (Python molurus) predation on a pig-tailed macaque (Macaca nemestrina) in Khao Yai National Park. *Hamadryad*, *34*, 176–178. https://doi.org/10.13140/2.1.3857.7449

King, S. L., & Janik, V. M. (2013). Bottlenose dolphins can use learned vocal labels to address each other. *Proceedings of the National Academy of Sciences*, *110*(32), 13216–13221. https://doi.org/10.1073/pnas.1304459110

Kingdon, J. (2015). *The Kingdon field guide to African mammals*. Bloomsbury Publishing.

Kirchhof, J., & Hammerschmidt, K. (2006). Functionally Referential Alarm Calls in Tamarins

(Saguinus fuscicollis and Saguinus mystax) – Evidence from Playback Experiments. *Ethology*, *112*(4), 346–354. https://doi.org/https://doi.org/10.1111/j.1439-0310.2006.01165.x

Koda, H., Shimooka, Y., & Sugiura, H. (2008). Effects of caller activity and habitat visibility on contact call rate of wild Japanese macaques (Macaca fuscata). *American Journal of Primatology*, *70*(11), 1055–1063. https://doi.org/10.1002/ajp.20597

Koné, I., McGraw, S., Gonedelé Bi, S., & Barrie, A. (2020). *Cercocebus atys*. The IUCN Red List of Threatened Species 2020: E.T136933A92248451. https://dx.doi.org/10.2305/IUCN.UK.2020-2.RLTS.T136933A92248451.en

Krause, M. A., & Beran, M. J. (2020). Words matter: Reflections on language projects with chimpanzees and their implications. *American Journal of Primatology*, *82*(10), e23187. https://doi.org/https://doi.org/10.1002/ajp.23187

Kuhl, P. K. (2000). A new view of language acquisition. *Proceedings of the National Academy of Sciences of the United States of America*, *97*(22), 11850–11857. https://doi.org/10.1073/pnas.97.22.11850

Lameira, A. R. (2017). Bidding evidence for primate vocal learning and the cultural substrates for speech evolution. *Neuroscience & Biobehavioral Reviews*, *83*, 429–439. https://doi.org/https://doi.org/10.1016/j.neubiorev.2017.09.021

Laporte, M. N. C., & Zuberbühler, K. (2010). Vocal greeting behaviour in wild chimpanzee females. *Animal Behaviour*, *80*(3), 467–473. https://doi.org/https://doi.org/10.1016/j.anbehav.2010.06.005

Lattenkamp, E. Z., & Vernes, S. C. (2018). Vocal learning: a language-relevant trait in need of a broad cross-species approach. *Current Opinion in Behavioral Sciences*, *21*, 209–215. https://doi.org/https://doi.org/10.1016/j.cobeha.2018.04.007

Lattenkamp, E. Z., Vernes, S. C., & Wiegrebe, L. (2018). Volitional control of social vocalisations and vocal usage learning in bats. *Journal of Experimental Biology*, *221*(14), jeb180729. https://doi.org/10.1242/jeb.180729

Lemasson, A., Gandon, E., & Hausberger, M. (2010). Attention to elders' voice in non-human primates. *Biology Letters*, *6*(3), 328. https://doi.org/10.1098/rsbl.2009.0875

Lemasson, A., Ouattara, K., Petit, E. J., & Zuberbühler, K. (2011). Social learning of vocal structure in a nonhuman primate? *BMC Evolutionary Biology*, *11*(1), 362. https://doi.org/10.1186/1471-2148-11-362

León, J., Thiriau, C., Bodin, C., Crockford, C., & Zuberbühler, K. (2022). Acquisition of predator knowledge from alarm calls via one-trial social learning in monkeys. *IScience*, *25*, 104853. https://doi.org/https://doi.org/10.1016/j.isci.2022.104853

León, J., Thiriau, C., Crockford, C., & Zuberbühler, K. (2022). *https://osf.io/y2gvc/.*

Leroux, M., & Townsend, S. W. (2020). Call combinations in great apes and the evolution of syntax. *Animal Behavior and Cognition*, *7*(2), 131–139.

Li, J., Smithwick, Q., & Chu, D. (2022). Holobricks: modular coarse integral holographic displays. *Light: Science & Applications*, *11*(1), 57. https://doi.org/10.1038/s41377-022-00742-7

Liebal, K., & Call, J. (2012). The origins of non-human primates' manual gestures. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *367*(1585), 118–128. https://doi.org/10.1098/rstb.2011.0044

Liebal, K., Waller, B. M., Burrows, A. M., & Slocombe, K. E. (2014). Primate communication: A multimodal approach. In *Primate communication: A multimodal approach.* Cambridge University Press.

Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, *68*(4), 619–640. https://doi.org/10.1139/z90-092

Luchkina, E., & Waxman, S. (2021). Acquiring verbal reference: The interplay of cognitive, linguistic, and general learning capacities. *Infant Behavior and Development*, *65*, 101624. https://doi.org/https://doi.org/10.1016/j.infbeh.2021.101624

Magrath, R. D., Haff, T. M., Fallow, P. M., & Radford, A. N. (2015). Eavesdropping on heterospecific alarm calls: from mechanisms to consequences. *Biological Reviews*, *90*(2), 560–586. https://doi.org/https://doi.org/10.1111/brv.12122

Manser, M. B. (2001). The acoustic structure of suricates’ alarm calls varies with predator type and the level of response urgency. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *268*(1483), 2315–2324. https://doi.org/10.1098/rspb.2001.1773

Manser, M. B., Bell, M. B., & Fletcher, L. B. (2001). The information that receivers extract from alarm calls in suricates. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *268*(1484), 2485–2491. https://doi.org/10.1098/rspb.2001.1772

Masataka, N., & Fujita, K. (1989). Vocal Learning of Japanese and Rhesus Monkeys. *Behaviour*, *109*(3–4), 191–199. https://doi.org/https://doi.org/10.1163/156853989X00222

McCowan, B., Franceschini, N. V, & Vicino, G. A. (2001). Age differences and developmental trends in alarm peep responses by squirrel monkeys (Saimiri sciureus). *American Journal of Primatology*, *53*(1), 19–31. https://doi.org/https://doi.org/10.1002/1098-2345(200101)53:1<19::AID-AJP2>3.0.CO;2-#

McCullagh, P., & Nelder, J. A. (1989). *Generalized linear models* (Second). Chapman & Hall/CRC.

McGraw, W. (1998). Comparative locomotion and habitat use of six monkeys in the Tai Forest, Ivory Coast. *American Journal of Physical Anthropology*, *105*(4), 493–510. https://doi.org/https://doi.org/10.1002/(SICI)1096-8644(199804)105:4<493::AID-AJPA7>3.0.CO;2-P

McGraw, W., & Bshary, R. (2002). Association of Terrestrial Mangabeys (Cercocebus atys) with Arboreal Monkeys: Experimental Evidence for the Effects of Reduced Ground Predator Pressure on Habitat Use. *International Journal of Primatology*, *23*(2), 311–325. https://doi.org/10.1023/A:1013883528244

McGraw, W. S., Zuberbühler, K., & Noë, R. (2007). *Monkeys of the Taï Forest: an African primate community* (Vol. 51). Cambridge University Press.

McGraw, W., & Zuberbühler, K. (2007). The monkeys of the Taï forest: an introduction. In Klaus Zuberbühler, R. Noë, & W. S. McGraw (Eds.), *Monkeys of the Taï Forest: An African Primate Community* (pp. 1–48). Cambridge University Press. https://doi.org/DOI: 10.1017/CBO9780511542121.002

McGraw, W., Zuberbühler, K., & Noë, R. (2007). *Monkeys of the Tai Forest*. Cambridge University Press. https://doi.org/10.1017/CBO9780511542121

Meno, W., Coss, R. G., & Perry, S. (2013a). Development of Snake-Directed Antipredator Behavior by Wild White-faced Capuchin Monkeys: I. Snake-Species Discrimination. *American Journal of Primatology*, *75*(3), 281–291. https://doi.org/https://doi.org/10.1002/ajp.22106

Meno, W., Coss, R. G., & Perry, S. (2013b). Development of Snake-Directed Antipredator Behavior by Wild White-Faced Capuchin Monkeys: II. Influence of the Social Environment. *American Journal of Primatology*, *75*(3), 292–300. https://doi.org/https://doi.org/10.1002/ajp.22109

Mery, F., & Burns, J. G. (2010). Behavioural plasticity: an interaction between evolution and experience. *Evolutionary Ecology*, *24*(3), 571–583. https://doi.org/10.1007/s10682-009-9336-y

Meyer, D., Hodges, J. K., Rinaldi, D., Wijaya, A., Roos, C., & Hammerschmidt, K. (2012). Acoustic structure of male loud-calls support molecular phylogeny of Sumatran and Javanese leaf monkeys (genus Presbytis). *BMC Evolutionary Biology*, *12*(1), 16.

Mielke, A., Crockford, C., & Wittig, R. M. (2019). Snake alarm calls as a public good in sooty mangabeys. *Animal Behaviour*, *158*, 201–209. https://doi.org/https://doi.org/10.1016/j.anbehav.2019.10.001

Mielke, A., & Zuberbühler, K. (2013). A method for automated individual, species and call type recognition in free-ranging animals. *Animal Behaviour*, *86*(2), 475–482. https://doi.org/https://doi.org/10.1016/j.anbehav.2013.04.017

Mineka, S. (1992). *Evolutionary Memories, Emotional Processing, and the Emotional Disorders* (D. L. B. T.-P. of L. and M. Medin (ed.); Vol. 28, pp. 161–206). Academic Press. https://doi.org/https://doi.org/10.1016/S0079-7421(08)60490-9

Mineka, S., & Cook, M. (1988). Social learning and the acquisition of snake fear in monkeys. In *Social learning: Psychological and biological perspectives.* (pp. 51–73). Lawrence Erlbaum Associates, Inc.

Mineka, S., & Cook, M. (1993). Mechanisms involved in the observational conditioning of fear. In *Journal of Experimental Psychology: General* (Vol. 122, Issue 1, pp. 23–38). American Psychological Association. https://doi.org/10.1037/0096-3445.122.1.23

Mittermeier, R., Wilson, D., & Rylands, A. B. (2013). *Handbook of the Mammals of the World: 3. Primates*. Lynx Edicions. https://books.google.com.co/books?id=P0-rMQEACAAJ

Mohamad Nor, N., & Rashid, R. A. (2018). A review of theoretical perspectives on language learning and acquisition. *Kasetsart Journal of Social Sciences*, *39*(1), 161–167. https://doi.org/https://doi.org/10.1016/j.kjss.2017.12.012

Mohr, T., Van de Waal, E., Zuberbühler, K., & Mercier, S. (2022). *https://osf.io/mjywg/.*

Morse, D. H. (1977). Feeding Behavior and Predator Avoidance in Heterospecific Groups. *BioScience*, *27*(5), 332–339. https://doi.org/10.2307/1297632

Munn, C. A. (1986). Birds that 'cry wolf.' *Nature*, *319*(6049), 143–145. https://doi.org/10.1038/319143a0

Newman, J. D., & Symmes, D. (1974). Vocal pathology in socially deprived monkeys. *Developmental Psychobiology*, *7*(4), 351–358. https://doi.org/https://doi.org/10.1002/dev.420070412

Oates, J. F., Whitesides, G. H., Davies, A. G., Waterman, P. G., Green, S. M., Dasilva, G. L., & Mole, S. (1990). Determinants of Variation in Tropical Forest Primate Biomass: New Evidence from West Africa. *Ecology*, *71*(1), 328–343. https://doi.org/10.2307/1940272

Oda, R. (1998). The responses of Verreaux's sifakas to anti-predator alarm calls given by sympatric ring-tailed lemurs. *Folia Primatologica; International Journal of Primatology*, *69*(6), 357–360. https://doi.org/10.1159/000021651

Oda, R., & Masataka, N. (1996). Interspecific Responses of Ringtailed Lemurs to Playback of Antipredator Alarm Calls Given by Verreaux's Sifakas. *Ethology*, *102*(3), 441–453. https://doi.org/https://doi.org/10.1111/j.1439-0310.1996.tb01138.x

Öhman, A. (2009). Of snakes and faces: An evolutionary perspective on the psychology of fear. *Scandinavian Journal of Psychology*, *50*(6), 543–552. https://doi.org/https://doi.org/10.1111/j.1467-9450.2009.00784.x

Ohman, A., & Mineka, S. (2001). Fears, phobias, and preparedness: toward an evolved module of fear and fear learning. *Psychological Review*, *108*(3), 483–522. https://doi.org/10.1037/0033-295x.108.3.483

Oliveira, L. C., & Dietz, J. M. (2011). Predation risk and the interspecific association of two Brazilian Atlantic forest primates in Cabruca agroforest. *American Journal of Primatology*, *73*(9), 852–860. https://doi.org/10.1002/ajp.20952

Olsson, A., & Phelps, E. A. (2007). Social learning of fear. *Nature Neuroscience*, *10*(9), 1095–1102. https://doi.org/10.1038/nn1968

Ouattara, K., Lemasson, A., & Zuberbühler, K. (2009a). Anti-predator strategies of free-ranging Campbell's monkeys. *Behaviour*, *146*(12), 1687–1708. https://doi.org/10.1163/000579509X12469533725585

Ouattara, K., Lemasson, A., & Zuberbühler, K. (2009b). Campbell's monkeys concatenate vocalizations into context-specific call sequences. In *PNAS Proceedings of the National Academy of Sciences of the United States of America* (Vol. 106, Issue 51, pp. 22026–22031). National Academy of Sciences. https://doi.org/10.1073/pnas.0908118106

Owren, M. J., Dieter, J. A., Seyfarth, R. M., & Cheney, D. L. (1992). "Food" Calls Produced by Adult Female Rhesus (Macaca mulatta) and Japanese (M. fuscata) Macaques, Their Normally-Raised Offspring, and Offspring Cross-Fostered between Species. *Behaviour*, *120*(3/4), 218–231. http://www.jstor.org/stable/4535009

Owren, M. J., Dieter, J. A., Seyfarth, R. M., & Cheney, D. L. (1993). Vocalizations of rhesus (Macaca mulatta) and Japanese (M. Fuscata) macaques cross-fostered between species show evidence of only limited modification. *Developmental Psychobiology*, *26*(7), 389–406. https://doi.org/https://doi.org/10.1002/dev.420260703

Owren, M. J., & Rendall, D. (1997). *An Affect-Conditioning Model of Nonhuman Primate Vocal Signaling BT - Communication* (D. H. Owings, M. D. Beecher, & N. S. Thompson (eds.); pp. 299–346). Springer US. https://doi.org/10.1007/978-1-4899-1745-4_10

Owren, M. J., & Rendall, D. (2001). Sound on the rebound: Bringing form and function back to the forefront in understanding nonhuman primate vocal signaling. *Evolutionary Anthropology: Issues, News, and Reviews*, *10*(2), 58–71.

https://doi.org/https://doi.org/10.1002/evan.1014

Peake, T. M., & Mcgregor, P. K. (2004). Information and aggression in fishes. *Animal Learning & Behavior*, *32*(1), 114–121. https://doi.org/10.3758/BF03196012

Penner, J., Fruteau, C., Range, F., & Rodel, M. (2008). Finding a needle in a haystack: new methods of locating and working with rhinoceros vipers (Bitis rhinoceros). *Herpetological Review*, *39*(3), 310.

Pepperberg, I. M. (2010). Vocal learning in Grey parrots: A brief review of perception, production, and cross-species comparisons. *Brain and Language*, *115*(1), 81–91. https://doi.org/https://doi.org/10.1016/j.bandl.2009.11.002

Pepperberg, I. M. (2017). Animal language studies: What happened? *Psychonomic Bulletin & Review*, *24*(1), 181–185. https://doi.org/10.3758/s13423-016-1101-y

Perry, S., Panger, M., Rose, L. M., Baker, M., Gros-Louis, J., Jack, K., Mackinnon, K. C., Manson, J., Fedigan, L., & Pyle, K. (2003). Traditions in wild white-faced capuchin monkeys. In *The Biology of Traditions* (pp. 391–425). Cambridge University Press. https://doi.org/10.1017/CBO9780511584022.015

Pessoa, D. M. A., Maia, R., de Albuquerque Ajuz, R. C., De Moraes, P. Z. P. M. R., Spyrides, M. H. C., & Pessoa, V. F. (2014). The adaptive value of primate color vision for predator detection. *American Journal of Primatology*, *76*(8), 721–729. https://doi.org/10.1002/ajp.22264

Pika, S., & Liebal, K. (2006). Differences and similarties between the natural gestural communication of the great apes and human children. In *The Evolution of Language* (pp. 267–274). WORLD SCIENTIFIC. https://doi.org/doi:10.1142/9789812774262_0034

Pika, S., Liebal, K., & Tomasello, M. (2003). Gestural communication in young gorillas (Gorilla gorilla): gestural repertoire, learning, and use. *American Journal of Primatology*, *60*(3), 95–111. https://doi.org/10.1002/ajp.10097

Poole, J. H., Tyack, P. L., Stoeger-Horwath, A. S., & Watwood, S. (2005). Elephants are capable of vocal learning. *Nature*, *434*(7032), 455–456. https://doi.org/10.1038/434455a

Potvin, D. A., Ratnayake, C. P., Radford, A. N., & Magrath, R. D. (2018). Birds Learn Socially to Recognize Heterospecific Alarm Calls by Acoustic Association. *Current Biology*, *28*(16), 2632-2637.e4. https://doi.org/https://doi.org/10.1016/j.cub.2018.06.013

Pozzi, L., Gamba, M., & Giacoma, C. (2013). Artificial Neural Networks: A New Tool for Studying Lemur Vocal Communication. In J. Masters, M. Gamba, & F. Génin (Eds.), *Leaping Ahead: Advances in Prosimian Biology* (pp. 305–313). Springer New York. https://doi.org/10.1007/978-1-4614-4511-1_34

Pozzi, L., Hodgson, J. A., Burrell, A. S., Sterner, K. N., Raaum, R. L., & Disotell, T. R. (2014). Primate phylogenetic relationships and divergence dates inferred from complete mitochondrial genomes. *Molecular Phylogenetics and Evolution*, *75*, 165–183. https://doi.org/10.1016/j.ympev.2014.02.023

Price, T., Ndiaye, O., Hammerschmidt, K., & Fischer, J. (2014). Limited geographic variation in the acoustic structure of and responses to adult male alarm barks of African green monkeys. *Behavioral Ecology and Sociobiology*, *68*(5), 815–825. https://doi.org/10.1007/s00265-014-1694-y

Price, T., Wadewitz, P., Cheney, D., Seyfarth, R., Hammerschmidt, K., & Fischer, J. (2015). Vervets revisited: A quantitative analysis of alarm call structure and context specificity. *Scientific Reports*, *5*, 13220. https://doi.org/10.1038/srep13220

Quam, R. M., Ramsier, M. A., Fay, R. R., & Popper, A. N. (2017). *Primate hearing and communication*. Springer.

Quintero, F., Touitou, S., Magris, M., & Zuberbühler, K. (2022a). An audience effect in sooty mangabey alarm calling. *Front Psychol*, *13*. https://doi.org/10.3389/fpsyg.2022.816744

Quintero, F., Touitou, S., Magris, M., & Zuberbühler, K. (2022b). The Evolution of Food Calls: Vocal Behaviour of Sooty Mangabeys in the Presence of Food . In *Frontiers in Psychology* (Vol. 13). https://www.frontiersin.org/articles/10.3389/fpsyg.2022.897318

R Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

Ramakrishnan, U., & Coss, R. G. (2000). Recognition of heterospecific alarm vocalization by Bonnet Macaques (Macaca radiata). In *Journal of Comparative Psychology* (Vol. 114, Issue 1, pp. 3–12). American Psychological Association. https://doi.org/10.1037/0735-7036.114.1.3

Ramakrishnan, U., Coss, R. G., Schank, J., Dharawat, A., & Kim, S. (2005). Snake Species Discrimination by Wild Bonnet Macaques (Macaca radiata). *Ethology*, *111*(4), 337–356. https://doi.org/10.1111/j.1439-0310.2004.01063.x

Range, F., & Fischer, J. (2004). Vocal Repertoire of Sooty Mangabeys (Cercocebus torquatus atys) in the Tai National Park. *Ethology*, *110*(4), 301–321. https://doi.org/10.1111/j.1439-0310.2004.00973.x

Range, F., & Noë, R. (2002). Familiarity and dominance relations among female sooty mangabeys in the Taï National Park. *American Journal of Primatology*, *56*(3), 137–153. https://doi.org/https://doi.org/10.1002/ajp.1070

Rapaport, L. G., & Brown, G. R. (2008). Social influences on foraging behavior in young nonhuman primates: Learning what, where, and how to eat. *Evolutionary Anthropology: Issues, News, and Reviews*, *17*(4), 189–201. https://doi.org/https://doi.org/10.1002/evan.20180

Rendall, D., Owren, M. J., & Ryan, M. J. (2009). What do animal signals mean? *Animal Behaviour*, *78*(2), 233–240. https://doi.org/https://doi.org/10.1016/j.anbehav.2009.06.007

Rescorla, L. A. (1980). Overextension in early language development. *Journal of Child Language*, *7*(2), 321–335. https://doi.org/DOI: 10.1017/S0305000900002658

Rescorla, R. A., & Wagner, A. (1972). A theory of Pavlovian conditioning: Variations in the effectiveness of reinforcement and nonreinforcement. In A. Black & P. W (Eds.), *Classical Conditioning II: Current Research and Theory: Vol. Vol. 2* (pp. 64–69). Appleton-Century-Crofts.

Ridgway, S., Carder, D., Jeffries, M., & Todd, M. (2012). Spontaneous human speech mimicry by a cetacean. *Current Biology*, *22*(20), R860–R861. https://doi.org/10.1016/j.cub.2012.08.044

Rödel, M., & Mahsberg, D. (2000). Vorläufige Liste der Schlangen des Taï-Nationalparks /

Elfenbeinküste und angrenzender Gebiete. *Salamandra*, *36*, 25–38.

Romano, D., Donati, E., Benelli, G., & Stefanini, C. (2019). A review on animal–robot interaction: from bio-hybrid organisms to mixed societies. *Biological Cybernetics*, *113*(3), 201–225. https://doi.org/10.1007/s00422-018-0787-5

Rosati, A. G., Machanda, Z. P., & Slocombe, K. E. (2022). Cognition in the wild: understanding animal thought in its natural context. *Current Opinion in Behavioral Sciences*, *47*, 101210. https://doi.org/https://doi.org/10.1016/j.cobeha.2022.101210

Roupe, S., Pistorio, A., & Wang, X. (2003). Vocal plasticity induced by auditory deprivation in the common marmoset. *Program No. 627.7 2003 Abstract Viewer and Itinerary Planner. Society for Neuroscience Online*.

Schel, A. M., Machanda, Z., Townsend, S. W., Zuberbühler, K., & Slocombe, K. E. (2013). Chimpanzee food calls are directed at specific individuals. *Animal Behaviour*, *86*(5), 955–965. https://doi.org/https://doi.org/10.1016/j.anbehav.2013.08.013

Schel, A. M., Townsend, S. W., Machanda, Z., Zuberbühler, K., & Slocombe, K. E. (2013). Chimpanzee Alarm Call Production Meets Key Criteria for Intentionality. *PLOS ONE*, *8*(10), e76674. https://doi.org/10.1371/journal.pone.0076674

Schel, A. M., & Zuberbühler, K. (2009). Responses to leopards are independent of experience in Guereza colobus monkeys. *Behaviour*, *146*(12), 1709–1737. https://doi.org/https://doi.org/10.1163/000579509X12483520922007

Schrago, C. G., & Russo, C. A. M. (2003). Timing the Origin of New World Monkeys. *Molecular Biology and Evolution*, *20*(10), 1620–1625. https://doi.org/10.1093/molbev/msg172

Schuppli, C., Meulman, E. J. M., Forss, S. I. F., Aprilinayati, F., van Noordwijk, M. A., & van Schaik, C. P. (2016). Observational social learning and socially induced practice of routine skills in immature wild orang-utans. *Animal Behaviour*, *119*, 87–98. https://doi.org/https://doi.org/10.1016/j.anbehav.2016.06.014

Searcy, W. A., & Nowicki, S. (2010). The Evolution of Animal Communication: Reliability and Deception in Signaling Systems. In *Reliability and Deception in Signaling Systems*.

Princeton University Press. https://doi.org/doi:10.1515/9781400835720

Seidenberg, M. S. (1997). Language Acquisition and Use: Learning and Applying Probabilistic Constraints. *Science*, *275*(5306), 1599–1603. https://doi.org/10.1126/science.275.5306.1599

Seiler, M., Schwitzer, C., Gamba, M., & Holderied, M. W. (2013). Interspecific Semantic Alarm Call Recognition in the Solitary Sahamalaza Sportive Lemur, Lepilemur sahamalazensis. *PLoS ONE*, *8*(6), e67397. https://doi.org/10.1371/journal.pone.0067397

Seppänen, J.-T., Forsman, J. T., Mönkkönen, M., & Thomson, R. L. (2007). Social information use is a process across time, space, and ecology, reaching heterospecifics. *Ecology*, *88*(7), 1622–1633. https://doi.org/10.1890/06-1757.1

Seyfarth, R. M., & Cheney, D. L. (1980). The Ontogeny of Vervet Monkey Alarm Calling Behavior: A Preliminary Report. *Zeitschrift Für Tierpsychologie*, *54*(1), 37–56. https://doi.org/10.1111/j.1439-0310.1980.tb01062.x

Seyfarth, R. M., & Cheney, D. L. (1986). Vocal development in vervet monkeys. *Animal Behaviour*, *34*(6), 1640–1658. https://doi.org/https://doi.org/10.1016/S0003-3472(86)80252-4

Seyfarth, R. M., & Cheney, D. L. (1997). Some general features of vocal development in nonhuman primates. In C. T. Snowdon & M. Hausberger (Eds.), *Social Influences on Vocal Development* (pp. 249–273). Cambridge University Press. https://doi.org/DOI: 10.1017/CBO9780511758843.013

Seyfarth, R. M., Cheney, D. L., & Marler, P. (1980). Vervet monkey alarm calls: semantic communication in a free-ranging primate. *Animal Behaviour*, *28*(4), 1070–1094.

Seyfarth, R, & Cheney, D. (2010). Production, usage, and comprehension in animal vocalizations. *Brain and Language*, *115*(1), 92–100. https://doi.org/https://doi.org/10.1016/j.bandl.2009.10.003

Seyfarth, R, Cheney, D., Bergman, T., Fischer, J., Zuberbühler, K., & Hammerschmidt, K. (2010). The central importance of information in studies of animal communication. *Animal Behaviour*, *80*(1), 3–8.

https://doi.org/https://doi.org/10.1016/j.anbehav.2010.04.012

Seyfarth, R, Cheney, D., & Marler, P. (1980). Monkey responses to three different alarm calls: evidence of predator classification and semantic communication. *Science*, *210*(4471), 801–803.

Seyfarth, R, & Cheney, D. (1990). The assessment by vervet monkeys of their own and another species' alarm calls. *Animal Behaviour*, *40*(4), 754–764. https://doi.org/https://doi.org/10.1016/S0003-3472(05)80704-3

Shannon, C. E. (1948). A Mathematical Theory of Communication. *Bell System Technical Journal*, *27*(3), 379–423. https://doi.org/https://doi.org/10.1002/j.1538-7305.1948.tb01338.x

Sheldon, B. C., Kruuk, L. E. B., & Alberts, S. C. (2022). The expanding value of long-term studies of individuals in the wild. *Nature Ecology & Evolution*. https://doi.org/10.1038/s41559-022-01940-7

Shibasaki, M., & Kawai, N. (2009). Rapid detection of snakes by Japanese monkeys (Macaca fuscata): An evolutionarily predisposed visual system. In *Journal of Comparative Psychology* (Vol. 123, pp. 131–135). American Psychological Association. https://doi.org/10.1037/a0015095

Shultz, S, & Thomsett, S. (2007). Interactions between African crowned eagles and their prey community. In Klaus Zuberbühler, R. Noë, & W. S. McGraw (Eds.), *Monkeys of the Taï Forest: An African Primate Community* (pp. 171–193). Cambridge University Press. https://doi.org/DOI: 10.1017/CBO9780511542121.008

Shultz, S, Noë, R., McGraw, W. S., & Dunbar, R. I. M. (2004). A community-level evaluation of the impact of prey behavioural and ecological characteristics on predator diet composition. *Proceedings. Biological Sciences*, *271*(1540), 725–732. https://doi.org/10.1098/rspb.2003.2626

Simmons, J. P., Nelson, L. D., & Simonsohn, U. (2011). False-Positive Psychology: Undisclosed Flexibility in Data Collection and Analysis Allows Presenting Anything as Significant. *Psychological Science*, *22*(11), 1359–1366. https://doi.org/10.1177/0956797611417632

Slater, P. J. B. (2006). *Animal Communication: Vocal Learning* (K. B. T.-E. of L. & L. (Second E. Brown (ed.); pp. 291–294). Elsevier. https://doi.org/https://doi.org/10.1016/B0-08-044854-2/00824-5

Slocombe, K E, & Zuberbühler, K. (2005). Functionally Referential Communication in a Chimpanzee. *Current Biology*, *15*(19), 1779–1784. https://doi.org/https://doi.org/10.1016/j.cub.2005.08.068

Slocombe, K E, & Zuberbühler, K. (2007). Chimpanzees modify recruitment screams as a function of audience composition. *Proceedings of the National Academy of Sciences*, *104*(43), 17228 LP – 17233. https://doi.org/10.1073/pnas.0706741104

Slocombe, K E, Waller, B. M., & Liebal, K. (2011). The language void: the need for multimodality in primate communication research. *Animal Behaviour*, *81*(5), 919–924. https://doi.org/https://doi.org/10.1016/j.anbehav.2011.02.002

Smid, S. C., McNeish, D., Miočević, M., & van de Schoot, R. (2020). Bayesian Versus Frequentist Estimation for Structural Equation Models in Small Sample Contexts: A Systematic Review. *Structural Equation Modeling: A Multidisciplinary Journal*, *27*(1), 131–161. https://doi.org/10.1080/10705511.2019.1577140

Snowdon, C. T. B. T.-A. in the S. of B. (2009). Chapter 7 Plasticity of Communication in Nonhuman Primates. In *Advances in the Study of Behavior* (Vol. 40, pp. 239–276). Academic Press. https://doi.org/https://doi.org/10.1016/S0065-3454(09)40007-X

Stansbury, A. L., & Janik, V. M. (2019). Formant Modification through Vocal Production Learning in Gray Seals. *Current Biology*, *29*(13), 2244-2249.e4. https://doi.org/10.1016/j.cub.2019.05.071

Stauffer, R. L., Walker, A., Ryder, O. A., Lyons-Weiler, M., & Hedges, S. B. (2001). Human and Ape Molecular Clocks and Constraints on Paleontological Hypotheses. *Journal of Heredity*, *92*(6), 469–474. https://doi.org/10.1093/jhered/92.6.469

Stensland, E., Angerbjörn, A., & Berggren, P. (2003). Mixed species groups in mammals. *Mammal Review*, *33*(3-4), 205–223. https://doi.org/https://doi.org/10.1046/j.1365-2907.2003.00022.x

Stephan, C., & Zuberbühler, K. (2008). Predation increases acoustic complexity in primate alarm calls. *Biology Letters*, *4*(6), 641–644. https://doi.org/10.1098/rsbl.2008.0488

Stephan, C., & Zuberbühler, K. (2014). Predation affects alarm call usage in female Diana monkeys (Cercopithecus diana diana). *Behavioral Ecology and Sociobiology*, *68*(2), 321–331. https://doi.org/10.1007/s00265-013-1647-x

Stephan, C., & Zuberbühler, K. (2021). *Alarm Calling and Kinship BT - Encyclopedia of Evolutionary Psychological Science* (T. K. Shackelford & V. A. Weekes-Shackelford (eds.); pp. 163–171). Springer International Publishing. https://doi.org/10.1007/978-3-319-19650-3_1512

Stevenson, M. (1973). Notes on pregnancy in the Sooty mangabey Cercocebus atys. *International Zoo Yearbook*, *13*(1), 134–135. https://doi.org/https://doi.org/10.1111/j.1748-1090.1973.tb02126.x

Stoeger, A. S., Mietchen, D., Oh, S., de Silva, S., Herbst, C. T., Kwon, S., & Fitch, W. T. (2012). An Asian Elephant Imitates Human Speech. *Current Biology*, *22*(22), 2144–2148. https://doi.org/10.1016/j.cub.2012.09.022

Struhsaker, T. T. (1967). Ecology of Vervet Monkeys (Cercopithecus Aethiops) in The Masai-Amboseli Game Reserve, Kenya. *Ecology*, *48*(6), 891–904. https://doi.org/https://doi.org/10.2307/1934531

Sugiura, H. (1998). Matching of acoustic features during the vocal exchange of coo calls by Japanese macaques. *Animal Behaviour*, *55*(3), 673–687. https://doi.org/https://doi.org/10.1006/anbe.1997.0602

Takahashi, D. Y., Liao, D. A., & Ghazanfar, A. A. (2017). Vocal Learning via Social Reinforcement by Infant Marmoset Monkeys. *Current Biology*, *27*(12), 1844-1852.e6. https://doi.org/10.1016/j.cub.2017.05.004

Talmage-Riggs, G., Winter, P., Ploog, D., & Mayer, W. (1972). Effect of deafening on the vocal behavior of the squirrel monkey (Saimiri sciureus). *Folia Primatologica; International Journal of Primatology*, *17*(5), 404–420. https://doi.org/10.1159/000155458

Team, J. (2020). *JASP (Version 0.14.1)*. https://jasp-stats.org/

Thinh, V. N., Hallam, C., Roos, C., & Hammerschmidt, K. (2011). Concordance between vocal and genetic diversity in crested gibbons. *BMC Evolutionary Biology*, *11*(1), 36. https://doi.org/10.1186/1471-2148-11-36

Thornton, A., & Clutton-Brock, T. (2011). Social learning and the development of individual and group behaviour in mammal societies. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*(1567), 978–987. https://doi.org/10.1098/rstb.2010.0312

Tomasello, M. (2010). *Why we cooperate*. Boston Review Books.

Tomasello, M, & Call, J. (1994). Social cognition of monkeys and apes. *American Journal of Physical Anthropology*, *37*(S19), 273–305. https://doi.org/https://doi.org/10.1002/ajpa.1330370610

Tomasello, M. (2008). *Origins of Human Communication*. MIT press.

Townsend, S. W., & Manser, M. B. (2013). Functionally Referential Communication in Mammals: The Past, Present and the Future. *Ethology*, *119*(1), 1–11. https://doi.org/https://doi.org/10.1111/eth.12015

Trape, J.-F., Trape, S., & Chirio, L. (2012). *Lézards, crocodiles et tortues d'Afrique occidentale et du Sahara*. IRD éditions.

Urbani, B. (2017). Humans as Primate Predators. In *The International Encyclopedia of Primatology* (pp. 1–3). https://doi.org/https://doi.org/10.1002/9781119179313.wbprim0258

Valente, D., De Gregorio, C., Torti, V., Miaretsoa, L., Friard, O., Randrianarison, R. M., Giacoma, C., & Gamba, M. (2019). Finding Meanings in Low Dimensional Structures: Stochastic Neighbor Embedding Applied to the Analysis of Indri indri Vocal Repertoire. *Animals : An Open Access Journal from MDPI*, *9*(5). https://doi.org/10.3390/ani9050243

van Doorn, J., van den Bergh, D., Böhm, U., Dablander, F., Derks, K., Draws, T., Etz, A., Evans, N. J., Gronau, Q. F., Haaf, J. M., Hinne, M., Kucharský, Š., Ly, A., Marsman, M., Matzke, D., Gupta, A. R. K. N., Sarafoglou, A., Stefan, A., Voelkel, J. G., &

Wagenmakers, E.-J. (2021). The JASP guidelines for conducting and reporting a Bayesian analysis. *Psychonomic Bulletin & Review*, *28*(3), 813–826. https://doi.org/10.3758/s13423-020-01798-5

van Schaik, C. P., van Noordwijk, M. A., Warsono, B., & Sutriono, E. (1983). Party size and early detection of predators in sumatran forest primates. *Primates*, *24*(2), 211–221. https://doi.org/10.1007/BF02381083

Vernes, S. C., & Wilkinson, G. S. (2020). Behaviour, biology and evolution of vocal learning in bats. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *375*(1789), 20190061. https://doi.org/10.1098/rstb.2019.0061

Verzani, J. (2004). *Using R for introductory statistics* (1st ed.). Chapman and Hall/CRC. https://doi.org/https://doi.org/10.4324/9780203499894

Wadewitz, P., Hammerschmidt, K., Battaglia, D., Witt, A., Wolf, F., & Fischer, J. (2015). Characterizing vocal repertoires - Hard vs. Soft classification approaches. *PLoS ONE*, *10*(4). https://doi.org/10.1371/journal.pone.0125785

Watson, S. K., Townsend, S. W., Schel, A. M., Wilke, C., Wallace, E. K., Cheng, L., West, V., & Slocombe, K. E. (2015). Vocal Learning in the Functionally Referential Food Grunts of Chimpanzees. *Current Biology*, *25*(4), 495–499. https://doi.org/https://doi.org/10.1016/j.cub.2014.12.032

Wegdell, F., Hammerschmidt, K., & Fischer, J. (2019). Conserved alarm calls but rapid auditory learning in monkey responses to novel flying objects. *Nature Ecology & Evolution*, *3*(7), 1039–1042. https://doi.org/10.1038/s41559-019-0903-5

Weiss, L., Brandl, P., & Frynta, D. (2015). Fear reactions to snakes in naïve mouse lemurs and pig-tailed macaques. *Primates*, *56*(3), 279–284. https://doi.org/10.1007/s10329-015-0473-3

Wheeler, B. C. (2009). Monkeys crying wolf? Tufted capuchin monkeys use anti-predator calls to usurp resources from conspecifics. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1669), 3013–3018. https://doi.org/10.1098/rspb.2009.0544

Wheeler, B. C., Fahy, M., & Tiddi, B. (2019). Experimental evidence for heterospecific alarm signal recognition via associative learning in wild capuchin monkeys. *Animal Cognition*, *22*(5), 687–695. https://doi.org/10.1007/s10071-019-01264-3

Wheeler, B. C., & Fischer, J. (2012). Functionally referential signals: A promising paradigm whose time has passed. *Evolutionary Anthropology: Issues, News, and Reviews*, *21*(5), 195–205. https://doi.org/https://doi.org/10.1002/evan.21319

Wheeler, B. C., & Hammerschmidt, K. (2013). Proximate factors underpinning receiver responses to deceptive false alarm calls in wild tufted capuchin monkeys: is it counterdeception? *American Journal of Primatology*, *75*(7), 715–725. https://doi.org/10.1002/ajp.22097

White, D. J. (2004). Influences of social learning on mate-choice decisions. *Animal Learning & Behavior*, *32*(1), 105–113. https://doi.org/10.3758/BF03196011

Whiten, A., & van de Waal, E. (2018). The pervasive role of social learning in primate lifetime development. *Behavioral Ecology and Sociobiology*, *72*(5), 80. https://doi.org/10.1007/s00265-018-2489-3

Whitesides, G. H. (1989). Interspecific associations of Diana monkeys, Cercopithecus diana, in Sierra Leone, West Africa: biological significance or chance? *Animal Behaviour*, *37*, 760–776. https://doi.org/https://doi.org/10.1016/0003-3472(89)90062-6

Wich, S. A., & Sterck, E. H. M. (2003). Possible audience effect in Thomas langurs (Primates; Presbytis thomasi): an experimental study on male loud calls in response to a tiger model. *American Journal of Primatology*, *60*(4), 155–159. https://doi.org/10.1002/ajp.10102

Winter, P., Handley, P., Ploog, D., & Schott, D. (1973). Ontogeny of squirrel monkey calls under normal conditions and under acoustic isolation. *Behaviour*, *47*(3), 230–239. https://doi.org/10.1163/156853973x00085

Wittig, R. M. (2018). 40 years of research at the Taï Chimpanzee Project. *Pan Africa News*, *25*(2), 16–18.

Wrangham, R. W., & Cheney, D. L. (1985). Predation rates and social-structure in primates. *American Journal of Primatology*, *8*(4), 372.

Zhang, Y. S., & Ghazanfar, A. A. (2018). Vocal development through morphological computation. *PLOS Biology*, *16*(2), e2003933. https://doi.org/10.1371/journal.pbio.2003933

Zuberbühler, K. (2000a). Interspecies semantic communication in two forest primates. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *267*(1444), 713–718. https://doi.org/10.1098/rspb.2000.1061

Zuberbühler, K. (2000b). Causal cognition in a non-human primate: field playback experiments with Diana monkeys. *Cognition*, *76*(3), 195–207. https://doi.org/10.1016/s0010-0277(00)00079-2

Zuberbühler, K. (2001). Predator-specific alarm calls in Campbell's monkeys, Cercopithecus campbelli. *Behavioral Ecology and Sociobiology*, *50*(5), 414–422.

Zuberbühler, K. (2003a). Natural semanticity in wild primates. In *Animal social complexity: Intelligence, culture, and individualized societies.* (pp. 362–367). Harvard University Press.

Zuberbühler, K. (2003b). Referential signaling in non-human primates: Cognitive precursors and limitations for the evolution of language. In *Advances in the study of behavior, Vol 33.* (pp. 265–307). Elsevier Academic Press. https://doi.org/10.1016/S0065-3454(03)33006-2

Zuberbühler, K. (2007). Monkey alarm calls. In Klaus Zuberbühler, R. Noë, & W. S. McGraw (Eds.), *Monkeys of the Taï Forest: An African Primate Community* (pp. 194–220). Cambridge University Press. https://doi.org/DOI: 10.1017/CBO9780511542121.009

Zuberbühler, K, & Jenny, D. (2002). Leopard predation and primate evolution. *Journal of Human Evolution*, *43*(6), 873–886. https://doi.org/https://doi.org/10.1006/jhev.2002.0605

Zuberbühler, K, & Jenny, D. (2007). Interaction between leopard and monkeys. In Klaus Zuberbühler, R. Noë, & W. S. McGraw (Eds.), *Monkeys of the Taï Forest: An African Primate Community* (pp. 133–154). Cambridge University Press. https://doi.org/DOI: 10.1017/CBO9780511542121.006

Zuberbühler, K, Jenny, D., & Bshary, R. (1999). The Predator Deterrence Function of Primate

Alarm Calls. *Ethology*, *105*(6), 477–490. https://doi.org/10.1046/j.1439-0310.1999.00396.x

Zuberbühler, K, Noë, R., & Seyfarth, R. M. (1997). Diana monkey long-distance calls: messages for conspecifics and predators. *Animal Behaviour*, *53*(3), 589–604.

Zuberbühler, K. (2000). Causal knowledge of predators' behaviour in wild Diana monkeys. *Animal Behaviour*, *59*(1), 209–220. https://doi.org/https://doi.org/10.1006/anbe.1999.1296

Zuberbühler, K. (2009). Survivor Signals: The Biology and Psychology of Animal Alarm Calling. *Advances in the Study of Behavior*, *40*, 277–322. https://doi.org/https://doi.org/10.1016/S0065-3454(09)40008-1

Zuberbühler, K, & Lemasson, A. (2014). *Primate Communication: Meaning from Strings of Calls BT - Language and Recursion* (F. Lowenthal & L. Lefebvre (eds.); pp. 115–125). Springer New York. https://doi.org/10.1007/978-1-4614-9414-0_9

Zuberbühler, K, León, J., Deshpande, A., & Quintero, F. (2022). Socially scripted vocal learning in primates. *Current Opinion in Behavioral Sciences*, *46*, 101153. https://doi.org/https://doi.org/10.1016/j.cobeha.2022.101153

2.13 Chapter 2: Appendix

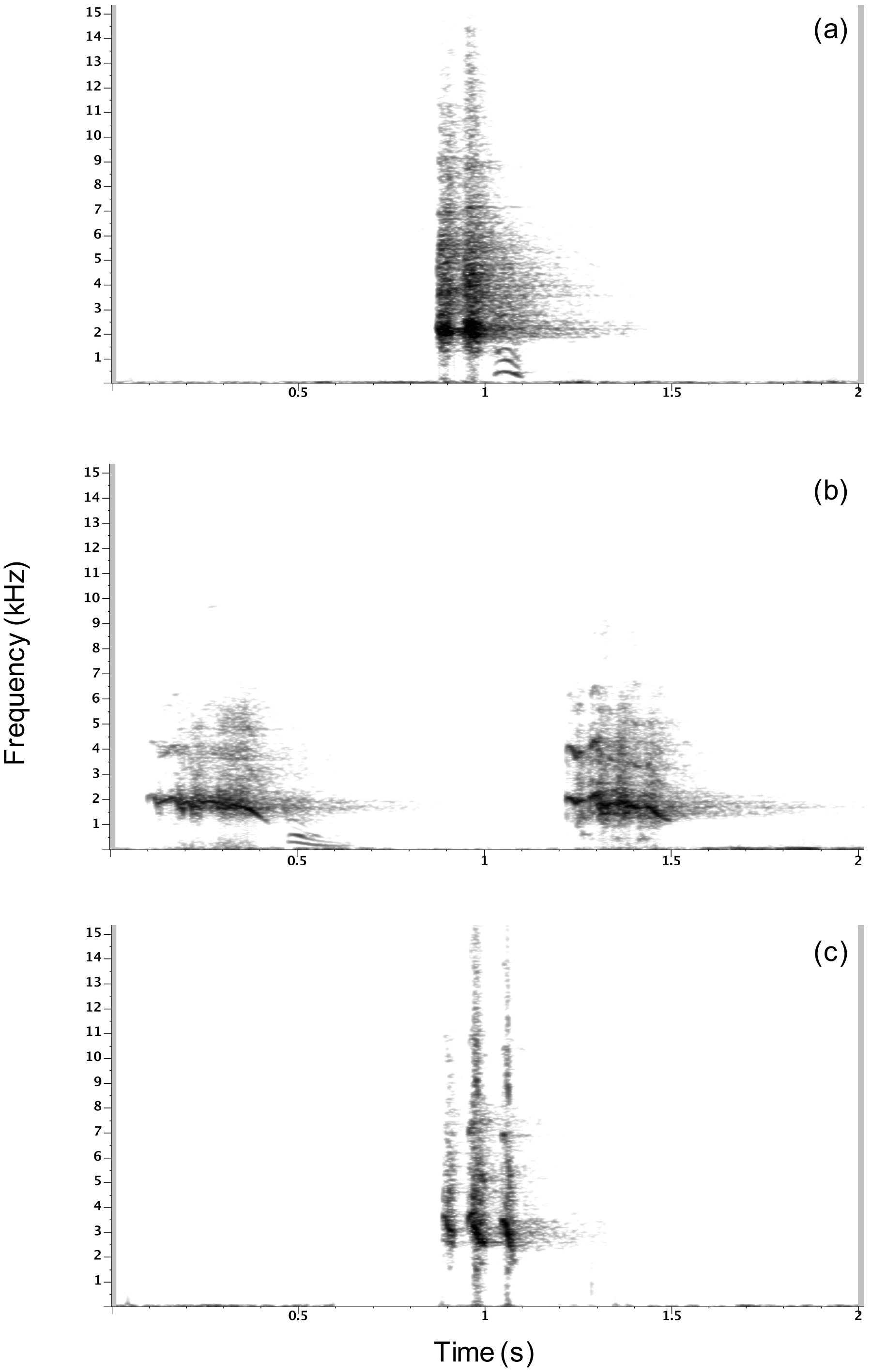

Figure S2.1 Representative samples of conspecific stimuli: Sooty mangabey alarm calls produce in response to (a) leopards, (b) eagles and (c) snakes. Spectrograms were made using Raven and the following settings: 1024 FFT, Hamming window, 75% overlap, 22.05 kHz sampling frequency.

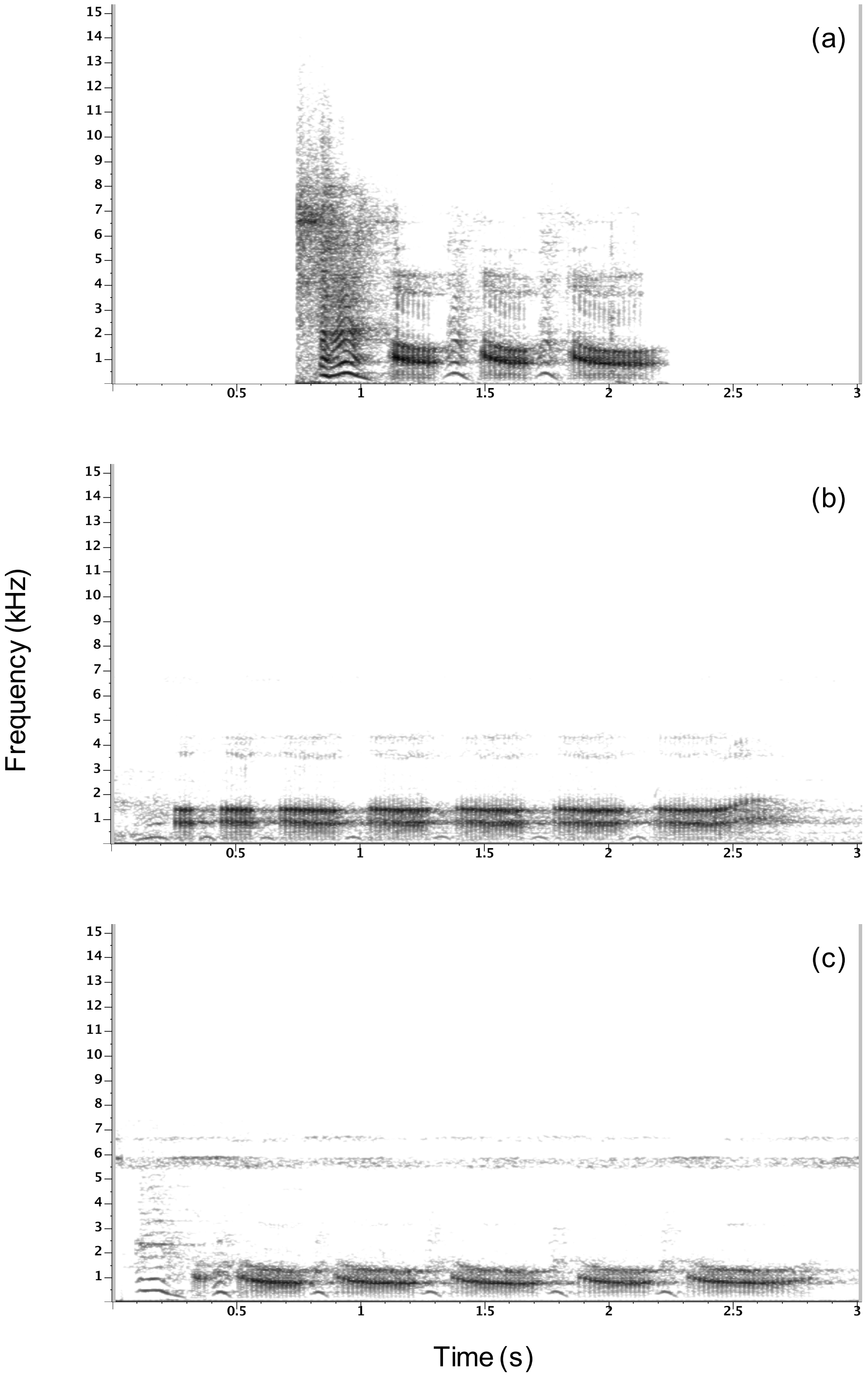

Figure S2.2 Representative samples of heterospecific stimuli: male Diana monkey loud alarm calls produce in response to (a) leopards, (b) eagles and (c) falling trees. Spectrograms were made using Raven and the following settings: 1024 FFT, Hamming window, 75% overlap, 22.05 kHz sampling frequency.

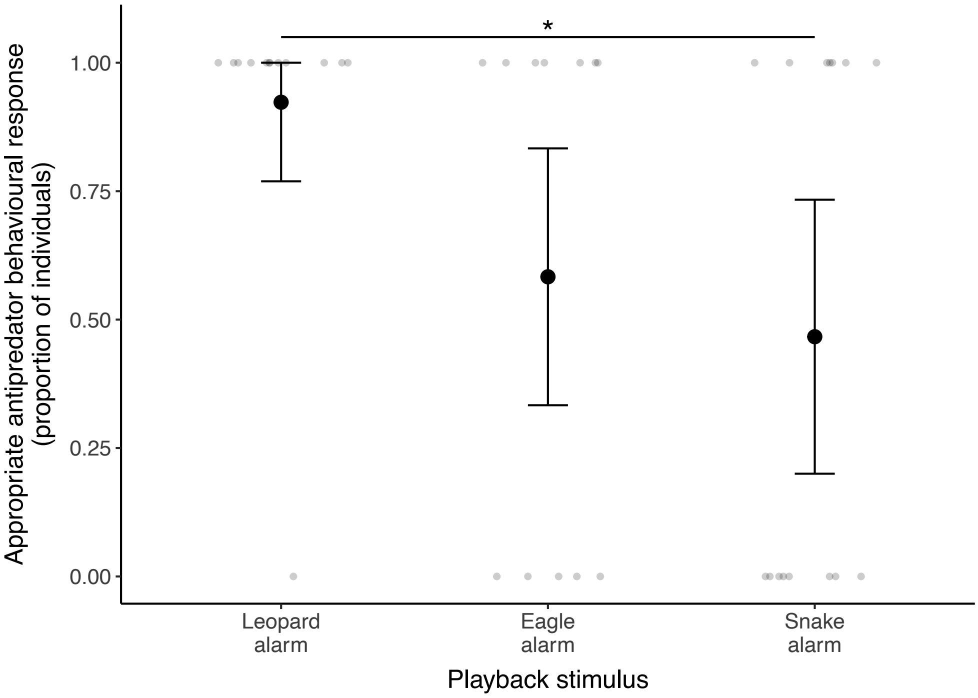

Figure S2.3 Responses to conspecific alarm calls: Proportion of individuals that showed appropriate specific antipredator behavioural responses to conspecific alarm call playbacks. Grey dots indicate individual values for each subjects' response. Post hoc pairwise comparisons: * *P*<0.05.

Table S2.1 Number of trials of the different playback conditions for each age class.

Conspecific trials

Age class	Adults	Old juveniles	Young juveniles
(number of subjects)	(N=10)	(N=11)	(N=10)
Playback stimulus	Number of trials		
Leopard alarm	4	7	6
Eagle alarm	6	5	5
Snake alarm	5	6	5

Heterospecific trials

Age class	Adults	Old juveniles	Young juveniles
	(N=15)	(N=13)	(N=11)
Playback stimulus	Number of trials		
Leopard alarm	5	6	6
Eagle alarm	8	8	7
Tree alarm	6	9	8

Sooty mangabey and Diana monkey alarm calls rates.

To carry out our experiments with a frequency no higher than the natural one, from August to October 2019 (N=47 days), we took *ad libitum* data during all-day samplings on the natural rate of sooty mangabeys' exposure to their own and Diana monkey different alarm call types. After an alarm call was registered, all following calls referring to the same threat were considered as part as one calling event and were not considered independent. We considered new calling events to occur only if no other predator-related vocalization was emitted by any primate species during the previous hour. JL and two field assistants (PK and LB) took the data with a perfect interrater reliability of Cohen's kappa=1 for calling events classification (Table S2.1).

Table S2.2 Natural occurrences of alarm calling events of sooty mangabeys (conspecifics) and Diana monkeys (heterospecifics).

	Alarm Call Type		
Conspecific alarm calls	Leopard	Eagle	Snake
Alarm calling events	7	60	19
Calling events/week (±SE)	1.04 (0.06)	8.94 (0.19)	2.83 (0.07)
Heterospecific alarm calls	Leopard	Eagle	Falling tree
Alarm calling events	4	72	49
Calling events/week (±SE)	0.6 (0.04)	10.72 (0.21)	7.3 (0.2)

Chapter 3: Acquisition of predator knowledge in sooty mangabeys

Julián León[1, 2, *], Fredy Quintero[1, 2] and Klaus Zuberbühler[1, 2, 3]

[1]Institute of Biology, University of Neuchâtel, 2000 Neuchâtel, Switzerland.

[2]Taï Monkey Project, Centre Suisse de Recherches Scientifiques, 01 BP1303 Abidjan 01, Cote d'Ivoire.

[3]School of Psychology and Neuroscience, University of St. Andrews, KY16 9JP Saint Andrews, Scotland (UK).

(Manuscript under review in Animal Behaviour)

3.1 Abstract

How do primates learn to communicate? An influential, but largely untested model proposes that primates go through a pruning process, guided by social learning, during which they increasingly restrict alarm calling from initially broad ranges of animals to few dangerous predators. To test this model, we conducted an experiment with free-ranging sooty mangabeys (*Cercocebus atys*) in which we systematically exposed different age groups to models of dangerous vipers and non-venomous colubrid snakes. We found that young juveniles perceived all snakes as dangerous and indiscriminately alarm called, although they had the longest response latencies. In contrast, adults showed antipredator behaviours faster to vipers than colubrids but never alarm called to the latter, unlike juveniles. Finally, all young and some older juveniles engaged in social referencing – gazing at others to obtain information from them for assessing the situation and guiding their own behaviour –, suggesting that social learning mostly occurred during the first two years of life. Our study provides a systematic, empirical demonstration that predator learning in non-human primates starts with over-generalisation followed by subsequent refinement via social learning.

3.2 Keywords:

Snake recognition, Vocal communication, Alarm calls, Predation, Learning

3.3 Introduction

Most animals share their habitats with other species that can be dangerous to them and require specific anti-predator responses, often accompanied by acoustically distinct predator-specific alarm calls, and primates are no exception (Cäsar & Zuberbühler, 2012; Fichtel, 2020; Fischer, 2020; Zuberbühler, 2009). Detecting and recognizing predators early is critical for effective anti-predator responses, including appropriate alarm calling, but how do young individuals learn to recognize their predators? Predation triggers some of the most basic interactions between organisms and is often considered a major force of natural selection (Abrams, 2001). As predation risk varies in time and space, it is unsurprising that in many species' anti-predator behaviour appears to result from a combination of rigid species-specific and flexible learned responses (reviewed in Edwards et al., 2021; Griffin, 2004; Kelley & Magurran, 2003; Mery & Burns, 2010).

Research has shown some degree of hardwired recognition and responses to predators for a diverse range of taxa, including invertebrates (Dalesman et al., 2006), fish (Zanuzzo et al., 2019), amphibians (Epp & Gabor, 2008), reptiles (Baxter-Gilbert et al., 2018), birds (Dessborn et al., 2012; Göth, 2001) and rodents (Apfelbach et al., 2005). For primates, there is experimental evidence for seemingly hardwired responses towards leopards (Schel & Zuberbühler, 2009) and snakes (Barros et al., 2002; Cook & Mineka, 1990; Weiss et al., 2015). Nonetheless, if antipredator responses are fully hardwired, it is not clear what kind of feedback might encourage novel signal-context associations (e.g., novel predators). A second way to acquire competence in antipredator behaviour is through learning, for example via trial-and-error or other forms of conditioning (Pika et al., 2003). This can be very rapid, as demonstrated in adult West African green monkeys exposed repeatedly to an abnormal threat, a remotely operated drone (Wegdell et al., 2019). Subject rapidly learned to avoid the drone, presumably building on pre-existing knowledge from natural encounters with raptors.

Generally, however, predation events are infrequent, fast and unpredictable, which poses the question of how inexperienced individuals can learn to avoid predators if there are no good learning opportunities and if eventual mistakes are extremely dangerous. One way by which group-living animals can overcome this predicament is by rapid social learning (for a review of social learning about predators by fish, birds, eutherian mammals and marsupials see Griffin, 2004), a process by which naive individuals learn from interacting with more experienced group members (Deshpande et al., 2022; Galef & Laland, 2005; Heyes & Galef Jr, 1996; León, Thiriau, Bodin, et al., 2022). This is especially beneficial for young individuals, which are often especially vulnerable to predators due to small body size, poor motor skills and inexperience (Curio, 1976; Genovart et al., 2010; Janson & van Schaik, 1993). Learning from more experienced individuals is adaptive because it spares inexperienced individuals from the expensive (and potentially lethal) consequences of learning by trial-and-error.

The bulk of social learning studies, and the theories that have emerged from them, have focused on mechanical problem-solving, typically how chimpanzees learn to open complex puzzle boxes that contain food and require sequences of manipulations, which can be learned most efficiently by observing others (Horner & Whiten, 2005). A much less studied, but arguably equally important form of social learning is by observing how others react to unfamiliar objects or events in the environment. This process of actively seeking information socially and using it to evaluate novel objects and events in order to guide responses is termed 'social referencing' (Feinman et al., 1992; Klinnert et al., 1983). Social referencing is especially important for infants and juveniles and is has the following features: (a) referential glances between another individual and the stimulus and (b) behavioural changes in response to the information received (Russell et al., 1997). Beside humans, social referencing has been studied mainly in other primates (chimpanzees: Evans & Tomasello, 1986; Itakura, 1995; Russell et al., 1997; vervet monkeys: Mohr et al., 2023; capuchin monkeys: Morimoto & Fujita, 2012; Barbary macaques: Roberts et al., 2008; orang-utans: Schuppli et al., 2016), domesticated animals (dogs: Merola et al., 2012; cats: Merola et al., 2015; horses: Schrimpf et al., 2020) and bats (Hall et al., 2011).

Here, we were interested in how terrestrial forest monkeys, sooty mangabeys, *Cercocebus atys atys,* rely on social learning to acquire knowledge about novel predators encountered naturally. Pioneering research on vervet monkeys suggested that young primates are born with some degree of predisposition towards discriminating between broad predator classes and then, as they grow up, go through a cognitive pruning process during which predator categories and corresponding alarm call behaviour become increasingly refined, guided by social learning from other group members (Seyfarth & Cheney, 1980, 1986). Vervets monkeys produce acoustically distinct alarm calls in response to leopards, eagles and snakes (Price et al., 2015). Field observations suggested that, around three months of age, vervet infants begin to give their first alarm calls, but often in incorrect ways until they are older than two years, although never in completely arbitrary ways. For example, leopard alarms are produced to a wide range of terrestrial mammals, eagle alarms mainly to airborne objects and snake alarms mainly to snake-shaped objects (e.g., long shaking vine) and also other reptiles, i.e., tortoises (Seyfarth & Cheney, 1980). But as the infants age, they become more selective and finally restrict their alarm calling and anti-predator behaviour to a small number of dangerous local predators. This process is guided by social learning insofar as infants were more likely to respond to alarm calls appropriately if they first looked at adults (Seyfarth & Cheney, 1986).

Seyfarth & Cheney's maturational model has been very influential in developmental theories of animal communication and has become somewhat of the default theory of primate vocal development, despite the fact that it has hardly been tested empirically in natural settings (for related research see Meno et al., 2013a, 2013b). This lack of evidence is problematic because, in all likelihood, communication and cognition have coevolved and close to nothing is known about the corresponding developmental patterns. In particular, it is unclear whether ontogenetic changes in primate alarm call behaviour are governed by underlying changes in conceptual organisation, i.e., an increase in an individual's knowledge of the local fauna (but see Gursky, 2003; León, Thiriau, Crockford, et al., 2022; Perry et al., 2003). Also unclear is how effective learning is, particularly whether competence develops rapidly with one or few key experiences (Brodbeck et al., 1992) or gradually over multiple trials, as predicted by standard animal learning theory (Rescorla & Wagner, 1972). There is recent experimental evidence that, in the predation context, monkeys can acquire predator knowledge very rapidly, requiring only one or a small number of experiences (Deshpande et al., 2022; León, Thiriau, Bodin, et al., 2022; Wegdell et al., 2019). Other learning appears to be more gradual (Castro & Snowdon, 2000; Fichtel, 2008; Fischer et al., 2000; McCowan et al., 2001; Ramakrishnan & Coss, 2000), although it is often unknown what sorts of experiences individuals have had throughout their early lives.

For most primate species, the main groups of predators consist of carnivores, raptors, snakes and human hunting (Isbell, 1994; Urbani, 2017). In the evolutionary history of the primate lineage, reptiles were most likely amongst the oldest predators, suggesting that the primate cognitive system has been adapted for snakes before other predator categories (Öhman, 2009).

Snakes are often cryptically hidden in vegetation, so that effective defence requires adaptations in the visual system (‘snake detection theory’: Isbell, 2006, 2009). It comes as no surprise that primates, including humans, are especially skilled at detecting snakes, even under difficult visual conditions (Kawai & He, 2016; Kawai & Koda, 2016; Ohman & Mineka, 2001; Shibasaki & Kawai, 2009), with further evidence of efficient processing, attentional prioritization and rapid fear acquisition in response to snakes (Öhman, 2009).

Although no species of snakes specializes in hunting primates, some do occasionally predate on them (Headland & Greene, 2011) and lethal accidents are likely to happen. Since most snakes hunt by stealth and ambush (Greene, 1997), their dangerousness decreases drastically once their location is known and they can be monitored. Interestingly, during interactions with detected snakes, primates generally remain at safe distances and spend considerable time monitoring and sometimes mobbing the snake. Some species have evolved specific alarm calls to snakes but calling is usually highly selective and restricted to a few dangerous species (Ouattara et al., 2009; Ramakrishnan et al., 2005). In chimpanzees and bonobos (and probably other species), alarm calls to snakes inform other group members about the snake’s location and usually cause careful approach and startling reduction, indicating less surprise about the presence of the snake (Crockford et al., 2012; Girard-Buttoz et al., 2020; Schel et al., 2013). Such combined responses of prolonged monitoring, alarm calling and low predation risk provide an ideal learning environment for young primates to refine their detection, recognition and response skills (Curio et al., 1978).

Here, we tested the core feature of Seyfarth & Cheney's model - the notion of cognitive refinement - with a field experimental study on snake anti-predator behaviour in sooty mangabeys. In the Taï Forest, Côte d’Ivoire, mangabeys are hunted by leopards (*Panthera pardus*) (Zuberbühler & Jenny, 2002), crowned eagles (*Stephanoaetus coronatus*) (Shultz & Thomsett, 2007) and, to a lesser extent, chimpanzees (*Pan troglodytes*) (Boesch & Boesch-Achermann, 2000). In addition, mangabeys sporadically come into contact with large pythons (*Python regius*) that also prey on smaller primates. Moreover, terrestrial mammals are generally vulnerable to snakebites (Supplementary Video 1), notably by vipers (Penner et al., 2008). Two highly venomous species are common in the Taï Forest, Gaboon (*Bitis gabonica*) and rhinoceros vipers (*Bitis nasicornis*), which are frequently encountered by mangabeys, two to three times per week (León, Thiriau, Bodin, et al., 2022; Range & Fischer, 2004). Importantly, although there are more than 50 different snake species in the Taï Forest (Ernst

& Rödel, 2002; Rödel & Mahsberg, 2000), only pythons and the two vipers normally elicit anti-predator-specific responses and alarm calls from adult mangabeys. All three snakes are ambush hunters, which do not pursue their prey and are no longer dangerous once discovered and monitored at a safe distance (Crockford et al., 2015). Once mangabeys detect a viper, they typically jump aside or show other types of startle responses. Then, they often stand bipedally and cautiously approach and scan the area around the snake and produce snake-specific alarm calls that attract other individuals (Penner et al., 2008; Range & Fischer, 2004) (Fig. A1; Supplementary Video 2).

During viper encounters, mangabeys show some evidence for audience awareness as they are more likely to alarm call when fewer individuals are present, if they have not heard other alarm calls before, and if socially important individuals are near (Mielke et al., 2019; Quintero et al., 2022). Predator encounters, in other words, evoke another psychological process that can be cognitively demanding. Although audience effects appear to be ubiquitous in group-living vertebrates and even present in partially solitary animals (fish: Doutrelant et al., 2001; birds: Karakashian et al., 1988; Marler et al., 1986; Meaux et al., 2023; Vignal et al., 2004; Zaccaroni et al., 2013; mammals: Dunlop, 2016; le Roux et al., 2008; Soldati et al., 2022; Townsend et al., 2012), it is often unclear what aspects of the audience is represented. Audience effects are present when signal production is not only determined by the triggering stimulus (e.g., predator or food) but moderated by the signaller 's social environment (Zuberbühler, 2008). Evidence is largely in terms of changes in vocal rates (screams: Fedurek et al., 2015; Slocombe & Zuberbühler, 2007; food calls: Caine et al., 1995; Di Bitetti, 2005; Kalan & Boesch, 2015; Pollick et al., 2005; mating calls: Townsend & Zuberbuhler, 2009 or alarm calls: Crockford et al., 2012; Girard-Buttoz et al., 2020; Wich & Sterck, 2003) but also present in gestural signalling (Cartmill & Byrne, 2007; Hobaiter et al., 2017).

Here, we examined how mangabeys from different age groups reacted to models of dangerous (vipers) and non-venomous (colubrids) snakes (Figure 3.1). Following the Seyfarth & Cheney’s refinement model, we predicted that young individuals would be less attentive and less able than adults to recognize viper models as predators and generally less proficient in distinguishing between dangerous and non- dangerous snakes. We also predicted that, relative to adults, young individuals would engage in more social referencing and be more indiscriminate in both alarm calling and anti-predator behaviour. Finally, we predicted age-related gradual changes, with viper models being increasingly more effective in triggering anti-predator behaviour and alarm calling than colubrid snake models with increasing age.

Figure 3.1 Snake models. Illustrations of two viper models (top) and two colubrid models (bottom). Viper models were custom-made using wood, acrylic paint and varnish, while colubrid models were prefabricated and made of rubber.

3.4 Methods

Study site and subjects

Experiments were conducted with one group of free-ranging sooty mangabeys in Taï National Park, Côte d’Ivoire. The study group was fully habituated to human observers, with a home range of a 2 km^2 core area, shared with groups of other monkey species studied since 1991, as part of a long-term research project, the Taï Monkey Project (TMP) (McGraw & Zuberbühler, 2007). Experiments were conducted in three blocks: N=8 trials from August 2013 to July 2014, N=7 trials from January to September 2015, and N=20 trials from August 2019 to March 2020 (main study period). To balance the number of trials, Auriane Le Floch provided one additional trial conducted on August 2022. During the main study period, the group was around 87 individuals, including 30 adults (23 females, 7 males; >5 years old), 12 subadults (6 females, 6 males; 4–5 years old), 17 old juveniles (9 females, 8 males; 3–4 years old), 22 young juveniles (10 females, 12 males; 1–2 years old) and 6 infants (2 females, 4 males; <1 year old). Snake models were presented to young and old juveniles and adults. Infants were not used for experiments due to the difficulty to present the model to the infant without the mother seeing it first.

Presentation of snake models

We conducted N=6 trials per age group and model type (viper or colubrid) for a total of N=36 trials distributed over an equal number of individuals (N=12 young juveniles; N=12 old juveniles; N=12 adults). JL conducted N=22 trials (N=4; viper model trials; N=18 colubrid model trials), FQ conducted N=13 viper model trials; Auriane Le Floch conducted N=1 viper model trial. We used eight different viper models, crafted from wood, acrylic paint and varnish, and two rubber prefabricated colubrid models (Figure 3.1). Models resembled real snakes, positioned with realistic postures to match real-life encounters in the wild. For logistical reasons, two of the viper models had an elongated position, which is a relatively rare posture for a viper in the wild. Nevertheless, subjects did not show any type of bias to these elongated viper models.

Each trial consisted of a snake model presentation to a focal subject. For each trial, we strategically placed the model on the anticipated travel path of the focal subject, in the leaf litter behind a log or bush, prior to the subject's arrival. Two experimenters conducted each trial: the first one placed the model, while the second continuously filmed the focal animal using Panasonic SDR-26 and HC-V500 video cameras, ~30 s before, during and ~30 s after the detection of the model. We ended a trial by removing the model after the subject had left the area and no other group member was within visual range. Trials were conducted by locating individuals suitable as subjects, provided they were alone or in small parties away from other group members, usually in the periphery of the group, assuring that they would be the first individual in the group to see the model. Finally, trials were conducted only if no other predator-related event had occurred during the previous hour.

To avoid habituation and minimize disruption, we conducted only one trial with a viper model and one trial with a colubrid model per day. We did not present snake models more than once every three days and usually only twice per week, which was within the monkeys' natural encounter frequencies with Gaboon and rhinoceros vipers (León, Thiriau, Bodin, et al., 2022). In total, snake model encounters ranged between one and three trials per individual. During trials, we were careful not use snake models that the subject had previously seen while in the audience of previous trials.

For each trial, we noted the identity, age and behavioural response of the subject, the type of model and the audience size. As soon as the subject detected the model, we scored the subject's response and determined the composition of the audience. Audience size was defined as the number of individuals within a 10 m range of the subject between the time of model detection and 30 s afterwards, as this radius and time window, respectively, should capture nearby group members who are at potential risk but also ignorant of the snake.

Coding behavioural responses

We used a Solomon coder (https://solomoncoder.com) to analyse video recordings on a frame-by-frame basis (25 frames s^{-1}) during the first 30 s after model detection. JL extracted eight behavioural responses from each video (see Table S3.1 for detailed definitions). Behavioural variables were selected to assess attentiveness (how much attention was showed towards the snake model), proficiency in snake recognition (how skilled was an individual to detect and classify a snake), cautious behaviour (the degree of alertness in a potentially dangerous situation), social referencing (the seeking of information from others to guide the subject reaction towards the snake model), and alarm calling behaviour. We measured attentiveness by the number of looks, body orientations and looking duration towards the model. Proficiency in snake recognition was measured by the latency from snake model detection to the first occurrence of the onset of any of the extracted behavioural responses. We measured cautious behaviour by the difference in the number of pauses 30 s before and after a model was detected. Social referencing was measured by counting the number of scans and scanning duration toward other individuals after the detection of a model. A scan was defined as a change in the head position while looking around to left or right, up or down outside a 45° arc of the snake model, typically gazing towards other individuals. Only abrupt changes in direction were noted, indicated by a prior cessation in head movement. Finally, alarm calling behaviour was measured by assessing whether or not focal subjects produced snake-specific alarm calls after spotting the models. Due to the difference between the number of alarm calls given as response to the two model types was too great (viper 59 snake alarm calls in 8 trials vs colubrid 4 snake alarm calls in 4 trials), we chose not to analyse the total number of alarm calls. To estimate inter-observer reliability, a second observer (Sasha Cárdenas) blind-coded (18/36) 50% of the trials, resulting in excellent interrater reliability (Interrater reliability measures: Intraclass Correlation Coefficient range: ICC=0.79–1.00; Cohen's kappa for Alarm calling $K = 1$; see Table S3.2 for each behavioural response ICC).

Statistical analysis

To investigate which factors had an impact on snake recognition and anti-predator behaviours towards snakes in mangabeys, we used a series of Linear and Generalized Linear Models (Bolker et al., 2009) using R version 4.0.3 (R Core Team, 2020) and the functions 'lm' (for numeric data) and 'glm' (for count data, family = Poisson; for binary data, family = Binomial) of the packages stats and nlme. To reduce multiple testing and redundancy between the behavioural variables, we conducted a factor analysis utilizing the 'factanal' function (also in R stats package). We calculated the number of factors to extract utilizing the 'fspe' function from the fspe package (Haslbeck & van Bork, 2022). We then chose the variable with the strongest loading from every one of the four coming about factors (Factor 1: Number of scans; Factor 2: Number of pauses; Factor 3: Alarm calling; Factor 4: Latency; Table S3.3). In total, these four factors accounted for almost 75% of the variance in the data (Number of scans: 27.8%, Number of pauses: 20.3%, Alarm calling: 17.0%, Latency: 9.5%). We tested these four variables as response variables in four separate models ('lm': Latency; 'glm': Number of scans, Number of pauses and Alarm calling). To achieve a normal distribution in the latency model, we calculated the square-root of the latency.

Initially, we observed standard errors particularly high for the Alarm calling model (GLM), indicating complete separation or a convergence issue (Hauck-Donner phenomenon). To solve the convergence problem and fit the model, we utilized the 'brglmFit' function from the brglm2 package (Kosmidis, 2023), which fits GLMs using implicit and explicit bias reduction methods (Kosmidis, 2014). We included focal age (i.e., young juvenile, old juvenile, adult) and the type of model (i.e., viper or colubrid) as fixed factors and test predictors. To test the significance of the fixed factors and their relations, we used the 'Anova' function (car package) in each model to perform a type III or II ANOVA Wald Chi-Square Tests, depending on whether or not there was a significant interaction in the model. Originally, we included the interaction involving the two fixed factors into the full models, to detect if the behavioural response towards one particular snake model changed with age. We then removed not significant interactions to simplify the models (Engqvist, 2005). Moreover, to check whether 'Audience size' influenced subjects' behavioural responses, we re-ran all the analyses including this variable as control predictor. Since results were robust, we decided not to include this variable in the models to avoid overparameterization. Finally, for each selected reduced model, we checked for overdispersion and verified homogeneity of variance.

When post hoc analyses were necessary, we conducted pairwise post hoc comparisons between levels of statistically significant control predictors by computing estimated marginal means for each model, using the 'emmeans' function (emmeans package). For these comparisons, we included a Tukey honest significant difference adjustment to account for running multiple tests on the same data of the Linear Model (Feise, 2002). Finally, to count for multiple testing of the same behavioural response, we determined critical P values following the Benjamini–Hochberg procedure: $P^* = (i/m)\alpha$, with $i = i$th test, $m =$ total number of tests and $\alpha =$ significance level.

3.5 Results

General patterns

We were able to observe subjects' responses to the snake models for at least 30s in all trials, N=36 (Tables S3.1 & S3.2). A subject was defined as the first individual to detect the snake model in a given trial. After detecting the model, subjects often grabbed leaves and other vegetal material near the snake to smell them, as if trying to gather additional information through olfactory cues. To reduce the need for multiple testing and redundancy between correlated behavioural variables (Number of looks, Number of body orientations, Looking duration, Latency, Number of pauses, Number of scans, Scanning duration and Alarm calling; Table S3.1), we conducted a factor analysis and then tested the resulting factors in separate LM and GLM models. Factor analyses do not reduce the original number of variables (unlike principal component analyses) but allow the identification of key variables (factors) that are causing variation in the observed data. The variables with the strongest loadings were: Latency, Number of pauses, Alarm calling and Number of scans (Table S3.3). In all four models, at least one test predictor showed a significant influence on the response variable (Table S3.4).

Development of predator knowledge

We first tested latencies to reaction (*latency* model), as a basic measure of predator knowledge, and found a significant interaction between subject age and model type (latency LM, $\chi^2_2 = 1$, $P = 0.024$). Adults reacted faster to the viper than colubrid models (post hoc tests: $t = 4.91$, $P < 0.001$; latency mean ± SE: vipers 0.43 s ± 0.08; colubrids 2.70 s ± 0.38). Juveniles also reacted faster to vipers than colubrids but differences were not statically significant (post hoc tests: old juveniles: $t = 0.87$, $P = 0.95$; latency mean ± SE: vipers:1.60 s ± 0.38; colubrids 2.13 s ± 0.53; young juveniles: $t = 2.19$, $P = 0.27$; latency mean ± SE: vipers 1.73 s ± 0.30; colubrids 3.1 s ± 0.51; Figure 3.2; Tables S3.4a & S3.5). Moreover, adults reacted faster to vipers than juveniles to colubrids (post hoc tests: latencies to reaction, adults to vipers vs old juveniles to colubrids: $t = 3.74$, $P = 0.009$; adults to vipers vs young juveniles to colubrids: $t = 5.44$, $P < 0.001$; Figure 3.2; Tables S3.4a & S3.5) or to vipers (post hoc tests: latencies to reaction to vipers, adults vs young juveniles: $t = –3.25$, $P = 0.03$; Figure 3.2; Tables S3.4a & S3.5).

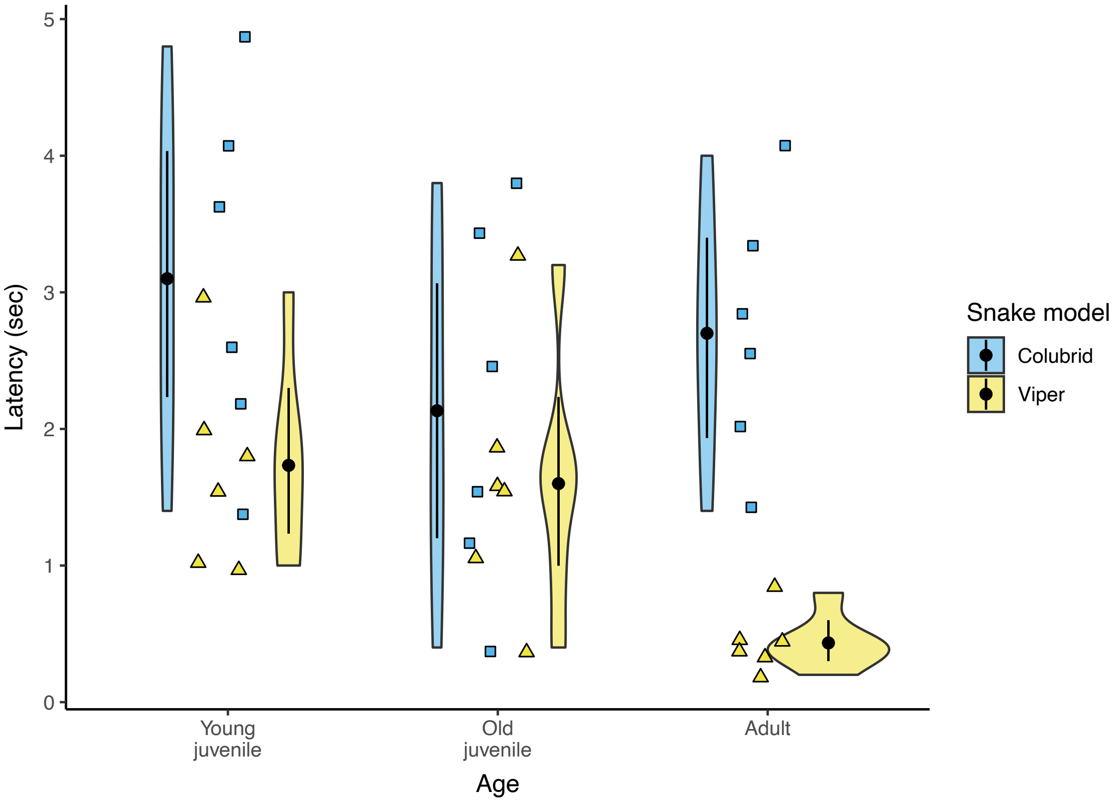

Figure 3.2 Development of predator knowledge: latency to reaction. Violin plots illustrating the kernel density distribution of the latency to exhibit a behavioural response during the first 30 s after the detection of the snake model, depending on age. Embedded black dots and vertical lines indicate means and 95% confidence intervals from model estimation, respectively. Blue squares indicate individual values per subject for the colubrid snake model condition, yellow triangles indicate values per subject for the viper snake model condition. Young and old juvenile and adult N=12 each.

As a second measure of snake knowledge, we tested if viper models elicited more cautious behaviour – cautious behaviour was measured by the number of travel pauses taken– than colubrid models across age groups (*number of pauses* model). Partially supporting our prediction, subjects of all age groups showed a tendency to pause more and move more cautiously after encountering viper models compared with colubrid models. (number of pauses GLM, $\chi^2_2 = 3.54$, $P = 0.059$; number of pauses mean ± SE: vipers 3.05 ± 0.23 vs colubrids 2.05 ± 0.23; Figure 3.3; Tables S3.4b & S3.5; Supplementary Videos 3.3 & 3.4). However, contrary to our predictions and despite the fact that old juveniles paused on average more than young juveniles in response to viper models, the differences between the number of pauses elicited by viper and colubrid models were the same in both juvenile age groups (young juveniles, number of pauses mean ± SE: vipers 2.83 ± 0.47 vs colubrids 2 ± 0.44; old juveniles, number of pauses mean ± SE: vipers: 3.16 ± 0.47 vs colubrids 2.33 ± 0.33; Figure 3.3; Table S3.5). Nevertheless, this difference in cautious behaviour between viper and colubrid models increased by 62% in adults (number of pauses mean ± SE: vipers 3.16 ± 0.3 vs colubrids 1.83 ± 0.47; Figure 3.3; Table S3.5).

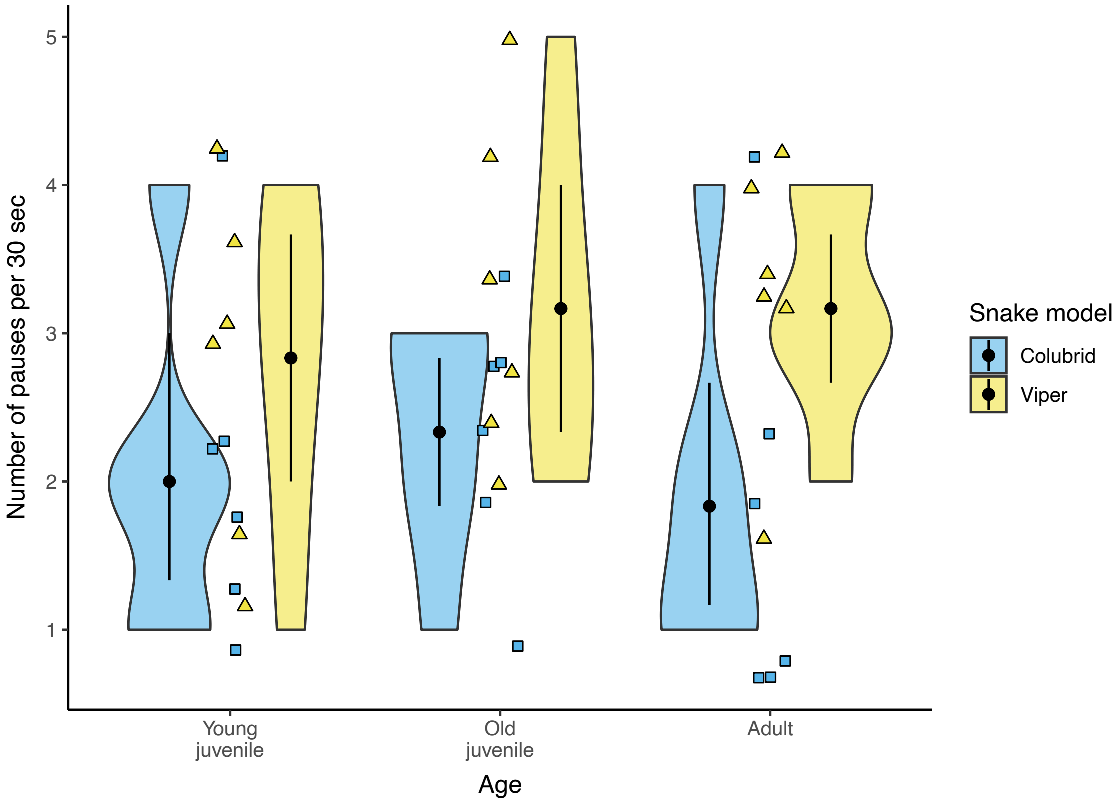

Figure 3.3 Development of predator knowledge: cautious behaviour. Violin plots illustrating the kernel density distribution of the number of pauses during first 30 s after the detection of the snake model, depending on age. Embedded black dots and vertical lines indicate means and 95% confidence intervals from model estimation, respectively. Blue squares indicate individual values per subject for the colubrid snake model condition, yellow triangles indicate values per subject for the viper snake model condition. Young and old juvenile and adult N=12 each.

Development of alarm calling

Subjects alarm called in 12 of 36 trials (33.3%; 4 of 12 colubrid model trials and 8 of 12 viper model trials). Crucially, no adult alarm called to the harmless colubrid model, while 2 of 6 (33.3%) young and 2 of 6 (33.3%) old juveniles alarm called. In contrast, 5 of 6 (83.3%) adults alarm called to the viper models, whereas again only 2 of 6 (33.3%) old juveniles and 1 of 6 (16.7%) young juveniles alarm called (Supplementary Material). In the *Alarm calling* model, we found a significant interaction between subjects' age and model type (alarm calling GLM, $\chi^2_2 = 8.16$, $P = 0.016$). Partially supporting our prediction, post hoc tests showed that young juveniles had a tendency to produce alarm calls in fewer viper model trials than adults (number of young juveniles vs adults who gave alarm calls during viper model trials: $z = 1.84$, $P = 0.06$; Figure 3.4; Tables S3.4c & S3.5; Supplementary Video 3.3). On average, callers gave 4.91 calls per encounter during viper model trials, but when counting only viper trials on adults the average number of calls per individual per trial increased to 7.66 calls (an increment of 64%). Moreover, adults produced 2.7 more alarm calls than juveniles (46 calls in 5 trials vs 17 calls in 7). Though, they restricted their alarm calls to viper models (number of adults who gave alarm calls during viper vs colubrid trials: $z = -2.06$, $P = 0.03$; average number of calls emitted by adults per viper encounter: 7.66; range: 0–13 calls; Figure 3.4; Tables S3.4c & S3.5, Supplementary Videos 3.3 & 3.4), while young juveniles alarm called evenly to colubrid (2 calls in 2 trials) and viper models (2 calls in 1 trial). Similarly, old juveniles emitted alarm calls in two trials for each type of snake model, but when occurred, the numbers of calls elicited by viper models variated considerably (1 vs 10 calls).

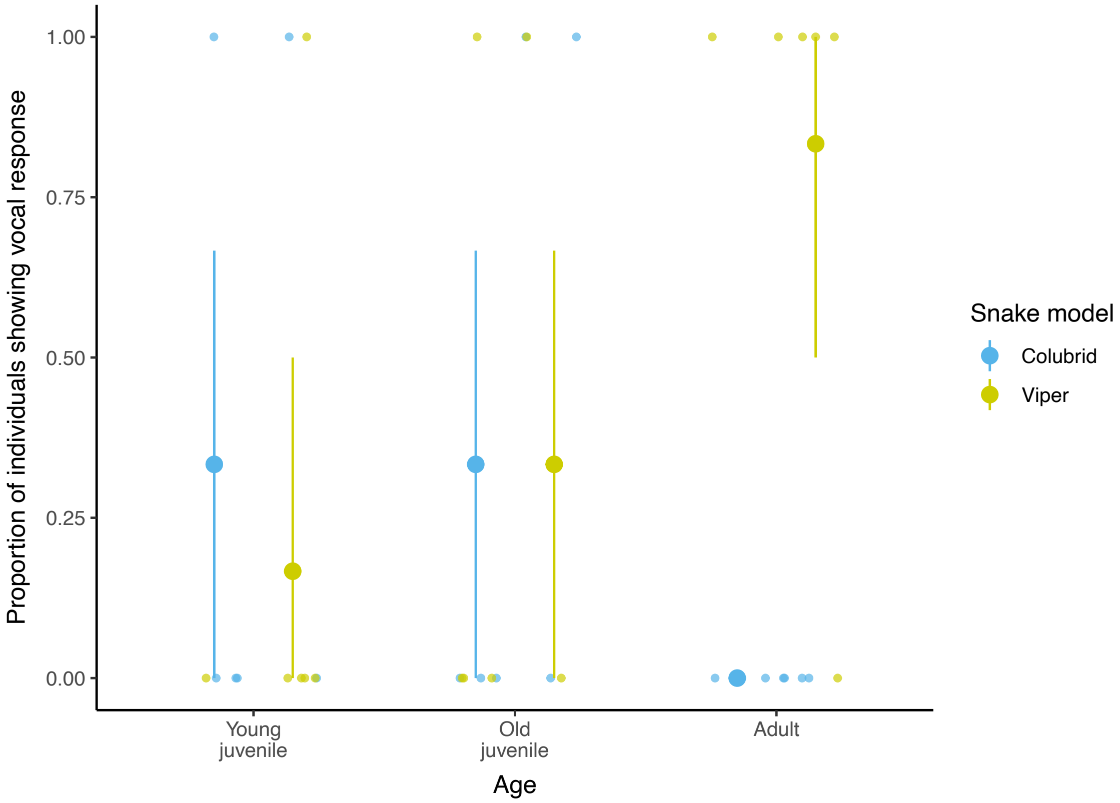

Figure 3.4 Development of alarm calling. Proportion of subjects that showed vocal responses during the first 30 s after the detection of the snake model, depending on age. Large dots indicate mean and vertical lines indicate a 95% confidence interval from model estimation, and small dots indicate individual values per subject per condition. Colour key, blue: colubrid snake model condition, yellow: viper snake model condition. Young and old juvenile and adult N=12 each.

Every time an individual (regardless of age) produced snake alarm calls, other individuals responded by approaching and looking actively for the snake model. When other group members arrived and detected the model, they cautiously approached further and scanned the surrounding area, and then passively monitored the model from about 1–2 meters, sometimes bipedally and sometimes by sitting on elevated places close by. We did not observe specific snake-directed behaviour (e.g., mobbing behaviour, threat gestures) towards the models. Finally, during both natural snake encounters and trials, young individuals, especially infants, showed particular interest in the conglomeration of mangabeys around the snake location, became more aroused, usually approached the area by climbing low branches around it and stayed around the snake whereabouts longer than older individuals.

Development of social referencing

For social referencing, i.e., number of head scans towards other individuals after the detection of the snake model, we found a significant age effect (χ^2_2 = 6.23, P = 0.04): once young juveniles detected the snake, they searched for and looked at other group members more than adults (number of scans GLM, estimate = 0.62, SE = 0.25, z = 2.4, P = 0.015; number of scans mean ± SE: young juveniles 3.58 ± 0.28 vs adults 1.91 ± 0.52; Figure 3.5; Tables S3.4d & S3.5; Supplementary Videos 3.3 & 3.4).

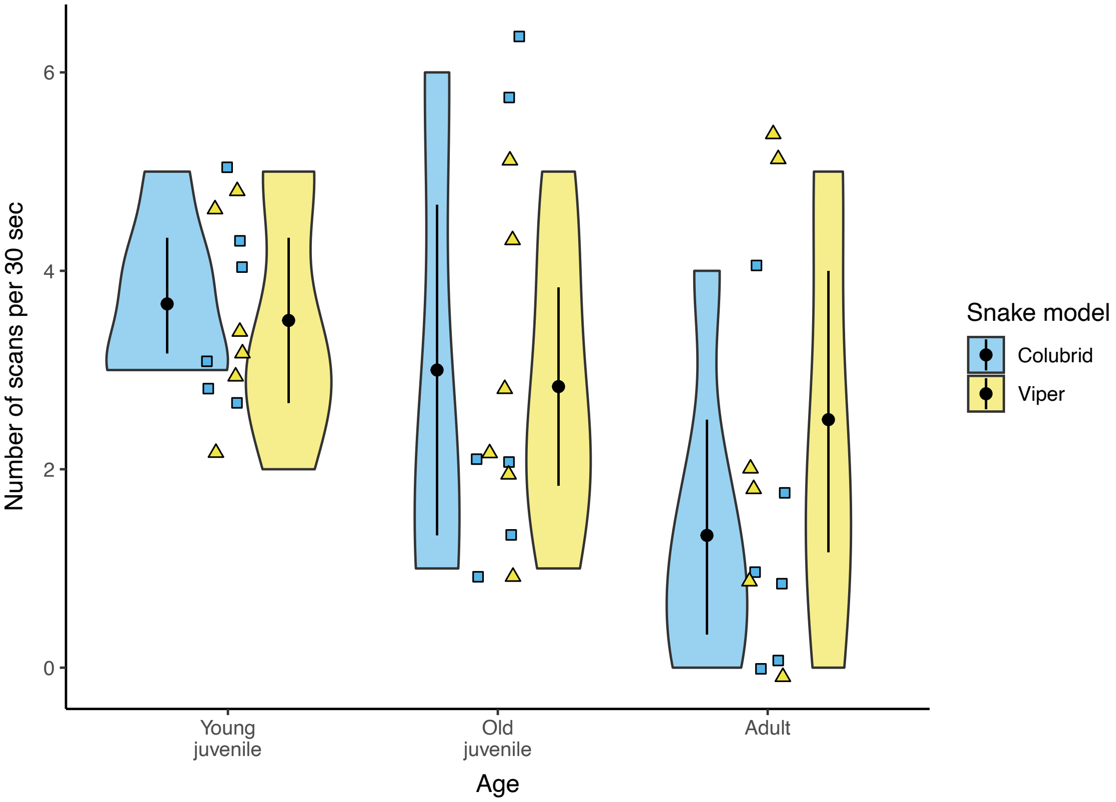

Figure 3.5 Development of social referencing. Violin plots illustrating the kernel density distribution of the number of head scans towards other individuals during first 30 s after the detection of the snake model, depending on age. Embedded black dots and vertical lines indicate means and 95% confidence intervals from model estimation, respectively. Blue squares indicate individual values per subject for the colubrid snake model condition, yellow triangles indicate values per subject for the viper snake model condition. Young and old juvenile and adult N=12 each.

Audience effects

Finally, we also looked at audience effects, since audience size may impact on social learning and social referencing opportunities. We found that audience size did not vary between model conditions (viper models trials: mean ± SE: adults 1.16 ± 0.40 vs old juveniles 1.66 ± 0.56 vs young juveniles 2.16 ± 0.65, range 0–4; colubrid models trials: mean ± SE: adults 1.66 ± 0.42 vs old juveniles 1.66 ± 0.49 vs young juveniles 2 ± 0.44, range 0–3; Supplementary Material). Moreover, when used as control predictor, audience size had no significant influence in any of the statistical models and was therefore excluded from the analyses to avoid overparameterization.

3.6 Discussion

West African forest primates are exposed to dozens of different snake species. Most of them are not dangerous but a small number can cause fatal accidents, and previous research has suggested that primates recognise the truly dangerous species. We investigated the development of this knowledge with an experimental field study on free-ranging sooty mangabeys in the Taï National Park, Côte d'Ivoire. In doing so, we tested an influential model of primate vocal development, the idea that individuals undergo a pruning process of cognitive refinement with corresponding changes in anti-predator and alarm calling behaviour. We tested this learning model by using realistic snake models of highly dangerous vipers and non-venomous colubrids to explore age-related snake recognition and antipredator behaviour. Our results showed that adults showed signs of competence by reacting to viper models faster than juveniles and by only producing alarm calls to the dangerous vipers. However, we also found that - across age groups - viper models elicited more cautious behaviour than colubrid models. When exposed to viper models, all young juveniles and some old juveniles actively engaged in social referencing and they also had longer response latencies, suggesting that they relied on more experienced individuals before deciding how to respond to snakes.

Mangabeys are vulnerable to snakebites by vipers which can cause lethal venom poisoning (León and Quintero, personal observations, Supplementary Video 3.1), which may have caused strong selection pressure (Öhman, 2009). Snake-predator core knowledge, in the form of fast recognition and identification, is essential for preventing accidents, particularly for camouflaged species such as vipers. Despite being harder to detect, vipers models elicited the shortest response latencies in all age groups (twice as fast as to colubrid models). Some studies have shown that naïve primates with no prior experience with snakes exhibit fear responses when presented with snake stimuli (Barros et al., 2002; Cook & Mineka, 1990; Weiss et al., 2015). Therefore, this difference in the latency of response to viper and colubrid models could be seen as part of a strong selection for the evolution of innate viper recognition in mangabeys. However, this disparity was caused by the shorter latency exhibited by adults towards viper models when compared to subjects of all ages who were exposed to colubrid models (Figure 3.2). Additionally, adults also reacted faster than young juveniles when spotting viper models. On the other hand, the fact that even 1–2 years olds moved more cautiously in response to viper than colubrid models suggests that monkeys are prepared to recognise dangerous snake species and that discrimination learning starts early (Mineka, 1992; Olsson & Phelps, 2007). Altogether, these results highlight the importance of experience in the development of snake-predator knowledge in mangabeys. Future studies on infant mangabeys should address the extent to which this difference is explained by the Öhman and Mineka's module of fear (Ohman & Mineka, 2001), where a fearful predisposition towards vipers might have facilitated their rapid and efficient recognition by mangabeys.

Overall, subjects gave 4.9 alarm calls per encounter during viper model trials, similar to what has been reported in a previous study (3.7 calls; Mielke et al., 2019). In line with our predictions, both young and old juveniles (occasionally) alarm called but then to both dangerous and harmless snake models, whereas adults regularly alarm called, but only to dangerous vipers (overall alarm call response rates: young juveniles: 25.0%; old juveniles: 33.3%; adults: 41.7%; N=12 each). In sum, adults not only produced more snake alarm calls but also restricted their calls to viper models. These findings are in line with the idea that subjects go through a pruning process during which they become more selective in their alarm calling behaviour during predator encounters (Seyfarth & Cheney, 1980, 1986). Interestingly, infant vervet monkeys begin to correctly produce alarm calls at around 4–6 months of age, but they do not regularly used them in the appropriate context until subjects are older than 2 years. In contrast, it takes more than 4 years for mangabeys to restrict their snake alarm calls to dangerous snakes. These differences suggest that, independently from eventual innate predisposition, vocal production and usage might develop in species-specific ways, with some species alarm calling from early on and other species refraining from alarm call production until cognitively competent.

Our study is in line with previous research showing that social referencing plays an important role in how inexperienced animals learn to associate their signals with the appropriate referents (Deshpande et al., 2022; León, Thiriau, Crockford, et al., 2022; Seyfarth & Cheney, 1986). In these studies, young primates were more likely to respond appropriately if they first looked at more experienced group members, a form of social referencing (Baldwin & Moses, 1996; Evans & Tomasello, 1986). Additionally, rhesus monkeys that were naive and initially fearless of snakes came to avoid them after observing the aversive response of a more experienced individual towards a snake (Mineka & Cook, 1993). Altogether, these results suggest that the process through which young monkeys acquire predator recognition, avoidance and alarm call knowledge is driven by active social learning.

In the case of mangabey snake-specific anti-predator behaviour, Seyfarth and Cheney's learning model appears to contain at least three distinguishable steps of refinement. First, an over-generalised and quasi-silent acquisition phase, where young individuals are born with general knowledge of predator classes that allows them to classify, via over-generalisation, all snake-like species and objects around them as a snake-type of danger (e.g., lizards, tortoises, crocodiles, amphibians, small logs). During this phase, infants produce few snake alarm calls to a broad range of stimuli that resemble the colour or the shape of vipers, i.e., juveniles producing a snake alarm call to a toad (Mathilde Grampp, personal communication). In the second step, young mangabeys learn that not all snakes are dangerous and start to discriminate between vipers and non-vipers snakes. During these first two phases, social referencing, and thus social learning, seems to be important for the subsequent refinement of snake anti-predator behaviour. Therefore, it is likely that learning about predator classes begins when infants start moving independently between 6–12 months old. Later, by the time juveniles are 2 years old, they have already learned to ignore non-viper snakes, probably from observing more experienced individuals. Finally, in the third step, after developing cognitive competence, mangabeys direct snake-specific anti-predator behaviour, including active alarm calling behaviour, almost exclusively to vipers. Experiments on wild capuchins monkeys revealed similar results. Even while capuchins started to exhibit predator detection and alarm calling behaviour as young as 4 months old, snake-species discrimination did not become apparent until juvenile stage (2–5 years old) (Meno et al., 2013a). Future studies should address if young mangabeys sharpen their snake anti-predator responses rapidly in response to very few key experiences or either gradually over multiple experiences across juvenile stage.

Social beings are affected by their social environments, and one manifestation of this is audience effects. Empirical studies providing evidence of changes in the signalling behaviour of individuals caused by the mere presence of others have been conducted with fish (Doutrelant et al., 2001), birds (Karakashian et al., 1988; Marler et al., 1986; Meaux et al., 2023) and mammals (Dunlop, 2016; le Roux et al., 2008), including non-human primates (Crockford et al., 2012; Girard-Buttoz et al., 2020; Wich & Sterck, 2003). In mangabeys, very often the first individual to detect a snake is also the first caller (Mielke et al., 2019). Snake alarm calls seem to facilitate snake detection by other individuals by increasing awareness and distance detection. Other experimental studies with viper models in mangabeys have shown that subjects are more likely to call if they had not heard other alarm calls before and if they are with small audiences, reinforcing that during viper encounters alarm calling is crucial to ensure that as many individuals as possible become aware of the snake location (Mielke et al., 2019; Quintero et al., 2022). Although it is clear that mangabeys adjust their snake anti-predator behaviour to their audiences, we are confident that this variable did not have any important undetected effect on our results since audience size, when used as a control predictor, showed no significant influence on any of the statistical models and audiences sizes did not considerably vary between conditions (Supplementary Material).

We have shown that mangabeys' snake-specific discrimination and competent snake anti-predator behaviour, including alarm calling, towards dangerous vipers arise and refine during juvenile stage. However, we did not determine the exact age at which infants begin to recognize the different snake species they are exposed to, nor the exact age at which they start to display snake anti-predator behaviour. This should be addressed in future research to test which socioecology and cognitive features may shape mangabeys' snake-species discrimination from early on. Moreover, our stationary snake models could be more similar to Gaboon and rhinoceros vipers, which are highly static snakes, unlikely to move even in response to agitated monkey mobbing behaviour (Quintero et al., 2022), than to more mobile colubrid species. Studies in vervet monkeys and wild jackdaws (*Corvus monedula*) have shown that the animacy of the objects (e.g., potential predator models) influences subjects' responses (Deshpande et al., 2022; Greggor et al., 2022). Future experiments taking into account the movement pattern of snake models are needed to examine the effect of animacy in monkeys' snake-species discrimination. One flaw of our study was not to include python models. In the Taï forest, mangabeys only exhibit strong snake anti-predator behaviour to pythons and Gaboon and rhinoceros vipers. Mangabeys are particularly vulnerable to snakebites by highly dangerous vipers (Penner et al., 2008), which they frequently encounter. On the other hand, mangabeys rarely come into contact with pythons, which are confirmed primates' predators (Headland & Greene, 2011; Jaffe & Isbell, 2010; Khamcha & Sukumal, 2009; Struhsaker, 1967; van Schaik et al., 1983). If encounter rates and the level of perceived threat posed by pythons and vipers influence mangabeys' snake-species recognition learning and their snake anti-predator responses remain to be tested in the future. Finally, because of the recruitment nature of snake alarm calls in mangabeys and how they acquire their snake-specific anti-predator behaviours, the mangabey-viper system may be an interesting model to investigate the conditioning and evolution of fear in primates and the role of vocal social learning in how they become communicatively competent in the production, usage and comprehension of their alarm calls.

Cognition is often defined as the capacity to gather, process and retain information—which can subsequently be used to make decisions (Shettleworth, 2010). Studying cognitive evolution, however, is notoriously hard, because neither brains nor behaviours fossilise. Thus, the highly selective and restricted nature of snake-specific anti-predator behaviour exhibited by adults allowed us to assess the development of cognitive competence in mangabeys. Snakes were amongst the earliest and most tenacious threats during the evolutionary history of primates and require, as demonstrated by this study, cognitive development to allow a safe coexistence with them. In the Taï Forest, mangabeys are exposed to a large number of snake species, but only three elicit anti-predator responses, suggesting that primates have evolved a capacity to learn to avoid false positives.

In sum, we have empirically corroborated Seyfarth and Cheney's learning model (Seyfarth & Cheney, 1980, 1986). Our results indicate that learning about snakes may begin with an over-generalized response to a wide variety of species, including some nonthreatening ones, that is winnowed down, probably via social learning, into a response directed toward specific dangerous species. This finding highlights snake-species recognition and threat assessment as prerequisites for effective snake avoidance. Our results also indicate that snakes, particularly vipers, are perceived by non-human primates as an important threat from an early age, but also that fast identification and alarm calling towards dangerous snakes are sharpened with experience. Furthermore, our study also builds up on the role of the social environment in primates snake-directed anti-predator behaviour (Meno et al., 2013b). Overall, these findings support the theories that state that competence in anti-predator behaviour is acquired through social learning during the juvenile stage by refining pre-existing snake fear (Griffin, 2004;

Mineka & Cook, 1988; Seyfarth & Cheney, 1980), and that snakes as predators have played a central role in the evolution of primate cognition (Isbell, 2006, 2009).

3.7 Acknowledgments

We thank the Centre Suisse de Recherches Scientifiques (CSRS), the Ministère de la Recherche Scientifique, the Ministère de l'Agriculture et des Ressources Animales and the Office Ivoirien des Parcs et Réserves (OIPR) of Côte d'Ivoire for support and permission to conduct research in the Taï National Park. Fieldwork was made possible thanks to Paterson Kalo, Landri Bele, Richard Peho, Benjamin Zehi, Gerard Gha and the rest of the Taï Monkey Project (TMP) assistants, to whom we express our gratitude. We thank Constance Thiriau, Martina Magris y Sonia Touitou the staff of the CRE research station in Taï for support in the field. We also thank Anderson Bitty for logistic support and Radu Slobodeanu for statistical advice. We thank Auriane Le Floch for providing one viper model trial and Sasha Cárdenas for blind-coding the videos to estimate inter-observer reliability.

3.8 Funding

This work was funded by the Swiss National Centre of Competence in Research (NCCR) Evolving Language, Swiss National Science Foundation Agreement #51NF40_180888 (KZ), and the Swiss National Science Foundation project grant 31003A_166458: "Social learning in primate communication" (KZ).

3.9 Author contributions

Conceptualization: JL, KZ; Methodology and experiments: JL, FQ; Formal analysis and investigation: JL; Writing - original draft preparation: JL; Writing - review and editing: JL, KZ; Funding acquisition: KZ; Supervision: KZ

3.10 Competing interests

All other authors declare they have no competing interests.

3.11 Data and code availability

All data reported in this paper are included in the supplementary materials. Code is available through the Open Science Framework (OSF) project: "Sooty mangabey-Snake project" (https://osf.io/5v6z8/). All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials. All supplementary videos have been deposited at OSF and are publicly available at the following link: https://osf.io/hw2r7/?view_only=c5581e1a8e6e4cdba8311ed18871239d. Additional data related to this paper is available from the lead contact upon request.

3.12 References

Abrams, P. A. (2001). Predator-Prey Interactions. In C. W. Fox, D. A. Roff, & D. J. Fairbairn (Eds.), *Evolutionary Ecology: Concepts and Case Studies* (p. 0). Oxford University Press. https://doi.org/10.1093/oso/9780195131543.003.0028

Apfelbach, R., Blanchard, C. D., Blanchard, R. J., Hayes, R. A., & McGregor, I. S. (2005). The effects of predator odors in mammalian prey species: a review of field and laboratory studies. *Neuroscience and Biobehavioral Reviews*, *29*(8), 1123–1144. https://doi.org/10.1016/j.neubiorev.2005.05.005

Baldwin, D. A., & Moses, L. J. (1996). The Ontogeny of Social Information Gathering. *Child Development*, *67*(5), 1915–1939. https://doi.org/10.2307/1131601

Barros, M., Boere, V., Mello, E. L., & Tomaz, C. (2002). Reactions to Potential Predators in Captive-Born Marmosets (Callithrix penicillata). *International Journal of Primatology*, *23*(2), 443–454. https://doi.org/10.1023/A:1013899931878

Baxter-Gilbert, J., Riley, J. L., & Whiting, M. J. (2018). Runners and fighters: clutch effects and body size drive innate antipredator behaviour in hatchling lizards. *Behavioral Ecology and Sociobiology*, *72*(6), 97. https://doi.org/10.1007/s00265-018-2505-7

Boesch, C., & Boesch-Achermann, H. (2000). *The chimpanzees of the Taï forest : behavioural* *ecology and evolution*. Oxford : Oxford university press. http://lib.ugent.be/catalog/rug01:000534901

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., & White, J.-S. S. (2009). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution*, *24*(3), 127–135. https://doi.org/10.1016/j.tree.2008.10.008

Brodbeck, D. R., Burack, O. R., & Shettleworth, S. J. (1992). One-trial associative memory in black-capped chickadees. *Journal of Experimental Psychology: Animal Behavior Processes*, *18*, 12–21. https://doi.org/10.1037/0097-7403.18.1.12

Caine, N. G., Addington, R. L., & Windfelder, T. L. (1995). Factors affecting the rates of food calls given by red-bellied tamarins. *Animal Behaviour*, *50*(1), 53–60. https://doi.org/10.1006/anbe.1995.0220

Cartmill, E. A., & Byrne, R. W. (2007). Orangutans modify their gestural signaling according to their audience's comprehension. *Current Biology : CB*, *17*(15), 1345–1348. https://doi.org/10.1016/j.cub.2007.06.069

Cäsar, C., & Zuberbühler, K. (2012). Referential alarm calling behaviour in New World primates. *Current Zoology*, *58*(5), 680–697. https://doi.org/10.1093/czoolo/58.5.680

Castro, N. A., & Snowdon, C. T. (2000). Development of Vocal Responses in Infant Cotton-Top Tamarins. *Behaviour*, *137*(5), 629–646. http://www.jstor.org/stable/4535727

Cook, M., & Mineka, S. (1990). Selective associations in the observational conditioning of fear in rhesus monkeys. *Journal of Experimental Psychology. Animal Behavior Processes*, *16*(4), 372–389.

Crockford, C, Wittig, R. M., Mundry, R., & Zuberbühler, K. (2012). Wild Chimpanzees Inform Ignorant Group Members of Danger. *Current Biology*, *22*(2), 142–146. https://doi.org/https://doi.org/10.1016/j.cub.2011.11.053

Crockford, Catherine, Wittig, R. M., & Zuberbühler, K. (2015). An intentional vocalization draws others' attention: a playback experiment with wild chimpanzees. *Animal Cognition*, *18*(3), 581–591. https://doi.org/10.1007/s10071-014-0827-z

Curio, E. (1976). *The ethology of predation* (Vol. 7). Springer Science & Business Media.

Curio, E., Ernst, U., & Vieth, W. (1978). Cultural Transmission of Enemy Recognition: One Function of Mobbing. *Science*, *202*(4370), 899 LP – 901. https://doi.org/10.1126/science.202.4370.899

Dalesman, S., Rundle, S. D., Coleman, R. A., & Cotton, P. A. (2006). Cue association and antipredator behaviour in a pulmonate snail, Lymnaea stagnalis. *Animal Behaviour*, *71*(4), 789–797. https://doi.org/https://doi.org/10.1016/j.anbehav.2005.05.028

Deshpande, A., Van Boekholt, B., & Zuberbuhler, K. (2022). Preliminary evidence for one-trial social learning of vervet monkey alarm calling. *Royal Society Open Science*, *9*(8), 210560. https://doi.org/10.1098/rsos.210560

Dessborn, L., Englund, G., Elmberg, J., & Arzél, C. (2012). Innate responses of mallard ducklings towards aerial, aquatic and terrestrial predators. *Behaviour*, *149*(13–14), 1299–1317. https://doi.org/https://doi.org/10.1163/1568539X-00003014

Di Bitetti, M. S. (2005). Food-associated calls and audience effects in tufted capuchin monkeys, Cebus apella nigritus. *Animal Behaviour*, *69*(4), 911–919. https://doi.org/https://doi.org/10.1016/j.anbehav.2004.05.021

Doutrelant, C., McGregor, P. K., & Oliveira, R. F. (2001). The effect of an audience on intrasexual communication in male Siamese fighting fish, Betta splendens. *Behavioral Ecology*, *12*(3), 283–286. https://doi.org/10.1093/beheco/12.3.283

Dunlop, R. A. (2016). Changes in vocal parameters with social context in humpback whales: considering the effect of bystanders. *Behavioral Ecology and Sociobiology*, *70*, 857–870. https://doi.org/10.1007/s00265-016-2108-0

Edwards, M. C., Ford, C., Hoy, J. M., FitzGibbon, S., & Murray, P. J. (2021). How to train your wildlife: A review of predator avoidance training. *Applied Animal Behaviour Science*, *234*, 105170. https://doi.org/https://doi.org/10.1016/j.applanim.2020.105170

Engqvist, L. (2005). The mistreatment of covariate interaction terms in linear model analyses of behavioural and evolutionary ecology studies. *Animal Behaviour*, *70*(4), 967–971. https://doi.org/https://doi.org/10.1016/j.anbehav.2005.01.016

Epp, K. J., & Gabor, C. R. (2008). Innate and Learned Predator Recognition Mediated by Chemical Signals in Eurycea nana. *Ethology*, *114*(6), 607–615. https://doi.org/https://doi.org/10.1111/j.1439-0310.2008.01494.x

Ernst, R., & Rödel, M. (2002). A new Atheris species (Serpentes: Viperidae), from Taï National Park, Ivory Coast. *Herpetological Journal*, *12*, 55–61.

Evans, A., & Tomasello, M. (1986). Evidence for social referencing in young chimpanzees (Pan troglodytes). *Folia Primatologica; International Journal of Primatology*, *47*(1), 49–54. https://doi.org/10.1159/000156263

Fedurek, P., Slocombe, K. E., & Zuberbühler, K. (2015). Chimpanzees communicate to two different audiences during aggressive interactions. *Animal Behaviour*, *110*, 21–28. https://doi.org/https://doi.org/10.1016/j.anbehav.2015.09.010

Feinman, S., Roberts, D., Hsieh, K.-F., Sawyer, D., & Swanson, D. (1992). *A Critical Review* *of Social Referencing in Infancy BT - Social Referencing and the Social Construction of Reality in Infancy* (S. Feinman (ed.); pp. 15–54). Springer US. https://doi.org/10.1007/978-1-4899-2462-9_2

Feise, R. J. (2002). Do multiple outcome measures require p-value adjustment? *BMC Medical Research Methodology*, *2*, 8. https://doi.org/10.1186/1471-2288-2-8

Fichtel, C. (2008). Ontogeny of conspecific and heterospecific alarm call recognition in wild Verreaux's sifakas (Propithecus verreauxi verreauxi). *American Journal of Primatology*, *70*(2), 127–135. https://doi.org/https://doi.org/10.1002/ajp.20464

Fichtel, C. (2020). Monkey Alarm Calling: It Ain't all Referential, or is It? *Animal Behavior and Cognition*, *7*, 101–107.

Fischer, J. (2020). Nonhuman primate alarm calls then and now. *Animal Behavior and Cognition*, *7*.

Fischer, J., Cheney, D. L., & Seyfarth, R. M. (2000). Development of infant baboons' responses to graded bark variants. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *267*(1459), 2317–2321. https://doi.org/10.1098/rspb.2000.1285

Galef, B. G., & Laland, K. N. (2005). Social learning in animals: empirical studies and theoretical models. *Bioscience*, *55*(6), 489–499.

Genovart, M., Negre, N., Tavecchia, G., Bistuer, A., Parpal, L., & Oro, D. (2010). The young, the weak and the sick: evidence of natural selection by predation. *PloS One*, *5*(3), e9774. https://doi.org/10.1371/journal.pone.0009774

Girard-Buttoz, C., Surbeck, M., Samuni, L., Tkaczynski, P., Boesch, C., Fruth, B., Wittig, R. M., Hohmann, G., & Crockford, C. (2020). Information transfer efficiency differs in wild chimpanzees and bonobos, but not social cognition. *Proceedings of the Royal Society B: Biological Sciences*, *287*(1929), 20200523. https://doi.org/10.1098/rspb.2020.0523

Göth, A. (2001). Innate predator-recognition in Australian brush-turkey (Alectura lathami, Megapodiidae) hatchlings. *Behaviour*, *138*, 117–136. https://doi.org/10.1163/156853901750077826

Greene, H. W. (1997). *Snakes: the evolution of mystery in nature*. Univ of California Press.

Greggor, A. L., McIvor, G. E., Clayton, N. S., & Thornton, A. (2022). Wild jackdaws are wary of objects that violate expectations of animacy. *Royal Society Open Science*, *5*(10), 181070. https://doi.org/10.1098/rsos.181070

Griffin, A. (2004). Social learning about predators: a review and prospectus. *Animal Learning & Behavior*, *32*(1), 131–140. https://doi.org/10.3758/BF03196014

Gursky, S. (2003). Predation Experiments on Infant Spectral Tarsiers (Tarsius spectrum). *Folia*

Primatologica, *74*(5–6), 272–284. https://doi.org/https://doi.org/10.1159/000073314

Hall, N. J., Udell, M. A. R., Dorey, N. R., Walsh, A. L., & Wynne, C. D. L. (2011). Megachiropteran bats (Pteropus) utilize human referential stimuli to locate hidden food. *Journal of Comparative Psychology (Washington, D.C. : 1983)*, *125*(3), 341–346. https://doi.org/10.1037/a0023680

Haslbeck, J. M. B., & van Bork, R. (2022). Estimating the number of factors in exploratory factor analysis via out-of-sample prediction errors. *Psychological Methods*. https://doi.org/10.1037/met0000528

Headland, T. N., & Greene, H. W. (2011). Hunter–gatherers and other primates as prey, predators, and competitors of snakes. *Proceedings of the National Academy of Sciences*, *108*(52), E1470–E1474. https://doi.org/10.1073/pnas.1115116108

Heyes, C., & Galef Jr, B. (1996). *Social learning in animals: the roots of culture*. Elsevier.

Hobaiter, C., Byrne, R. W., & Zuberbühler, K. (2017). Wild chimpanzees' use of single and combined vocal and gestural signals. *Behavioral Ecology and Sociobiology*, *71*(6), 96. https://doi.org/10.1007/s00265-017-2325-1

Horner, V., & Whiten, A. (2005). Causal knowledge and imitation/emulation switching in chimpanzees (Pan troglodytes) and children (Homo sapiens). *Animal Cognition*, *8*(3), 164–181. https://doi.org/10.1007/s10071-004-0239-6

Isbell, L. A. (1994). Predation on primates: Ecological patterns and evolutionary consequences. *Evolutionary Anthropology: Issues, News, and Reviews*, *3*(2), 61–71. https://doi.org/10.1002/evan.1360030207

Isbell, L. A. (2006). Snakes as agents of evolutionary change in primate brains. *Journal of Human Evolution*, *51*(1), 1–35. https://doi.org/https://doi.org/10.1016/j.jhevol.2005.12.012

Isbell, L. A. (2009). *The Fruit, the Tree, and the Serpent*. Harvard University Press. https://doi.org/10.2307/j.ctvjnrvj0

Itakura, S. (1995). An exploratory study of social referencing in chimpanzees. *Folia Primatologica*, *64*, 44–48. https://doi.org/10.1159/000156831

Jaffe, K. . E., & Isbell, L. (2010). The Guenons: Polyspecific associations in sociological perspective. In C. J. Campbell, A. Fuentes, K. C. MacKinnon, S. K. Bearder, & R. Stumpf (Eds.), *Primates in Perspective* (pp. 277–300). Oxford University Press.

Janson, C. H., & van Schaik, C. P. (1993). Ecological risk aversion in juvenile primates: slow and steady wins the race. In M. E. Pereira & L. A. Fairbanks (Eds.), *Juvenile primates: life history, development, and behavior* (pp. 57–74). Oxford Univ. Press.

Kalan, A. K., & Boesch, C. (2015). Audience effects in chimpanzee food calls and their potential for recruiting others. *Behavioral Ecology and Sociobiology*, *69*(10), 1701–1712. http://www.jstor.org/stable/43599678

Karakashian, S. J., Gyger, M., & Marler, P. (1988). Audience effects on alarm calling in chickens (Gallus gallus). In *Journal of Comparative Psychology* (Vol. 102, pp. 129–135). American Psychological Association. https://doi.org/10.1037/0735-7036.102.2.129

Kawai, N., & He, H. (2016). Breaking Snake Camouflage: Humans Detect Snakes More Accurately than Other Animals under Less Discernible Visual Conditions. *PLOS ONE*, *11*(10), e0164342. https://doi.org/10.1371/journal.pone.0164342

Kawai, N., & Koda, H. (2016). Japanese monkeys (Macaca fuscata) quickly detect snakes but not spiders: Evolutionary origins of fear-relevant animals. In *Journal of Comparative Psychology* (Vol. 130, pp. 299–303). American Psychological Association. https://doi.org/10.1037/com0000032

Kelley, J. L., & Magurran, A. E. (2003). Learned predator recognition and antipredator responses in fishes. *Fish and Fisheries*, *4*(3), 216–226. https://doi.org/https://doi.org/10.1046/j.1467-2979.2003.00126.x

Khamcha, D., & Sukumal, N. (2009). Burmese python (Python molurus) predation on a pig-tailed macaque (Macaca nemestrina) in Khao Yai National Park. *Hamadryad*, *34*, 176–178. https://doi.org/10.13140/2.1.3857.7449

Klinnert, M., Campos, J., Sorce, J., Emde, R., & Svejda, M. (1983). Emotions as behavior regulators: social referencing in infancy. In R. Plutchik & H. B. T.-E. in E. D. Kellerman (Eds.), *Emotions in Early Development* (pp. 57–86). Academic Press. https://doi.org/https://doi.org/10.1016/B978-0-12-558702-0.50009-1

Kosmidis, I. (2014). Bias in parametric estimation: reduction and useful side-effects. *WIREs Computational Statistics*, *6*(3), 185–196. https://doi.org/https://doi.org/10.1002/wics.1296

Kosmidis, I. (2023). *brglm2: Bias Reduction in Generalized Linear Models* (R package version 0.9). https://cran.r-project.org/package=brglm2

le Roux, A., Cherry, M. I., & Manser, M. B. (2008). The audience effect in a facultatively social mammal, the yellow mongoose, Cynictis penicillata. *Animal Behaviour*, *75*(3), 943–949. https://doi.org/https://doi.org/10.1016/j.anbehav.2007.07.014

León, J., Thiriau, C., Bodin, C., Crockford, C., & Zuberbühler, K. (2022). Acquisition of predator knowledge from alarm calls via one-trial social learning in monkeys. *IScience*, *25*, 104853. https://doi.org/https://doi.org/10.1016/j.isci.2022.104853

León, J., Thiriau, C., Crockford, C., & Zuberbühler, K. (2022). *https://osf.io/y2gvc/.*

Marler, P., Dufty, A., & Pickert, R. (1986). Vocal communication in the domestic chicken: II. Is a sender sensitive to the presence and nature of a receiver? *Animal Behaviour*, *34*(PART 1), 194–198. https://doi.org/10.1016/0003-3472(86)90023-0

McCowan, B., Franceschini, N. V, & Vicino, G. A. (2001). Age differences and developmental trends in alarm peep responses by squirrel monkeys (Saimiri sciureus). *American Journal of Primatology*, *53*(1), 19–31. https://doi.org/https://doi.org/10.1002/1098-2345(200101)53:1<19::AID-AJP2>3.0.CO;2-#

McGraw, W., & Zuberbühler, K. (2007). The monkeys of the Taï forest: an introduction. In Klaus Zuberbühler, R. Noë, & W. S. McGraw (Eds.), *Monkeys of the Taï Forest: An African Primate Community* (pp. 1–48). Cambridge University Press. https://doi.org/DOI: 10.1017/CBO9780511542121.002

Meaux, E., He, C., Zeng, X., He, R., Jiang, A., & Goodale, E. (2023). Audience effects in a group-living bird: How contact call rate is affected by vegetation and group size and composition. *Ecology and Evolution*, *13*(3), e9909. https://doi.org/https://doi.org/10.1002/ece3.9909

Meno, W., Coss, R. G., & Perry, S. (2013a). Development of Snake-Directed Antipredator Behavior by Wild White-faced Capuchin Monkeys: I. Snake-Species Discrimination. *American Journal of Primatology*, *75*(3), 281–291. https://doi.org/https://doi.org/10.1002/ajp.22106

Meno, W., Coss, R. G., & Perry, S. (2013b). Development of Snake-Directed Antipredator Behavior by Wild White-Faced Capuchin Monkeys: II. Influence of the Social Environment. *American Journal of Primatology*, *75*(3), 292–300. https://doi.org/https://doi.org/10.1002/ajp.22109

Merola, I., Lazzaroni, M., Marshall-Pescini, S., & Prato-Previde, E. (2015). Social referencing and cat–human communication. *Animal Cognition*, *18*(3), 639–648. https://doi.org/10.1007/s10071-014-0832-2

Merola, I., Prato-Previde, E., & Marshall-Pescini, S. (2012). Social referencing in dog-owner dyads? *Animal Cognition*, *15*(2), 175–185. https://doi.org/10.1007/s10071-011-0443-0

Mery, F., & Burns, J. G. (2010). Behavioural plasticity: an interaction between evolution and experience. *Evolutionary Ecology*, *24*(3), 571–583. https://doi.org/10.1007/s10682-009-9336-y

Mielke, A., Crockford, C., & Wittig, R. M. (2019). Snake alarm calls as a public good in sooty mangabeys. *Animal Behaviour*, *158*, 201–209.

https://doi.org/https://doi.org/10.1016/j.anbehav.2019.10.001

Mineka, S. (1992). *Evolutionary Memories, Emotional Processing, and the Emotional Disorders* (D. L. B. T.-P. of L. and M. Medin (ed.); Vol. 28, pp. 161–206). Academic Press. https://doi.org/https://doi.org/10.1016/S0079-7421(08)60490-9

Mineka, S., & Cook, M. (1988). Social learning and the acquisition of snake fear in monkeys. In *Social learning: Psychological and biological perspectives.* (pp. 51–73). Lawrence Erlbaum Associates, Inc.

Mineka, S., & Cook, M. (1993). Mechanisms involved in the observational conditioning of fear. In *Journal of Experimental Psychology: General* (Vol. 122, Issue 1, pp. 23–38). American Psychological Association. https://doi.org/10.1037/0096-3445.122.1.23

Mohr, T., van de Waal, E., Zuberbühler, K., & Mercier, S. (2023). Juvenile vervet monkeys rely on others when responding to danger. *Animal Cognition*. https://doi.org/10.1007/s10071-023-01765-2

Morimoto, Y., & Fujita, K. (2012). Capuchin monkeys (Cebus apella) use conspecifics' emotional expressions to evaluate emotional valence of objects. *Animal Cognition*, *15*(3), 341–347. https://doi.org/10.1007/s10071-011-0458-6

Öhman, A. (2009). Of snakes and faces: An evolutionary perspective on the psychology of fear. *Scandinavian Journal of Psychology*, *50*(6), 543–552. https://doi.org/https://doi.org/10.1111/j.1467-9450.2009.00784.x

Ohman, A., & Mineka, S. (2001). Fears, phobias, and preparedness: toward an evolved module of fear and fear learning. *Psychological Review*, *108*(3), 483–522. https://doi.org/10.1037/0033-295x.108.3.483

Olsson, A., & Phelps, E. A. (2007). Social learning of fear. *Nature Neuroscience*, *10*(9), 1095–1102. https://doi.org/10.1038/nn1968

Ouattara, K., Lemasson, A., & Zuberbühler, K. (2009). Anti-predator strategies of free-ranging Campbell's monkeys. *Behaviour*, *146*(12), 1687–1708. https://doi.org/10.1163/000579509X12469533725585

Penner, J., Fruteau, C., Range, F., & Rodel, M. (2008). Finding a needle in a haystack: new methods of locating and working with rhinoceros vipers (Bitis rhinoceros). *Herpetological Review*, *39*(3), 310.

Perry, S., Panger, M., Rose, L. M., Baker, M., Gros-Louis, J., Jack, K., Mackinnon, K. C., Manson, J., Fedigan, L., & Pyle, K. (2003). Traditions in wild white-faced capuchin monkeys. In *The Biology of Traditions* (pp. 391–425). Cambridge University Press. https://doi.org/10.1017/CBO9780511584022.015

Pika, S., Liebal, K., & Tomasello, M. (2003). Gestural communication in young gorillas (Gorilla gorilla): gestural repertoire, learning, and use. *American Journal of Primatology*, *60*(3), 95–111. https://doi.org/10.1002/ajp.10097

Pollick, A. S., Gouzoules, H., & de Waal, F. B. M. (2005). Audience effects on food calls in captive brown capuchin monkeys, Cebus apella. *Animal Behaviour*, *70*(6), 1273–1281. https://doi.org/https://doi.org/10.1016/j.anbehav.2005.03.007

Price, T., Wadewitz, P., Cheney, D., Seyfarth, R., Hammerschmidt, K., & Fischer, J. (2015). Vervets revisited: A quantitative analysis of alarm call structure and context specificity. *Scientific Reports*, *5*, 13220. https://doi.org/10.1038/srep13220

Quintero, F., Touitou, S., Magris, M., & Zuberbühler, K. (2022). An audience effect in sooty mangabey alarm calling. *Front Psychol*, *13*. https://doi.org/10.3389/fpsyg.2022.816744

R Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

Ramakrishnan, U., & Coss, R. G. (2000). Recognition of heterospecific alarm vocalization by Bonnet Macaques (Macaca radiata). In *Journal of Comparative Psychology* (Vol. 114, Issue 1, pp. 3–12). American Psychological Association. https://doi.org/10.1037/0735-7036.114.1.3

Ramakrishnan, U., Coss, R. G., Schank, J., Dharawat, A., & Kim, S. (2005). Snake Species Discrimination by Wild Bonnet Macaques (Macaca radiata). *Ethology*, *111*(4), 337–356. https://doi.org/10.1111/j.1439-0310.2004.01063.x

Range, F., & Fischer, J. (2004). Vocal Repertoire of Sooty Mangabeys (Cercocebus torquatus atys) in the Tai National Park. *Ethology*, *110*(4), 301–321. https://doi.org/10.1111/j.1439-0310.2004.00973.x

Rescorla, R. A., & Wagner, A. (1972). A theory of Pavlovian conditioning: Variations in the effectiveness of reinforcement and nonreinforcement. In A. Black & P. W (Eds.), *Classical Conditioning II: Current Research and Theory: Vol. Vol. 2* (pp. 64–69). Appleton-Century-Crofts.

Roberts, S. G. B., McComb, K., & Ruffman, T. (2008). An experimental investigation of referential looking in free-ranging Barbary macaques (Macaca sylvanus). In *Journal of Comparative Psychology* (Vol. 122, pp. 94–99). American Psychological Association. https://doi.org/10.1037/0735-7036.122.1.94

Rödel, M., & Mahsberg, D. (2000). Vorläufige Liste der Schlangen des Taï-Nationalparks / Elfenbeinküste und angrenzender Gebiete. *Salamandra*, *36*, 25–38.

Russell, C. L., Bard, K. A., & Adamson, L. B. (1997). Social referencing by young chimpanzees (Pan troglodytes). In *Journal of Comparative Psychology* (Vol. 111, pp. 185–193). American Psychological Association. https://doi.org/10.1037/0735-7036.111.2.185

Schel, A. M., Townsend, S. W., Machanda, Z., Zuberbühler, K., & Slocombe, K. E. (2013). Chimpanzee Alarm Call Production Meets Key Criteria for Intentionality. *PLOS ONE*, *8*(10), e76674. https://doi.org/10.1371/journal.pone.0076674

Schel, A. M., & Zuberbühler, K. (2009). Responses to leopards are independent of experience in Guereza colobus monkeys. *Behaviour*, *146*(12), 1709–1737. https://doi.org/https://doi.org/10.1163/000579509X12483520922007

Schrimpf, A., Single, M.-S., & Nawroth, C. (2020). Social Referencing in the Domestic Horse. In *Animals* (Vol. 10, Issue 1). https://doi.org/10.3390/ani10010164

Schuppli, C., Meulman, E. J. M., Forss, S. I. F., Aprilinayati, F., van Noordwijk, M. A., & van Schaik, C. P. (2016). Observational social learning and socially induced practice of routine skills in immature wild orang-utans. *Animal Behaviour*, *119*, 87–98. https://doi.org/https://doi.org/10.1016/j.anbehav.2016.06.014

Seyfarth, R. M., & Cheney, D. L. (1980). The Ontogeny of Vervet Monkey Alarm Calling Behavior: A Preliminary Report. *Zeitschrift Für Tierpsychologie*, *54*(1), 37–56. https://doi.org/10.1111/j.1439-0310.1980.tb01062.x

Seyfarth, R. M., & Cheney, D. L. (1986). Vocal development in vervet monkeys. *Animal Behaviour*, *34*(6), 1640–1658. https://doi.org/https://doi.org/10.1016/S0003-3472(86)80252-4

Shettleworth, S. J. (2010). *Cognition, Evolution, and Behavior* (2nd ed.). Oxford University Press.

Shibasaki, M., & Kawai, N. (2009). Rapid detection of snakes by Japanese monkeys (Macaca fuscata): An evolutionarily predisposed visual system. In *Journal of Comparative Psychology* (Vol. 123, pp. 131–135). American Psychological Association. https://doi.org/10.1037/a0015095

Shultz, S., & Thomsett, S. (2007). Interactions between African crowned eagles and their prey community. In Klaus Zuberbühler, R. Noë, & W. S. McGraw (Eds.), *Monkeys of the Taï Forest: An African Primate Community* (pp. 171–193). Cambridge University Press. https://doi.org/DOI: 10.1017/CBO9780511542121.008

Slocombe, K. E., & Zuberbühler, K. (2007). Chimpanzees modify recruitment screams as a function of audience composition. *Proceedings of the National Academy of Sciences*, *104*(43), 17228 LP – 17233. https://doi.org/10.1073/pnas.0706741104

Soldati, A., Fedurek, P., Dezecache, G., Call, J., & Zuberbühler, K. (2022). Audience sensitivity in chimpanzee display pant hoots. *Animal Behaviour*, *190*, 23–40. https://doi.org/https://doi.org/10.1016/j.anbehav.2022.05.010

Struhsaker, T. T. (1967). Ecology of Vervet Monkeys (Cercopithecus Aethiops) in The Masai-Amboseli Game Reserve, Kenya. *Ecology*, *48*(6), 891–904. https://doi.org/https://doi.org/10.2307/1934531

Townsend, S, Rasmussen, M., Clutton-Brock, T., & Manser, M. (2012). Flexible alarm calling in meerkats: the role of the social environment and predation urgency. *Behavioral Ecology*, *23*(6), 1360–1364. https://doi.org/10.1093/beheco/ars129

Townsend, Simon, & Zuberbuhler, K. (2009). Audience effects in chimpanzee copulation calls. *Communicative & Integrative Biology*, *2*(3), 282–284. https://doi.org/10.4161/cib.2.3.6796

Urbani, B. (2017). Humans as Primate Predators. In *The International Encyclopedia of Primatology* (pp. 1–3). https://doi.org/https://doi.org/10.1002/9781119179313.wbprim0258

van Schaik, C. P., van Noordwijk, M. A., Warsono, B., & Sutriono, E. (1983). Party size and early detection of predators in sumatran forest primates. *Primates*, *24*(2), 211–221. https://doi.org/10.1007/BF02381083

Vignal, C., Mathevon, N., & Mottin, S. (2004). Audience drives male songbird response to partner's voice. *Nature*, *430*(6998), 448–451. https://doi.org/10.1038/nature02645

Wegdell, F., Hammerschmidt, K., & Fischer, J. (2019). Conserved alarm calls but rapid auditory learning in monkey responses to novel flying objects. *Nature Ecology & Evolution*, *3*(7), 1039–1042. https://doi.org/10.1038/s41559-019-0903-5

Weiss, L., Brandl, P., & Frynta, D. (2015). Fear reactions to snakes in naïve mouse lemurs and pig-tailed macaques. *Primates*, *56*(3), 279–284. https://doi.org/10.1007/s10329-015-0473-3

Wich, S. A., & Sterck, E. H. M. (2003). Possible audience effect in Thomas langurs (Primates; Presbytis thomasi): an experimental study on male loud calls in response to a tiger model. *American Journal of Primatology*, *60*(4), 155–159. https://doi.org/10.1002/ajp.10102

Zaccaroni, M., Binazzi, R., Massolo, A., & Dessì-Fulgheri, F. (2013). Audience effect on aerial alarm calls in the monogamous red-legged partridge. *Ethology Ecology & Evolution*, *25*(4), 366–376. https://doi.org/10.1080/03949370.2013.798352

Zanuzzo, F. S., de C. Bovolato, A. L., Pereira, R. T., Valença-Silva, G., Barcellos, L. J. G., & Barreto, R. E. (2019). Innate response based on visual cues of sympatric and allopatric predators in Nile tilapia. *Behavioural Processes*, *164*, 109–114. https://doi.org/https://doi.org/10.1016/j.beproc.2019.05.004

Zuberbühler, K. (2008). Audience effects. *Current Biology*, *18*(5), R189–R190. https://doi.org/10.1016/j.cub.2007.12.041

Zuberbühler, K, & Jenny, D. (2002). Leopard predation and primate evolution. *Journal of Human Evolution*, *43*(6), 873–886. https://doi.org/https://doi.org/10.1006/jhev.2002.0605

Zuberbühler, Klaus. (2009). Survivor Signals: The Biology and Psychology of Animal Alarm Calling. *Advances in the Study of Behavior*, *40*, 277–322. https://doi.org/https://doi.org/10.1016/S0065-3454(09)40008-1

3.13 Chapter 3: Appendix

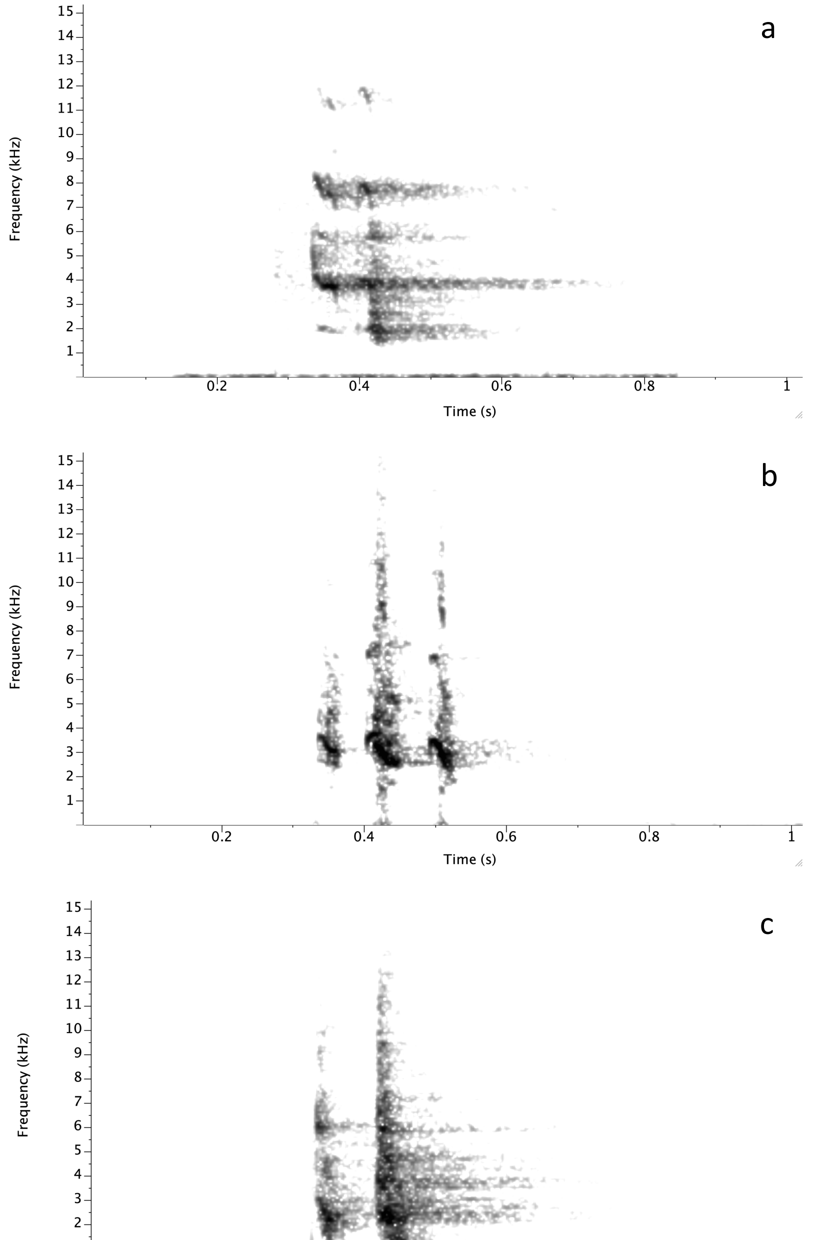

Figure S3.1 Representative samples of sooty mangabey alarm calls produce in response to snakes, depending on age: (a) young juvenile, (b) old juvenile and (c) adult. Spectrograms were made using Raven and the following settings: 512 FFT, Hamming window, 75% overlap, 22.05 kHz sampling frequency.

Table S3.1 Definitions of behavioural responses.

Behavioural responses	**Definition**
Number of looks	Number of times the subject's head turned and paused within a 30° arc of the snake model location.
Number of body orientations	Number of times the subject turned more than halfway from the direction of travel toward the snake model location as sign of high attentiveness.
Looking duration	Total duration of all looks within a 30° arc of the snake model location.
Latency	Time between snake model detection and first occurrence of onset of response.
Number of pauses	Difference in the number of pauses during the 30 s after and before the model was detected. Pauses were defined as halts in walking or climbing caused by all four limbs stopping movement at the same time.
Number of scans	Number of times the position of the subject's head changed while looking left or right, up or down outside a 45° arc of the snake model, typically gazing towards other individuals, after the detection of the model. Only abrupt changes in direction were noted, indicated by a prior cessation in head movement.
Scanning duration	Total duration of all scans toward other individuals after the detection of the snake model.
Alarm calling	Whether or not subjects produced snake-specific alarm calls after spotting the snake models.

Table S3.2 Interrater reliability measures for each behavioural response. Intraclass Correlation Coefficient (ICC) is used for continuous variables and Cohen's kappa (*K*) for the binary variable. To estimate inter-observer reliability, a second observer blind-coded 50% of the trials. Results indicate excellent interrater reliability.

Behavioural responses	**Interrater reliability measures**
Number of looks	ICC = 0.90
Number of body orientations	ICC = 0.83
Looking duration	ICC = 0.79
Latency	ICC = 0.87
Number of pauses	ICC = 1
Number of scans	ICC = 0.91
Scanning duration	ICC = 0.82
Alarm calling	*K* = 1

Table S3.3 Factor loadings of behavioural response variables.

Variable	Factor 1	Factor 2	Factor 3	Factor 4
Number of looks	0.643	0.452	0.242	0.379
Number of body orientations	0.411	0.472	0.213	–0.198
Looking duration	0.231	0.468	0.543	0.340
Latency		–0.149	–0.111	**0.589**
Number of pauses		**0.974**		–0.206
Number of scans	**0.891**			0.124
Scanning duration	0.889			
Alarm calling			**0.966**	–0.245

Table S3.4. Influence of predictor variables on behavioural responses to snake models.

Fixed effects	Estimate	SE	Z value [a]	Pr(>|z|)
a. Latency				
Intercept	1.62	0.14	[b]	[b]
Age (old juvenile)	–0.23	0.19	–1.67	0.25
Age (young juvenile)	0.10	0.19	0.53	0.59
Model type (viper)	–0.97	0.19	–4.90	**<0.001 ****
Age (old juvenile)*Model type (viper)	0.80	0.28	2.85	**<0.01 ****
Age (young juvenile)*Model type (viper)	0.54	0.28	1.92	0.06 ·
b. Number of pauses				
Intercept	0.69	0.22	[b]	[b]
Age (old juvenile)	0.09	0.25	0.37	0.70
Age (young juvenile)	–0.03	0.26	–0.13	0.89
Model type (viper)	0.39	0.21	1.86	0.06 ·
c. Alarm calling				
Intercept	–2.56	1.58	[b]	[b]
Age (old juvenile)	1.97	1.80	1.09	0.27
Age (young juvenile)	1.97	1.80	1.09	0.27
Model type (viper)	3.86	1.87	2.06	**0.038 ***
Age (old juvenile)*Model type (viper)	–3.86	2.22	–1.73	0.08
Age (young juvenile)*Model type (viper)	–4.57	2.28	–2.00	**0.045 ***
d. Number of scans				
Intercept	0.59	0.23	[b]	[b]
Age (old juvenile)	0.41	0.26	1.56	0.11
Age (young juvenile)	0.62	0.25	2.42	**0.01 ***
Model type (viper)	0.09	0.19	0.49	0.61

[a] t values are shown for the Latency model (LM).

[b] Omitted given that there is no interpretable result.

Parentheses denote the variable level that reflects the estimate when tested against the alternative level: Old and Young juvenile vs Adult, Viper vs Colubrid.

* $P < 0.05$ and ** $P < 0.01$, all P values < 0.05 are in bold and are below the critical value determined by the Benjamini-Hochberg correction for multiple testing and hence considered as evidence for a significant effect.

In all four models, the interaction between the two test predictors was originally included into the full models. We then removed it when no significant to simplify the models. To check whether 'Audience size' influenced behavioural responses, we re-ran all the analyses with this variable as control predictor. Since results were robust, we did not include this variable in the models to avoid overparameterization.

Table S3.5 Response variables and descriptive statistics from N=36 trials with colubrid and viper snake models. Mean ± SE per age group per model type.

	Young juveniles		**Old Juveniles**		**Adults**	
Response variable:	Colubrid	Viper	Colubrid	Viper	Colubrid	Viper
Number of looks	5.5 ± 1.02	5.16 ± 0.54	6 ± 1.21	5.33 ± 0.76	3.33 ± 0.42	5.33 ± 0.99
Number of body orientations	1 ± 0.51	1.83 ± 0.54	1.5 ± 0.5	1.66 ± 0.21	0.16 ± 0.16	1.66 ± 0.56
Looking duration (s)	10.82 ± 2.79	12.5 ± 2.99	10.37 ± 3.06	9.7 ± 2.84	4.68 ± 1.28	11.1 ± 2.19
Latency (s)	3.1 ± 0.51	1.73 ± 0.3	2.13 ± 0.53	1.6 ± 0.38	2.7 ± 0.38	0.43 ± 0.08
Number of pauses	2 ± 0.44	2.83 ± 0.47	2.33 ± 0.33	3.16 ± 0.47	1.83 ± 0.47	3.16 ± 0.3
Number of scans	3.66 ± 0.33	3.5 ± 0.5	3 ± 0.96	2.83 ± 0.6	1.33 ± 0.61	2.5 ± 0.84
Scanning duration (s)	4.7 ± 0.83	4.86 ± 1.67	4.24 ± 1.77	3 ± 1.07	1.44 ± 0.83	3.2 ± 1.43
Alarm calling (binary)	0.33 ± 0.21	0.16 ± 0.16	0.33 ± 0.21	0.33 ± 0.21	0 ± 0	0.83 ± 0.16

Chapter 4: Acquisition of predator knowledge from alarm calls via one-trial social learning in monkeys

Julián León[1, 2, *], Constance Thiriau[2], Clémentine Bodin[2], Catherine Crockford[3,4] and Klaus Zuberbühler[1, 2, 5]

[1]Institute of Biology, University of Neuchâtel, 2000 Neuchâtel, Switzerland.

[2]Taï Monkey Project, Centre Suisse de Recherches Scientifiques, 01 BP1303 Abidjan 01, Cote d'Ivoire.

[3]Institute of Cognitive Sciences Marc Jeannerod, CNRS, 69330, Lyon, France

[4]Taï Chimpanzee Project, Centre Suisse de Recherches Scientifiques, 01 BP1303 Abidjan 01, Cote d'Ivoire.

[5]School of Psychology and Neuroscience, University of St. Andrews, KY16 9JP Saint Andrews, Scotland (UK).

(Manuscript published in iScience; DOI: https://doi.org/10.1016/j.isci.2022.104853)

4.1 Abstract

How do animals learn to classify the world and what is the role of social learning during this process? Here, we show that young sooty mangabeys, Cercocebus atys, of Taï Forest, Côte d'Ivoire, learn to rapidly classify an unfamiliar predator by attending to others' alarm calls and that such knowledge is retained over long periods. We experimentally exposed subjects to chimeric predator models with both snake- and leopard-like features, combined with playbacks of conspecific snake (N=12) or leopard alarms (N=13). Adults classified the chimeras as non-threatening but for juveniles, we found that one single alarm call exposure was sufficient to allocate the chimera to the snake or leopard category, suggesting plausibility judgments in experienced adults. We then retested N=10 juveniles with the same models more than a year after their first experience and found that they continued to show their original response, indicating long-term retention of socially learned predator categorisation.

4.2 Keywords:

Vocal communication, Predation, Social learning, Fast-mapping, Long-term retention

4.3 Introduction

How do non-human primates learn to classify predators? Early research on the vervet monkey alarm call system have shown that infants are, to some extent, predisposed from birth to discriminate between the basic predator classes (aerial vs terrestrial), but with experience become increasingly more competent in recognising the few predatory species that pose an actual threat (e.g., martial eagles, leopards). Social learning is a likely driver during this process, with behavioural effects on alarm call production and antipredator responses (Hauser, 1989; Seyfarth & Cheney, 1980, 1986). More recent fieldwork has shown that predator category formation can be astonishingly rapid. West African green monkeys produced aerial alarm calls when exposed to a drone for a first time (Wegdell et al., 2019), while in subsequent encounters the mere sound of the drone was already sufficient to elicit scanning the sky and running for cover. In another field experiment, Wheeler and colleagues (2019) showed that, after a small number of trials, capuchin monkeys learned to associate novel sounds with the presence of predators and that they could retain such knowledge for many months.

Rapid and efficient learning is clearly adaptive in the predation context, a powerful selection force with considerable fitness consequences, but often very limited learning opportunities (Curio, 1976). Moreover, many species are faced with a range of regionally varying predator species that require different antipredator responses (Bidner, 2014; Stephan & Zuberbühler, 2008, 2014). Rapid learning has been also demonstrated in the foraging context, such as taste aversion in laboratory rats (Garcia et al., 1955) or fast-mapping in a dog trained to fetch toys (Kaminski et al., 2004). While rapid learning is well documented, it still remains unclear how exactly animals acquire such knowledge. Group-living animals grow up surrounded by more experienced group members, suggesting that social learning is important to obtain information from interacting or observing more experienced ones (Galef & Laland, 2005; Heyes & Galef, 1996). A classic example is Curio and colleagues' (1978) study on blackbird mobbing behaviour, which could be conditioned to novel raptor models and even random objects (plastic bottles), as long as the social input was adequate. Similar experiments with rhesus monkeys showed that individuals that were naive and initially fearless of snakes came to avoid them, after observing the aversive response of a more experienced individual towards a snake (Mineka & Cook, 1993).

In this study, we investigated the role of social learning in predator category formation in a terrestrial forest primate, the sooty mangabeys (*Cercocebus atys*). In Taï Forest, Côte d'Ivoire, mangabeys are hunted by leopards (*Panthera pardus*) (Zuberbühler & Jenny, 2002), crowned eagles (*Stephanoaetus coronatus*) (Shultz & Thomsett, 2007) but they are also vulnerable to accidental snakebites, notably by highly venomous Gaboon and rhinoceros vipers (*Bitis gabonica*; *B nasicornis*) (Penner et al., 2008). Sooty mangabeys frequently encounter leopards (1.04 per observation week), crowned eagles (8.94 per observation week), and large vipers (2.83 per observation week; Supplementary Methods S4.1). Leopards attack primates on the ground or in the lower canopy but monkeys can protect themselves by rapid climbing. Vipers do not pursue and are no longer dangerous once discovered and monitored (Crockford et al., 2015). Mangabeys produce acoustically distinct alarm calls to both predators (Range & Fischer, 2004). Predator detection is probably strongly visually guided, with evidence from other primates that the spotted leopard coat and distinct body shape of vipers are sufficient to trigger alarm calling (Coss et al., 2005; Coss & Ramakrishnan, 2000; Crockford et al., 2015; Pessoa et al., 2014; Schel & Zuberbühler, 2009).

Here, we experimentally tested whether free-ranging sooty mangabeys could socially learn to categorise a visually ambiguous animal model with features of both leopards and vipers (Figure 4.1). We first examined how subjects from different age groups reacted spontaneously to these chimeric animal models, deliberately designed to create ambiguity for classification and thus preventing individuals from making predictions about dangerousness, hunting technique or appropriate alarm call behaviour. We were interested in whether subjects would rely on other group members' apparent assessments of the chimera, if given the opportunity. We operationalised this this in a second experiment with juveniles, by first letting a subject encountered the chimera, immediately followed by playbacks of snake or leopard alarm calls by a familiar (but invisible) group member. Later that same day, we presented the chimeric model for a second time to the same subjects and registered their responses. If subjects attended to others' alarm calls (i.e., their categorisations), we predicted that they should use this information in the future encounters with the chimera (see Table 4.1 for definitions of antipredator behaviours).

Table 4.1. Definitions and predictions of behavioural responses.

Behavioural response	**Definition**	**Prediction**[*]
Snake antipredator behaviours	Subject stays and scans the forest floor, approaches and inspects, jumps aside, stands bipedally and/or emits snake alarm calls	Snake > Leopard
Number of pauses	Subject stops walking by halting all limb movement at the same time. Individuals pause more when caution is required to ascertain the nature and location of a nearby stationary threat.	Snake > Leopard
Leopard antipredator behaviours	Subject escapes climbing into a tree, flees and/or emits leopard alarm calls	Leopard > Snake
Move >10 m	Subject displaces more than 10 m away from the model after detecting it. Individuals increase their distance from a nearby chaser threat.	Leopard > Snake

4.4 Methods

Experimental Model and Subject Details

The study was conducted from August 2019 to March 2020 and March to August 2021 with two groups of free-ranging sooty mangabeys in Taï National Park, Côte d'Ivoire. Both groups were fully habituated to human observers (McGraw & Zuberbühler, 2007). We first collected baseline data to the chimera model from 15 subjects (6 adults, 3 old and 5 young juveniles) from the main study group and 4 juveniles (3 old and 1 young juveniles) from one group whose home range was about 4 km Northwest of the main study group (Mielke et al., 2019). All experiments were conducted on the main study group, whose size was around 81 individuals during the study period, including 30 adults (23 females, 7 males; >5 years old), 12 subadults (6 females, 6 males; 4–5 years old), 17 old juveniles (9 females, 8 males; 3–4 years old) and 22 young juveniles (10 females, 12 males; 1–2 years old).

Figure 4.1. Chimeric models. Illustrations of two custom-made, snake-leopard chimeric animal models with visual features of two predators; leopard colour pattern and viper body shape. The two models differed in the surface structure, one being a painted wooden item (left) and the other being covered with commercially printed fabric (right).

Method Details

Experimental design

We fabricated two chimeric animal models with mixed visual features of leopards and vipers, using wood, acrylic paint and fabric as materials (Figure 4.1). Natural encounters with leopards, Gaboon and rhinoceros vipers are common occurrences in the study area. To avoid habituation and minimize stress, we presented chimeric animal models once per week, which was within the monkeys' natural range of experience with the mentioned ground predators (Supplementary Methods 4.1, Figure S4.1 and Table S4.1).

We followed sooty mangabeys and collected behavioural data from dawn to dusk for a second study. We used 20-min focal animal samples (Altmann, 1974) to record detailed behavioural data for all members of the main study group. We chose the first focal subject opportunistically and then sampled all individuals of the same age-sex class before making repeated samples of the same individual. During 930 focal samples (531 samples on adult and 399 on immatures subjects), we were able to document natural encounters with leopards (N=4) and Gaboon and rhinoceros vipers (N=14). Additionally, we recorded the vocal responses produced in N=5 leopard model, a realistic-looking plush toy, presentations. We recorded all alarm calls with a Marantz PMD 661 MKII digital recorder and an MKH 416-P48U3 Sennheiser directional microphone. Sound files were stored and processed as .wav files with 44.1 kHz sampling rate, 16 bits amplitude resolution using Audacity 2.2.2 (Audacity Team, 2020) and Raven 1.4 software (Center for Conservation Bioacoustics, 2014). Recordings were screened for exemplars with low signal-to-noise ratio, absence of signal overlap and recording distances of less than 10 m. We extracted 31 alarm calls (leopard alarm: N=15; snake alarm: N=16, see Figure S4.2) from 29 individuals (N=26 adults, N=2 old and N=1 young juveniles) that were used as playback stimuli.

Baseline condition

The study consisted of a baseline and two assessment conditions (Supplementary Methods S.2). In the baseline condition, we presented a chimeric model to N=6 adults, N=7 old and N=6 young juveniles, to describe the non-primed, spontaneous reactions to the models. All focal subjects were in the periphery of the group. As subjects had no prior experience with the model, they were prevented from making predictions about its dangerousness, hunting technique, mode of attack or appropriate alarm call. We decided to exclude adults from further experimental trials, as they consistently ignored the chimeric models in the baseline condition (N=6) (Table S4.2).

Experiment 1: Categorisation of chimeras

We conducted a total of N=26 experimental trials (N=13 old; N=13 young juveniles), each consisting of a model presentation in conjunction with an alarm playback (presentation trial), followed by a subsequent assessment (assessment trial), consisting of a second model presentation sometime after the first one (Table S4.3). One trial with a young female juvenile was aborted because of a technical problem with the playback speaker during the presentation of the chimeric model, resulting in a final dataset of N=25 trials.

During the presentation trial, the chimeric model was shown to a subject and, as soon as it detected the model, we played back either leopard alarms (N=13) or snake alarms (N=13). By simultaneously broadcasting another individual's alarm calls when model detection occurred, subjects were offered pivotal information on how to interpret the unfamiliar animal model. To avoid pseudo-replication, we used a different playback stimulus (N=26 alarm calls from 24 call providers) for each trial and ensured that we never broadcast a call from a call provider that was in the audience. 12 adult and 1 juvenile female and 8 adult, 2 subadult and 1 juvenile male were used as call providers (Table S4.4). We could not ascertain if some call providers were more effective in instilling knowledge in juveniles than others (e.g., hierarchy, kin or social bond effects), but by always broadcasting a different call stimulus and trying to avoid using call providers twice, we are confident that the identity of the caller did not have a major effect on our results. All stimuli were broadcasted using an Apple iPod touch digital player connected to an AER alpha speaker amplifier. The two types of chimeric models and the playback stimuli were presented in a randomized but counterbalanced way.

We then presented the chimeric model for a second time to the same subject and registered his or her response. Assessment trials were usually conducted on the same day (mean = 2.75 h; range: 1.2–20.0 h), but only after the subject had left the area of the first encounter and had engaged in other activities. Assessment trials were conducted only if no other predator-related event had occurred during the previous hour and when subjects were in the periphery of the group, usually isolated with no other individual within 5–10 m.

Experiment 2: Long-term retention

After a break of nearly two years (mean = 603 days; range: 534–718 days), an experimenter (CB) naive to the original study revisited the group and managed to retest N=11 subjects (N=7 old, N=4 young juveniles). N=4 subjects were originally primed with leopard alarm calls and N=7 originally with snake alarm calls. N=1 trial (old juvenile primed with snake alarms) was aborted because the subject became interrupted by a social interaction during the model presentation, resulting in a final dataset of N=10. Experimental conditions were identical to experiment 1.

Behavioural response variables

For each trial, we noted the identity and behavioural responses of the subject, type of model (paint or fabric), play backed alarm call (snake or leopard), time of model detection and audience composition within a 10–15 m radius of the subject. We distinguished four behavioural responses: snake antipredator behaviour (scored as 1 when subject stays and scans the forest floor, approaches and inspects, jumps aside, stands bipedally and/or emits snake alarm calls; binary), number of locomotor pauses 30 s before and after a model was detected (numeric), leopard antipredator behaviour (scored as 1 when subject escapes climbing into a tree, flees and/or emits leopard alarm calls; binary), and whether or not the subject moved >10 m from the model (scored as 1 when subject displaces more than 10 m away from the model after detecting it; binary) (Table 4.1). To estimate observer reliability, a second observer (Auriane Le Floch) blind-coded (21/43) 48.8% of trials, resulting in an excellent interrater reliability (Cohen's kappa for Snake antipredator behaviours: K=1; Leopard antipredator behaviours: K=1; Move >10 m: K=0.84 and intraclass correlation coefficient for the number of pauses: ICC=0.91). We used a Panasonic HC-V500 camera for video recordings and a Solomon coder (solomon.andraspeter.com) to analyse video recordings on a frame-by-frame basis (25 frames s^{-1}).

Quantification and statistical analysis

Contrary to frequentist methods, Bayesian analyses do not rely on asymptotic theory, a property that can be a drawback when analysing small sample size datasets (Smid et al., 2020). Hence, we used a mix of GLMs and Bayesian analyses as a way to overcome any potential small sample size issue, an inherent problem in primate cognition research, both in captivity and in the wild.

We used a series of Generalized Linear Models (McCullagh & Nelder, 1989) using R version 4.0.3 (R Core Team, 2020) and the functions 'bayesglm' (for binary variables; family = Binomial) and 'glm' (for numeric variable; family = Poisson) of the packages arm (Gelman & Su, 2020) and stats (R Core Team, 2020), respectively.

Each model tested a different behavioural response variable, coded from the assessment trials videos, against the same set of four fixed effects predictor variables. The predictor variables were as follows: (1) Playback Stimulus (snake or leopard alarm calls), (2) Juvenile Age (young or old), (3) Audience (alone or in company) and (4) Model Type (paint or fabric). Playback stimulus was our main variable of interest and was considered the test predictor, with the other three variables considered to be control predictors. None of the control predictors had a significant effect on the behavioural responses (Table S4.5). To check whether the control factor Model Type (paint or fabric) drove the results (Simmons et al., 2011), we re-ran all the analyses without it. The results were robust. Additionally, we included the interaction Playback Stimulus and Juvenile Age, to detect if younger individuals had any association preference for the chimeric model to a particular predator type. In all models, this interaction was not significant; thus, we removed it, and then reran the models (Table S4.5). A test of over-dispersion showed no cause for concern with dispersion parameters <1. To count for multiple testing, of the same behavioural response, P values were subjected to Bonferroni corrections, such that values below $P = 0.0125$ were considered significant.

Finally, we conducted one-sided Bayesian binomial tests, on JASP (Team, 2020) to analyse subjects' behavioural responses during control condition and retest trials and their vocal response during assessment trials. We specified a test value of 0.5, and a=b=1 for the prior distribution of θ under $\mathscr{H}1$. To interpret Bayes factors, we followed the classification of strength of evidence proposed by van Doorn et al. (van Doorn et al., 2021) in line with Jeffreys (Jeffreys, 1939): a Bayes factor smaller than 3 was interpreted as weak evidence, a Bayes factor between 3 and 10 was interpreted as moderate evidence, and a Bayes factor greater than 10 was interpreted as strong evidence for the alternative H_1 relative to the null hypothesis H_0. We also conducted frequentist statistics (binomial test) on the same behavioural and vocal responses to help interpretability of the results. We found no change in our results and conclusions (Table S4.6).

4.5 Results & Discussion

Baseline responses

We tested two immobile chimeric predator models with both snake-like and leopard-like features, which we positioned on a subject's anticipated travel path (Supplementary Methods 4.2). We collected data from subjects belonging to two different groups (TMP group: adults: N=6 adults, old juveniles (OJ): N=4, young juveniles (YJ): N=5; TCP group: OJ: N=3, YJ: N=1); see methods section for group sizes and composition). Adults consistently ignored the model (Bayes factor BF_{10} = 18.14, see methods section for interpretation of Bayes factors and Table S4.6 for equivalent frequentist statistics; Table S4.2), suggesting that they perceived the chimeras as irrelevant or at least non-threatening. In contrast, 9 of 13 juveniles treated the model as a potential predator. However, we did not find that juveniles had any clear bias to classify the chimera as a threat (Bayes factor BF_{10} = 1.49; Table S4.6). Specifically, 5 of 7 old juveniles and 4 of 6 young juveniles showed strong antipredator behaviour (Table S4.2). Although, at first sight, the models looked more similar to a snake-like animal than to a leopard-like one, there was no evidence for subjects having an overall bias to one or the other predator (snake response: OJ: N=2; YJ: N=3; leopard response: OJ: N=3; YJ: N=1; Bayes factor BF_{10} = 0.3; Table S4.6). These results suggest that juveniles categorised the chimeric models either as non-threatening animal or that, if they considered it a threat, either as snake or a leopard.

Experiment 1: Categorisation of chimeras

We then carried out the first experiment on individuals other than those used in the baseline condition (N=25; OJ: N=13, YJ: N=12; Table 4.2 and Table S4.3). Experimental trials consisted of two conditions: 1) presentation of a model, this time in conjunction with a playback of either snake or leopard alarms and 2) a subsequent assessment (Supplementary

Methods S4.2). As in the baseline condition adults consistently ignored the models, we decided to conduct the experiment with juveniles only. In each presentation trial, the chimera was shown to a subject and, as soon it had detected it, we played back either snake or leopard alarm calls of a familiar group member from a nearby concealed speaker (Figure S4.1). In subsequent assessment trials a few hours later (mean = 2.75h; range: 1.2–20.0h), we investigated whether subjects retained the relevant knowledge by presenting the model for a second time, this time without accompanying alarm calls.

Table 4.2. Juveniles' behavioural responses in assessment trials (N=26; one trial was aborted). Snake and leopard refers to antipredator behaviours. Leopard and move > 10 m responses are not mutually exclusive.

	Responses				
Play back alarm call	Snake	$\bar{x}$ N pauses (sd)	Leopard	Move > 10 m	Ignore
Snake (N=13)	9	2.38 (1.85)	0	1	3
Leopard (N=12)	1	1 (1.04)	4	7	4

In the assessment trials, we found that 5 of 25 juveniles (20.0%) produced alarm calls (N=4 snake condition, N=1 leopard condition; Table S4.3) that matched the ones experienced during playback. This suggests that subjects had learned to categorise the chimeric models from attending to others and that they were able to transmit this new knowledge with their own alarm calls (Bayes factor BF_{10} = 10.5; Table S4.6). These response rates may not seem particularly high, but they are comparable to what is usually observed in juveniles during natural encounters. During 177 and 133 hours of focal animal data on adults and immatures, respectively, we registered N=14 viper and N=4 leopard encounters events. In only N=3 viper and N=1 leopard encounters, a juvenile was the first individual to alarm call (22.2% of all observed snake and leopard natural encounters), suggesting that alarm calling was mainly initiated by more experienced adults and subadults, an effect also found in other primate studies (Dezecache et al., 2019; Hollén et al., 2008; Mielke et al., 2019). We found no evidence that juvenile age, the presence of audiences within 10 m or model type (paint or fabric) explained differences in alarm responses (Bayes factor, Age: BF_{10} = 0.7; Audience: BF_{10} = 0.7; Model

Type: BF_{10} = 1.9; Table S.41). Finally, the call providers during the presentation trials were always different and did not follow any evident categorisation pattern (two adult females and one adult, subadult and juvenile male each).

Regarding non-vocal responses, 13 of 25 subjects (52.0%) showed evidence that they treated the chimera as belonging to either the snake or the leopard category. These learned associations were more easily established with snake (snake GLM, estimate = −3.29, SE = 1.16, z = −2.82, P = 0.004; Figure 4.2a; Table 4.1 and Table S4.5a; Supplementary Video S4.1) than leopard alarms (leopard GLM, estimate = 2.99, SE = 1.57, z = 1.9, P = 0.05; Figure 4.3a, Table 4.1 and Table S4.5c; Supplementary Video S4.2), suggesting that the chimera was perceived as more snake-like than leopard-like (9 of 13 (69.2%) juveniles responded with snake antipredator behaviour; while only 4 of 12 (33.3%) responded with leopard antipredator behaviour). The fact that subjects exposed to snake alarm calls moved more cautiously when encountering the chimeric model again supports this idea (number of pauses GLM, estimate = −0.86, SE = 0.34, z = −2.51, P = 0.011; Figure 4.2b; Table 4.1 and Table S4.5b; Supplementary Video S4.1). Nevertheless, 7 of 12 subjects (58.3%) that heard leopard alarms increased their distance to the model (move >10m GLM, estimate = 2.8, SE = 1.1, z = 2.53, P = 0.011; Figure 4.3b; Table 4.1 and Table S4.5d; Supplementary Video S4.3). Although we did not record many strong leopard-type escape responses to the chimera when hearing leopard alarms during the model presentations, the observed behaviours were in line with what occurs during natural encounters with smaller cat-like species, particularly genets (*Genetta* spp.) and civets (*Civettictis civetta*; J León, unpublished data), suggesting that juveniles classified the chimera as a cat-like carnivore. Finally, seven more individuals ignored the model and two subjects that heard each type of alarm responded with mismatched behaviours: the one that heard snake alarms increased her distance to the model, while the subject that heard leopard alarms showed snake-type antipredator behaviour (Table 4.2 and Table S4.3).

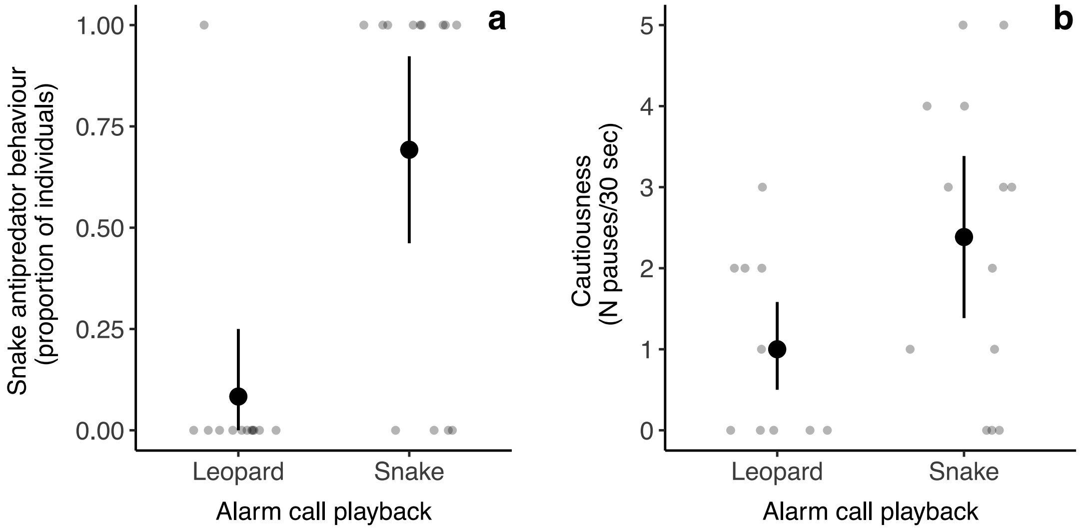

Figure 4.2. Sooty mangabey behavioural responses after detecting the chimeric model during the assessment trials. a) Proportion of individuals showing snake antipredator behaviour. b) Number of pauses. Black dots indicate medians, vertical lines indicate a 95% percentage interval, and grey dots indicate individual values for each subjects' response. Leopard condition N=12, snake condition N=13.

We also tested if the time interval between presentation and assessment trials had an effect on the responses of subjects. Although both trials were usually conducted on the same day, the number of hours since the presentation trials did not have a significant effect on the response to the chimeric model during the assessment trials, suggesting that learning was stable in the short-term (corresponding response in function of time interval between trials GLMM: estimate = 0.01, SE = 0.01, $z = 1.04$, $P = 0.29$).

In contrast to subjects in the baseline condition, who equally –and spontaneously– treated the chimera as a predator animal belonging equally to the snake and leopard category, subjects in experiment 1 categorised more easily the chimera as a snake-like threat. This is not very surprising since the chimeric model looked more similar to a snake-like animal than a leopard-like one. Thus, the learned associations were probably more readily established with snake alarm calls. Similarly, only a slight majority of subjects showed strong antipredator responses after categorising the chimeras as either a snake or a leopard, which was in line with natural observations. In fact, during natural predator encounters juveniles showed low response rates, while most antipredator behaviours, including alarm calls, were initiated by adults. This suggests that primate antipredator behaviours develop through a combination of simple maturation, personal experience and social inputs from other group members.

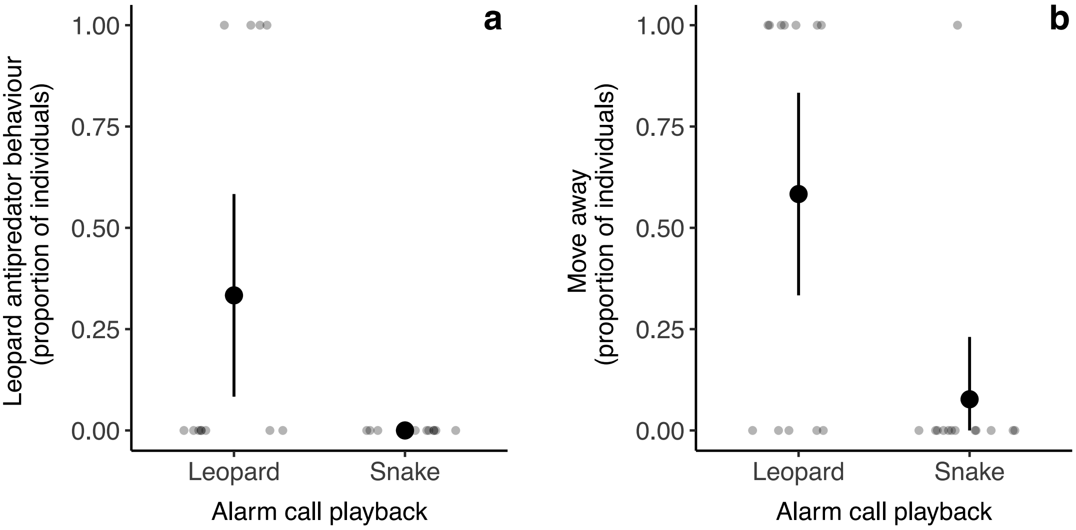

Figure 4.3. Sooty mangabey behavioural responses after detecting the chimeric model during the assessment trials. a) Proportion of individuals showing leopard antipredator behaviour. b) Proportion of individuals moving >10 m away from the model. Black dots indicate medians, vertical lines indicate a 95% percentage interval, and grey dots indicate individual values for each subjects' response. Leopard condition N=12, snake condition N=13.

In sum, our study demonstrated that sooty mangabeys can socially learn to classify novel objects from one single social learning experience, by attending to the referential properties of others' alarm calls. This finding aligns with the hypothesis that non-human primates become communicatively competent by learning to understand of how natural events usually unfold, specially by observing how others behave in unfamiliar situations (Zuberbühler et al., 2022).

Although predation is a major force of natural selection, actual predation attempts on particular individuals are often rare, while inconsequential encounters with predators are quite common. Hence, young individuals probably have opportunities to see predators, but it may be much more difficult to learn how to categorise them. To overcome this challenge, the ability to socially learn from how experienced group members react during predator sightings is clearly adaptive (Curio et al., 1978; Keen et al., 2020; Magrath et al., 2015; Potvin et al., 2018). Our field experiment adds to this line of research by showing how categorisation of novel objects can occur by attending to the referential information of others' vocalizations.

Experiment 2: Long-term retention

To assess whether the socially learned categorisation of the chimeric models was retained, we conducted retest trials almost 2 years after the first encounters. We were able to expose 10 of the original subjects to the same chimeric model for a third time after an average interval of 603 days (range 534–718 days). Remarkably, 9 of 10 subjects (90.0%) still exhibited the same reaction as in the assessment trials, indicating that associations formed during the initial exposure were retained permanently (Bayes factor BF_{10} = 18.51; Tables S4.1 and S4.7). It should be noted, though, that 3 of 10 subjects ignored the models in the initial exposure, so it is unknown if they have retained a previously learned association or relied on other cues to categorise the chimeras. Moreover, we found no evidence of any memory decay, when taking into account intervals between assessment and retest trials (Figure 4.4). We could retest only one of the five subjects who had a vocal response during the first experiment. One of ten subjects (10.0%) produced an alarm call (snake) during the retests; however, he was the same subject who gave a vocal response before and we were able to retest. This caller heard snake alarms when first presented to the chimera, suggesting that alarm calling could be part of socially learned antipredator behaviour to some extent. However, the variation in the responses and the small sample size in the retest trials suggests that the role of social learning in the retention of knowledge partially acquired through vocal signals should be interpreted with some caution.

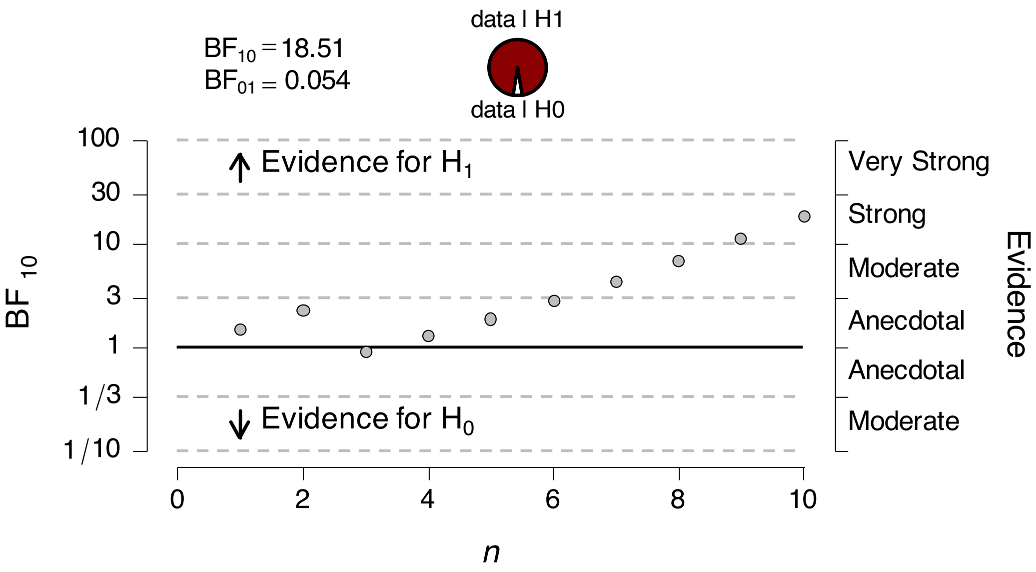

Figure 4.4. Bayes factor sequential sampling plot for retest trials. Accumulation of evidence after each of the N=10 retest trial data points is added as a function of its time interval between its corresponding assessment trials. The probability wheel at the top illustrates the ratio of the evidence in favour of the two hypotheses. Estimated Bayes factors for null (BF_{01}) and alternative (BF_{10}) hypotheses suggested that the data were 0.054:1 in favour of the absence of effect, or rather, 18.51 times more likely to occur under the presence of a long-term association effect than without it.

Limitations of study

We have shown that mangabeys can rapidly acquire predator knowledge from others' alarm calls by one-trial social learning, a conclusion based on the following limitations. First, a general problem in animal cognition research, especially in the wild, is low sample size, and our study is no exception. Habituation of wild primates to human observers is extremely time-consuming and a major financial commitment so it is difficult to see how address the problem at our study site. The main alternative is by replication in other species or with novel experimental designs. Specific to this study, it was impossible to find the 'perfect' chimera, i.e., a creature with equal amounts of 'leopard-ness' and 'snake-ness'. Although we found no evidence for a bias towards one of the two predator classes in naïve subjects, a wider range of chimera models would have been preferable, varying both in shape and colour patterns. Related to this, it would be interesting to see how far into the 'unnatural' models could have been made (e.g., random objects) before subjects no longer accepted them as a potential predator (see Curio et al., 1978). Future research may want to explore these avenues.

Conclusions

Rapid learning and long-term retention is highly adaptive in the predation context (Griffin, 2004; Wegdell et al., 2019; Wheeler et al., 2019). Despite the limitations of the study, here, we showed that alarm calls can serve as vehicles for rapid and highly efficient one-trail social learning, provided the subject has not yet reached adulthood. Remarkably, one such experience is sufficient to permanently stamp such knowledge into the monkey's mind, with no clear evidence for memory decay. Our study thus demonstrates that non-human primates can learn to identify and classify a novel danger by attending to referential signals and potentially retain such knowledge and communicate it subsequently to others. The effect was not seen in adults who ignored the models, suggesting they were better capable of distinguishing plausible from implausible events, and likely classified the model as irrelevant and non-threatening. Among the juvenile cohort, however, there were no performance differences in the categorisation of the chimeric model, with individuals up to 4 years attending to others' alarm calls as a basis for social learning. Whilst alarm call production is relatively inflexible at the species level, local variation in predators might drive selection for social learning of appropriate local alarm call usage. Whether such a selection pressure drives social learning of call usage more broadly, for example also in social contexts, remains to be tested.

4.6 Acknowledgments

We thank the Centre Suisse de Recherches Scientifiques (CSRS), the Ministère de la Recherche Scientifique, the Ministère de l'Agriculture et des Ressources Animales and the Office Ivoirien des Parcs et Réserves (OIPR) of Côte d'Ivoire for support and permission to conduct research in the Taï National Park. Fieldwork was made possible thanks to Paterson Kalo, Landri Bele and the rest of the Taï Monkey Project (TMP) assistants, to whom we express our gratitude. We thank the Taï Chimpanzee Project (TCP) and its staff for support in the field. We also thank Mélissa Berthet and Alison Ashbury for helpful discussions and comments on the early drafts of this manuscript.

4.7 Funding

This work was funded by the Swiss National Science Foundation Agreement project grants 31003A_166458 (KZ) and 310030_185324 (KZ), and the Swiss National Centre of Competence in Research (NCCR) Evolving Language, Swiss National Science Foundation Agreement #51NF40_180888 (KZ).

4.8 Author Contributions

Conceptualization: JL, KZ; Methodology and experiments: JL, CT, CB; Formal analysis and investigation: JL; Access to the TCP study group: CC; Writing - original draft preparation: JL; Writing - review and editing: JL, KZ; Funding acquisition: KZ; Supervision: KZ

4.9 Competing interests

The authors declare no competing interests.

4.10 Data and code availability

All data reported in this paper are included in the Supplemental Information file. All original code has been deposited at OSF: https://osf.io/t93xa/. All supplementary videos have been deposited at OSF and are publicly available at the following link: https://osf.io/hw2r7/?view_only=c5581e1a8e6e4cdba8311ed18871239d.

4.11 References

Abdai, J., Uccheddu, S., Gácsi, M., & Miklósi, Á. (2022). Exploring the advantages of using artificial agents to investigate animacy perception in cats and dogs. *Bioinspiration & Biomimetics*, *17*(6). https://doi.org/10.1088/1748-3190/ac93d9

Abrams, P. A. (2001). Predator-Prey Interactions. In C. W. Fox, D. A. Roff, & D. J. Fairbairn (Eds.), *Evolutionary Ecology: Concepts and Case Studies* (p. 0). Oxford University Press. https://doi.org/10.1093/oso/9780195131543.003.0028

Adams, D. B., & Kitchen, D. M. (2020). Model vs. playback experiments: The impact of sensory mode on predator-specific escape responses in saki monkeys. *Ethology*, *126*(5), 563–575. https://doi.org/https://doi.org/10.1111/eth.13008

Altmann, J. (1974). Observational Study of Behavior: Sampling Methods. *Behaviour*, *49*(3/4), 227–267. http://www.jstor.org/stable/4533591

Amici, F., Aureli, F., & Call, J. (2010). Monkeys and apes: are their cognitive skills really so different? *American Journal of Physical Anthropology*, *143*(2), 188–197. https://doi.org/10.1002/ajpa.21305

Araya-Salas, M., & Wright, T. (2013). Open-ended song learning in a hummingbird. *Biology Letters*, *9*(5), 20130625. https://doi.org/10.1098/rsbl.2013.0625

Arnold, K., Pohlner, Y., & Zuberbühler, K. (2008). A forest monkey's alarm call series to predator models. *Behavioral Ecology and Sociobiology*, *62*(4), 549–559. https://doi.org/10.1007/s00265-007-0479-y

Arnold, K., & Zuberbühler, K. (2006). Semantic combinations in primate calls. *Nature*, *441*(7091), 303.

Audacity Team. (2020). *Audacity: Free Audio Editor and Recorder* (2.2.2).

Baldwin, D. A., & Moses, L. J. (1996). The Ontogeny of Social Information Gathering. *Child Development*, *67*(5), 1915–1939. https://doi.org/10.2307/1131601

Barros, M., Boere, V., Mello, E. L., & Tomaz, C. (2002). Reactions to Potential Predators in Captive-Born Marmosets (Callithrix penicillata). *International Journal of Primatology*, *23*(2), 443–454. https://doi.org/10.1023/A:1013899931878

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software; Vol 1, Issue 1 (2015)* . https://doi.org/10.18637/jss.v067.i01

Bergman, T. J., Beehner, J. C., Painter, M. C., & Gustison, M. L. (2019). The speech-like properties of nonhuman primate vocalizations. *Animal Behaviour*, *151*, 229–237. https://doi.org/https://doi.org/10.1016/j.anbehav.2019.02.015

Bidner, L. R. (2014). Primates on the Menu: Direct and Indirect Effects of Predation on Primate Communities. *International Journal of Primatology*, *35*(6), 1164–1177. https://doi.org/10.1007/s10764-014-9797-x

Boesch, C., & Boesch-Achermann, H. (2000). *The chimpanzees of the Taï forest : behavioural ecology and evolution*. Oxford : Oxford university press. http://lib.ugent.be/catalog/rug01:000534901

Boesch, C., & Boesch, H. (1989). Hunting behavior of wild chimpanzees in the Taï National Park. *American Journal of Physical Anthropology*, *78*(4), 547–573. https://doi.org/https://doi.org/10.1002/ajpa.1330780410

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., & White, J.-S. S. (2009). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution*, *24*(3), 127–135. https://doi.org/10.1016/j.tree.2008.10.008

Borrow, N. (2014). *Field Guide to Birds of Western Africa*. Bloomsbury Publishing.

Bradbury, J. W., & Balsby, T. J. S. (2016). The functions of vocal learning in parrots. *Behavioral Ecology and Sociobiology*, *70*(3), 293–312. https://doi.org/10.1007/s00265-016-2068-4

Brodbeck, D. R., Burack, O. R., & Shettleworth, S. J. (1992). One-trial associative memory in black-capped chickadees. *Journal of Experimental Psychology: Animal Behavior Processes*, *18*, 12–21. https://doi.org/10.1037/0097-7403.18.1.12

Brumm, H., Voss, K., Köllmer, I., & Todt, D. (2004). Acoustic communication in noise:

regulation of call characteristics in a New World monkey. *The Journal of Experimental Biology*, *207*(Pt 3), 443–448. https://doi.org/10.1242/jeb.00768

Bshary, R., & Noë, R. (1997). Red colobus and Diana monkeys provide mutual protection against predators. *Animal Behaviour*, *54*(6), 1461–1474. https://doi.org/https://doi.org/10.1006/anbe.1997.0553

Carlson, N. V, Kelly, E. M., & Couzin, I. (2020). Individual vocal recognition across taxa: a review of the literature and a look into the future. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *375*(1802), 20190479. https://doi.org/10.1098/rstb.2019.0479

Cäsar, C., & Zuberbühler, K. (2012). Referential alarm calling behaviour in New World primates. *Current Zoology*, *58*(5), 680–697. https://doi.org/10.1093/czoolo/58.5.680

Castro, N. A., & Snowdon, C. T. (2000). Development of Vocal Responses in Infant Cotton-Top Tamarins. *Behaviour*, *137*(5), 629–646. http://www.jstor.org/stable/4535727

Center for Conservation Bioacoustics. (2014). Raven Pro: Interactive Sound Analysis Software. In *Ithaca, NY: The Cornell Lab of Ornithology.* (1.5).

Cheney, D. L., & Seyfarth, R. M. (1985). Social and non-social knowledge in vervet monkeys. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences*, *308*(1135), 187–201. https://doi.org/10.1098/rstb.1985.0019

Cheney, D, & Seyfarth, R. (2018). Flexible usage and social function in primate vocalizations. *Proceedings of the National Academy of Sciences*, *115*(9), 1974–1979. https://doi.org/10.1073/pnas.1717572115

Cheney, DL, & Seyfarth, R. (1990). How monkeys see the world: Inside the mind of another species. In *How monkeys see the world: Inside the mind of another species.* University of Chicago Press.

Chippaux, J.-P. (2006). *Les serpents d'Afrique occidentale et centrale*. IRD éditions.

Chomsky, N. (1965). *Aspects of the Theory of Syntax*. MIT press.

Chomsky, N. (2017). Language architecture and its import for evolution. *Neuroscience &*

Biobehavioral Reviews, *81*, 295–300. https://doi.org/https://doi.org/10.1016/j.neubiorev.2017.01.053

Chouinard-Thuly, L., Gierszewski, S., Rosenthal, G. G., Reader, S. M., Rieucau, G., Woo, K. L., Gerlai, R., Tedore, C., Ingley, S. J., Stowers, J. R., Frommen, J. G., Dolins, F. L., & Witte, K. (2017). Technical and conceptual considerations for using animated stimuli in studies of animal behavior. *Current Zoology*, *63*(1), 5–19. https://doi.org/10.1093/cz/zow104

Chow, C. P., Mitchell, J. F., & Miller, C. T. (2015). Vocal turn-taking in a non-human primate is learned during ontogeny. *Proceedings. Biological Sciences*, *282*(1807), 20150069. https://doi.org/10.1098/rspb.2015.0069

Clark, E. (2003). *First language acquisition*. Cambridge University Press.

Clarke, E., Reichard, U. H., & Zuberbühler, K. (2006). The syntax and meaning of wild gibbon songs. *PloS One*, *1*(1), e73.

Clay, Z., & Zuberbühler, K. (2011). Bonobos Extract Meaning from Call Sequences. *PLoS ONE*, *6*(4), e18786. https://doi.org/10.1371/journal.pone.0018786

Cook, M., & Mineka, S. (1990). Selective associations in the observational conditioning of fear in rhesus monkeys. *Journal of Experimental Psychology. Animal Behavior Processes*, *16*(4), 372–389.

Coss, R. G., McCowan, B., & Ramakrishnan, U. (2007). Threat-Related Acoustical Differences in Alarm Calls by Wild Bonnet Macaques (Macaca radiata) Elicited by Python and Leopard Models. *Ethology*, *113*(4), 352–367. https://doi.org/https://doi.org/10.1111/j.1439-0310.2007.01336.x

Coss, R. G., & Ramakrishnan, U. (2000). Perceptual Aspects of Leopard Recognition by Wild Bonnet Macaques (Macaca radiata). *Behaviour*, *137*(3), 315–335. http://www.jstor.org/stable/4535708

Coss, R. G., Ramakrishnan, U., & Schank, J. (2005). Recognition of partially concealed leopards by wild bonnet macaques (Macaca radiata): The role of the spotted coat. *Behavioural Processes*, *68*(2), 145–163.

https://doi.org/https://doi.org/10.1016/j.beproc.2004.12.004

Crockford, C, & Boesch, C. (2005). Call combinations in wild chimpanzees. *Behaviour*, *142*, 397–421.

Crockford, C, Wittig, R. M., Mundry, R., & Zuberbühler, K. (2012). Wild Chimpanzees Inform Ignorant Group Members of Danger. *Current Biology*, *22*(2), 142–146. https://doi.org/https://doi.org/10.1016/j.cub.2011.11.053

Crockford, C, Wittig, R. M., & Zuberbühler, K. (2015). An intentional vocalization draws others' attention: a playback experiment with wild chimpanzees. *Animal Cognition*, *18*(3), 581–591. https://doi.org/10.1007/s10071-014-0827-z

Crockford, C, Wittig, R. M., & Zuberbühler, K. (2017). Vocalizing in chimpanzees is influenced by social-cognitive processes. *Science Advances*, *3*(11), e1701742. https://doi.org/10.1126/sciadv.1701742

Curio, E. (1976). *The ethology of predation* (Vol. 7). Springer Science & Business Media.

Curio, E., Ernst, U., & Vieth, W. (1978). Cultural Transmission of Enemy Recognition: One Function of Mobbing. *Science*, *202*(4370), 899 LP – 901. https://doi.org/10.1126/science.202.4370.899

Davenport, T. R. B., Stanley, W. T., Sargis, E. J., De Luca, D. W., Mpunga, N. E., Machaga, S. J., & Olson, L. E. (2006). A New Genus of African Monkey, Rungwecebus: Morphology, Ecology, and Molecular Phylogenetics. *Science*, *312*(5778), 1378–1381. https://doi.org/10.1126/science.1125631

de Boer, B. (2005). Evolution of Speech and Its Acquisition. *Adaptive Behavior*, *13*(4), 281–292. https://doi.org/10.1177/105971230501300405

Deshpande, A. (2021). *Social learning and flexibility in vocal communication of wild vervet monkeys* [Université de Neuchâtel]. https://unine.swisscovery.slsp.ch/permalink/41SLSP_UNE/b1j16q/alma991009764729505517%0A

Deshpande, A., Van Boekholt, B., & Zuberbuhler, K. (2022). Preliminary evidence for one-trial social learning of vervet monkey alarm calling. *Royal Society Open Science*, *9*(8), 210560. https://doi.org/10.1098/rsos.210560

Dezecache, G., Crockford, C., & Zuberbühler, K. (2019). The development of communication in alarm contexts in wild chimpanzees. *Behavioral Ecology and Sociobiology*, *73*(8), 104. https://doi.org/10.1007/s00265-019-2716-6

Di Bitetti, M., & Wheeler, B. (2017). The vocal repertoire of the black horned capuchin monkey (Cebus [Sapajus] nigritus): an acoustic and contextual analysis. In M. Kowalewski & L. Oklander (Eds.), *Primatology in Argentina* (Vol. 2, pp. 171–199). Sociedad Argentina para el Estudio de los Mamíferos, Buenos Aires.

Ducheminsky, N., Henzi, S. P., & Barrett, L. (2014). Responses of vervet monkeys in large troops to terrestrial and aerial predator alarm calls. *Behavioral Ecology*, *25*(6), 1474–1484. https://doi.org/10.1093/beheco/aru151

Edwards, M. C., Ford, C., Hoy, J. M., FitzGibbon, S., & Murray, P. J. (2021). How to train your wildlife: A review of predator avoidance training. *Applied Animal Behaviour Science*, *234*, 105170. https://doi.org/https://doi.org/10.1016/j.applanim.2020.105170

Egnor, S. E. R., & Hauser, M. D. (2004). A paradox in the evolution of primate vocal learning. *Trends in Neurosciences*, *27*(11), 649–654. https://doi.org/https://doi.org/10.1016/j.tins.2004.08.009

Egnor, S. E. R., & Hauser, M. D. (2006). Noise-induced vocal modulation in cotton-top tamarins (Saguinus oedipus). *American Journal of Primatology*, *68*(12), 1183–1190. https://doi.org/10.1002/ajp.20317

Egnor, S. E. R., Iguina, C. G., & Hauser, M. D. (2006). Perturbation of auditory feedback causes systematic perturbation in vocal structure in adult cotton-top tamarins. *The Journal of Experimental Biology*, *209*(Pt 18), 3652–3663. https://doi.org/10.1242/jeb.02420

Eisenberg, J. F. (1976). Communication mechanisms and social integration in the black spider monkey, Ateles fusciceps robustus, and related species. *Smithson. Contrib. to Zool.*, 1–108. https://doi.org/doi:10.5479/si.00810282.213

Elowson, A. M., Snowdon, C. T., & Sweet, C. J. (1992). Ontogeny of trill and J-call vocalizations in the pygmy marmoset, Cebuella pygmaea. *Animal Behaviour*, *43*(5), 703–715. https://doi.org/https://doi.org/10.1016/S0003-3472(05)80195-2

Engqvist, L. (2005). The mistreatment of covariate interaction terms in linear model analyses of behavioural and evolutionary ecology studies. *Animal Behaviour*, *70*(4), 967–971. https://doi.org/https://doi.org/10.1016/j.anbehav.2005.01.016

Ernst, R., & Rödel, M. (2002). A new Atheris species (Serpentes: Viperidae), from Taï National Park, Ivory Coast. *Herpetological Journal*, *12*, 55–61.

Etting, S. F., Isbell, L. A., & Grote, M. N. (2014). Factors increasing snake detection and perceived threat in captive rhesus macaques (Macaca mulatta). *American Journal of Primatology*, *76*(2), 135–145. https://doi.org/10.1002/ajp.22216

Evans, A., & Tomasello, M. (1986). Evidence for social referencing in young chimpanzees (Pan troglodytes). *Folia Primatologica; International Journal of Primatology*, *47*(1), 49–54. https://doi.org/10.1159/000156263

Fedurek, P., & Slocombe, K. E. (2011). Primate vocal communication: a useful tool for understanding human speech and language evolution? *Human Biology*, *83*(2), 153–173. https://doi.org/10.3378/027.083.0202

Fedurek, P., Slocombe, K. E., & Zuberbühler, K. (2015). Chimpanzees communicate to two different audiences during aggressive interactions. *Animal Behaviour*, *110*, 21–28. https://doi.org/https://doi.org/10.1016/j.anbehav.2015.09.010

Feise, R. J. (2002). Do multiple outcome measures require p-value adjustment? *BMC Medical Research Methodology*, *2*, 8. https://doi.org/10.1186/1471-2288-2-8

Fichtel, C. (2004). Reciprocal recognition of sifaka (Propithecus verreauxi verreauxi) and redfronted lemur (Eulemur fulvus rufus) alarm calls. *Animal Cognition*, *7*(1), 45–52. https://doi.org/10.1007/s10071-003-0180-0

Fichtel, C. (2008). Ontogeny of conspecific and heterospecific alarm call recognition in wild Verreaux's sifakas (Propithecus verreauxi verreauxi). *American Journal of Primatology*, *70*(2), 127–135. https://doi.org/https://doi.org/10.1002/ajp.20464

Fichtel, C. (2020). Monkey Alarm Calling: It Ain't all Referential, or is It? *Animal Behavior* *and Cognition*, *7*, 101–107.

Fichtel, C., & Kappeler, P. M. (2002). Anti-Predator Behavior of Group-Living Malagasy Primates: Mixed Evidence for a Referential Alarm Call System. *Behavioral Ecology and Sociobiology*, *51*(3), 262–275. http://www.jstor.org/stable/4602047

Fichtel, C., & Kappeler, P. M. (2011). Variation in the Meaning of Alarm Calls in Verreaux's and Coquerel's Sifakas (Propithecus verreauxi, P. coquereli). *International Journal of Primatology*, *32*(2), 346–361. https://doi.org/10.1007/s10764-010-9472-9

Fischer, J. (2017). Primate vocal production and the riddle of language evolution. *Psychonomic Bulletin & Review*, *24*(1), 72–78. https://doi.org/10.3758/s13423-016-1076-8

Fischer, J, & Hammerschmidt, K. (2020). Towards a new taxonomy of primate vocal production learning. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *375*(1789), 20190045. https://doi.org/10.1098/rstb.2019.0045

Fischer, J, Metz, M., Cheney, D., & Seyfarth, R. (2001). Baboon responses to graded bark variants. *Animal Behaviour*, *61*(5), 925–931. https://doi.org/https://doi.org/10.1006/anbe.2000.1687

Fischer, J, & Price, T. (2017). Meaning, intention, and inference in primate vocal communication. *Neuroscience & Biobehavioral Reviews*, *82*, 22–31. https://doi.org/https://doi.org/10.1016/j.neubiorev.2016.10.014

Fischer, J. (2020). Nonhuman primate alarm calls then and now. *Animal Behavior and Cognition*, *7*.

Fischer, J. (2021). Primate Vocal Communication and the Evolution of Speech. *Current Directions in Psychological Science*, *30*(1), 55–60. https://doi.org/10.1177/0963721420979580

Fischer, J, Cheney, D. L., & Seyfarth, R. M. (2000). Development of infant baboons' responses to graded bark variants. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *267*(1459), 2317–2321. https://doi.org/10.1098/rspb.2000.1285

Fischer, J, & Hammerschmidt, K. (2001). Functional referents and acoustic similarity revisited: the case of Barbary macaque alarm calls. *Animal Cognition*, *4*(1), 29–35.

https://doi.org/10.1007/s100710100093

Fischer, J, Kitchen, D. M., Seyfarth, R. M., & Cheney, D. L. (2004). Baboon loud calls advertise male quality: acoustic features and their relation to rank, age, and exhaustion. *Behavioral Ecology and Sociobiology*, *56*(2), 140–148. https://doi.org/10.1007/s00265-003-0739-4

Foerster, S. (2008). Two incidents of venomous snakebite on juvenile blue and Sykes monkeys (Cercopithecus mitis stuhlmanni and C. m. albogularis). *Primates*, *49*(4), 300–303. https://doi.org/10.1007/s10329-008-0098-x

Friard, O., & Gamba, M. (2016). BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. *Methods in Ecology and Evolution*, *7*(11), 1325–1330. https://doi.org/10.1111/2041-210X.12584

Fröhlich, M., & van Schaik, C. P. (2020). Must all signals be evolved? A proposal for a new classification of communicative acts. *WIREs Cognitive Science*, *11*(4), e1527. https://doi.org/https://doi.org/10.1002/wcs.1527

Fugate, J. M. B., Gouzoules, H., & Nygaard, L. C. (2008). Recognition of rhesus macaque (Macaca mulatta) noisy screams: evidence from conspecifics and human listeners. *American Journal of Primatology*, *70*(6), 594–604. https://doi.org/https://doi.org/10.1002/ajp.20533

Galat, G., & Galat-Luong, A. (1985). La communauté de primates diurnes de la forêt de Taï, Côte-d'Ivoire. *Revue d'écologie (Terre Vie)*, *40*, 3–32.

Galef, B. G., & Giraldeau, L.-A. (2001). Social influences on foraging in vertebrates: causal mechanisms and adaptive functions. *Animal Behaviour*, *61*(1), 3–15. https://doi.org/https://doi.org/10.1006/anbe.2000.1557

Galef, B. G., & Laland, K. N. (2005). Social learning in animals: empirical studies and theoretical models. *Bioscience*, *55*(6), 489–499.

Gamba, M., Friard, O., Riondato, I., Righini, R., Colombo, C., Miaretsoa, L., Torti, V., Nadhurou, B., & Giacoma, C. (2015). Comparative analysis of the vocal repertoire of Eulemur: a dynamic time warping approach. *International Journal of Primatology*, *36*(5), 894–910.

Garcia, J., Kimeldorf, D. J., & Koelling, R. A. (1955). Conditioned aversion to saccharin resulting from exposure to gamma radiation. In *Science* (Vol. 122, pp. 157–158). American Assn for the Advancement of Science. https://doi.org/10.1126/science.122.3179.1089

Gautier-Hion, A., Quris, R., & Gautier, J.-P. (1983). Monospecific vs polyspecific life: A comparative study of foraging and antipredatory tactics in a community of Cercopithecus monkeys. *Behavioral Ecology and Sociobiology*, *12*(4), 325–335. https://doi.org/10.1007/BF00302901

Gelman, A., & Su, Y.-S. (2020). *arm: Data analysis using regression and multilevel/hierarchical models* (R package version 1.11-1). https://cran.r-project.org/package=arm

Genovart, M., Negre, N., Tavecchia, G., Bistuer, A., Parpal, L., & Oro, D. (2010). The young, the weak and the sick: evidence of natural selection by predation. *PloS One*, *5*(3), e9774. https://doi.org/10.1371/journal.pone.0009774

Genty, E., Breuer, T., Hobaiter, C., & Byrne, R. W. (2009). Gestural communication of the gorilla (Gorilla gorilla): repertoire, intentionality and possible origins. *Animal Cognition*, *12*(3), 527–546. https://doi.org/10.1007/s10071-009-0213-4

Ghazanfar, A. A., Liao, D. A., & Takahashi, D. Y. (2019). Volition and learning in primate vocal behaviour. *Animal Behaviour*, *151*, 239–247. https://doi.org/https://doi.org/10.1016/j.anbehav.2019.01.021

Gill, S. A., & Bierema, A. M.-K. (2013). On the Meaning of Alarm Calls: A Review of Functional Reference in Avian Alarm Calling. *Ethology*, *119*(6), 449–461. https://doi.org/https://doi.org/10.1111/eth.12097

Girard-Buttoz, C., Zaccarella, E., Bortolato, T., Friederici, A. D., Wittig, R. M., & Crockford, C. (2022). Chimpanzees produce diverse vocal sequences with ordered and recombinatorial properties. *Communications Biology*, *5*(1), 410. https://doi.org/10.1038/s42003-022-03350-8

Goodale, E., Beauchamp, G., Magrath, R. D., Nieh, J. C., & Ruxton, G. D. (2010). Interspecific information transfer influences animal community structure. *Trends in Ecology & Evolution*, *25*(6), 354–361. https://doi.org/10.1016/j.tree.2010.01.002

Goris, R. C. (2011). Infrared Organs of Snakes: An Integral Part of Vision. *Journal of Herpetology*, *45*(1), 2–14. https://doi.org/10.1670/10-238.1

Greene, H. W. (1997). *Snakes: the evolution of mystery in nature*. Univ of California Press.

Greggor, A. L., McIvor, G. E., Clayton, N. S., & Thornton, A. (2022). Wild jackdaws are wary of objects that violate expectations of animacy. *Royal Society Open Science*, *5*(10), 181070. https://doi.org/10.1098/rsos.181070

Griffin, A. (2004). Social learning about predators: a review and prospectus. *Animal Learning & Behavior*, *32*(1), 131–140. https://doi.org/10.3758/BF03196014

Grubb, P., Butynski, T. M., Oates, J. F., Bearder, S. K., Disotell, T. R., Groves, C. P., & Struhsaker, T. T. (2003). Assessment of the Diversity of African Primates. *International Journal of Primatology*, *24*(6), 1301–1357. https://doi.org/10.1023/B:IJOP.0000005994.86792.b9

Gursky, S. (2003). Predation Experiments on Infant Spectral Tarsiers (Tarsius spectrum). *Folia Primatologica*, *74*(5–6), 272–284. https://doi.org/https://doi.org/10.1159/000073314

Gust, D. A. (1994). A brief report on the social behavior of the crested mangabey (Cercocebus galeritus galeritus) with a comparison to the sooty mangabey (C. torquatus atys). *Primates*, *35*(3), 375–383. https://doi.org/10.1007/BF02382734

Gust, D. A., Busse, C. D., & Gordon, T. P. (1990). Reproductive parameters in the sooty mangabey (Cercocebus torquatus atys). *American Journal of Primatology*, *22*(4), 241–250. https://doi.org/10.1002/ajp.1350220404

Gust, D. A., & Gordon, T. P. (1993). Conflict resolution in sooty mangabeys. *Animal Behaviour*, *46*(4), 685–694. https://doi.org/https://doi.org/10.1006/anbe.1993.1245

Haff, T. M., & Magrath, R. D. (2013). To call or not to call: parents assess the vulnerability of their young before warning them about predators. *Biology Letters*, *9*(6), 20130745. https://doi.org/10.1098/rsbl.2013.0745

Hammerschmidt, K., & Fischer, J. (2008). Constraints in Primate Vocal Production. In *Evolution of Communicative Flexibility*. The MIT Press. https://doi.org/10.7551/mitpress/9780262151214.003.0005

Hammerschmidt, K., Freudenstein, T., & Jürgens, U. (2001). Vocal Development in Squirrel Monkeys. *Behaviour*, *138*(9), 1179–1204. http://www.jstor.org/stable/4535882

Hammerschmidt, K., Newman, J. D., Champoux, M., & Suomi, S. J. (2000). Changes In Rhesus Macaque ‘Coo’ Vocalizations during Early Development. *Ethology*, *106*(10), 873–886. https://doi.org/https://doi.org/10.1046/j.1439-0310.2000.00611.x

Harvey, P. H., & Clutton-Brock, T. H. (1985). Life History Variation in Primates. *Evolution*, *39*(3), 559–581. https://doi.org/10.2307/2408653

Hauser, M. D. (1988). How Infant Vervet Monkeys Learn To Recognize Starling Alarm Calls: the Role of Experience. *Behaviour*, *105*(3–4), 187–201. https://doi.org/https://doi.org/10.1163/156853988X00016

Hauser, M. D. (1989). Ontogenetic changes in the comprehension and production of vervet monkey (Cercopithecus aethiops) vocalizations. *Journal of Comparative Psychology*, *103*(2), 149–158. https://doi.org/10.1037/0735-7036.103.2.149

Hauser, M. D., Chomsky, N., & Fitch, W. T. (2002). The Faculty of Language: What Is It, Who Has It, and How Did It Evolve? *Science*, *298*(5598), 1569–1579. https://doi.org/10.1126/science.298.5598.1569

Hayes, C. (1951). The ape in our house. In *The ape in our house.* Harper.

Headland, T. N., & Greene, H. W. (2011). Hunter–gatherers and other primates as prey, predators, and competitors of snakes. *Proceedings of the National Academy of Sciences*, *108*(52), E1470–E1474. https://doi.org/10.1073/pnas.1115116108

Heyes, C., & Galef Jr, B. (1996). *Social learning in animals: the roots of culture*. Elsevier.

Heymann, E. W., & Buchanan-Smith, H. M. (2000). The behavioural ecology of mixed-species troops of callitrichine primates. *Biological Reviews of the Cambridge Philosophical Society*, *75*(2), 169–190. https://doi.org/10.1017/s0006323199005460

Hollén, L. I., Clutton-Brock, T., & Manser, M. B. (2008). Ontogenetic Changes in Alarm-Call Production and Usage in Meerkats (Suricata suricatta): Adaptations or Constraints? *Behavioral Ecology and Sociobiology*, *62*(5), 821–829. http://www.jstor.org/stable/25511757

Höner, O. P., Leumann, L., & Noë, R. (1997). Dyadic associations of red Colobus and diana monkey groups in the Taï National Park, Ivory Coast. *Primates*, *38*(3), 281–291. https://doi.org/10.1007/BF02381615

Hotchkin, C. F., Parks, S. E., & Weiss, D. J. (2013). Vocal modifications in primates: Effects of noise and behavioral context on vocalization structure. *Proceedings of Meetings on Acoustics. Acoustical Society of America*, *19*. https://doi.org/10.1121/1.4799257

Isbell, L. A. (1994). Predation on primates: Ecological patterns and evolutionary consequences. *Evolutionary Anthropology: Issues, News, and Reviews*, *3*(2), 61–71. https://doi.org/10.1002/evan.1360030207

Isbell, L. A. (2006). Snakes as agents of evolutionary change in primate brains. *Journal of Human Evolution*, *51*(1), 1–35. https://doi.org/https://doi.org/10.1016/j.jhevol.2005.12.012

Isbell, L. A. (2009). *The Fruit, the Tree, and the Serpent*. Harvard University Press. https://doi.org/10.2307/j.ctvjnrvj0

Jaffe, K. . E., & Isbell, L. (2010). The Guenons: Polyspecific associations in sociological perspective. In C. J. Campbell, A. Fuentes, K. C. MacKinnon, S. K. Bearder, & R. Stumpf (Eds.), *Primates in Perspective* (pp. 277–300). Oxford University Press.

Janik, V. M., & Slater, P. J. B. (2000). The different roles of social learning in vocal communication. *Animal Behaviour*, *60*(1), 1–11. https://doi.org/https://doi.org/10.1006/anbe.2000.1410

Janson, C. H., & van Schaik, C. P. (1993). Ecological risk aversion in juvenile primates: slow and steady wins the race. In M. E. Pereira & L. A. Fairbanks (Eds.), *Juvenile primates: life history, development, and behavior* (pp. 57–74). Oxford Univ. Press.

Jeffreys, H. (1939). *The theory of probability* (1st ed.). Oxford University Press.

Johnson, K. E., & Clark, C. J. (2020). Ontogeny of vocal learning in a hummingbird. *Animal Behaviour*, *167*, 139–150. https://doi.org/https://doi.org/10.1016/j.anbehav.2020.07.010

Johnson, K. E., & Clark, C. J. (2022). Costa's hummingbird has an extended sensitive phase of vocal learning. *Animal Behaviour*, *188*, 75–84. https://doi.org/https://doi.org/10.1016/j.anbehav.2022.04.001

Kaminski, J., Call, J., & Fischer, J. (2004). Word learning in a domestic dog: evidence for "fast mapping". *Science (New York, N.Y.)*, *304*(5677), 1682–1683. https://doi.org/10.1126/science.1097859

Kawai, N., & He, H. (2016). Breaking Snake Camouflage: Humans Detect Snakes More Accurately than Other Animals under Less Discernible Visual Conditions. *PLOS ONE*, *11*(10), e0164342. https://doi.org/10.1371/journal.pone.0164342

Kawai, N., & Koda, H. (2016). Japanese monkeys (Macaca fuscata) quickly detect snakes but not spiders: Evolutionary origins of fear-relevant animals. In *Journal of Comparative Psychology* (Vol. 130, pp. 299–303). American Psychological Association. https://doi.org/10.1037/com0000032

Keen, S. C., Cole, E. F., Sheehan, M. J., & Sheldon, B. C. (2020). Social learning of acoustic anti-predator cues occurs between wild bird species. *Proceedings of the Royal Society B: Biological Sciences*, *287*(1920), 20192513. https://doi.org/10.1098/rspb.2019.2513

Kelley, J. L., & Magurran, A. E. (2003). Learned predator recognition and antipredator responses in fishes. *Fish and Fisheries*, *4*(3), 216–226. https://doi.org/https://doi.org/10.1046/j.1467-2979.2003.00126.x

Kellogg, W. N., & Kellogg, L. A. (1933). The ape and the child: a study of environmental influence upon early behavior. In *The ape and the child: a study of environmental influence upon early behavior.* Whittlesey House.

Kendal, R. L., Coolen, I., van Bergen, Y., & Laland, K. N. B. T.-A. in the S. of B. (2005). *Trade-Offs in the Adaptive Use of Social and Asocial Learning* (Vol. 35, pp. 333–379). Academic Press. https://doi.org/https://doi.org/10.1016/S0065-3454(05)35008-X

Khamcha, D., & Sukumal, N. (2009). Burmese python (Python molurus) predation on a pig-tailed macaque (Macaca nemestrina) in Khao Yai National Park. *Hamadryad*, *34*, 176–178. https://doi.org/10.13140/2.1.3857.7449

King, S. L., & Janik, V. M. (2013). Bottlenose dolphins can use learned vocal labels to address each other. *Proceedings of the National Academy of Sciences*, *110*(32), 13216–13221. https://doi.org/10.1073/pnas.1304459110

Kingdon, J. (2015). *The Kingdon field guide to African mammals*. Bloomsbury Publishing.

Kirchhof, J., & Hammerschmidt, K. (2006). Functionally Referential Alarm Calls in Tamarins (Saguinus fuscicollis and Saguinus mystax) – Evidence from Playback Experiments. *Ethology*, *112*(4), 346–354. https://doi.org/https://doi.org/10.1111/j.1439-0310.2006.01165.x

Koda, H., Shimooka, Y., & Sugiura, H. (2008). Effects of caller activity and habitat visibility on contact call rate of wild Japanese macaques (Macaca fuscata). *American Journal of Primatology*, *70*(11), 1055–1063. https://doi.org/10.1002/ajp.20597

Koné, I., McGraw, S., Gonedelé Bi, S., & Barrie, A. (2020). *Cercocebus atys*. The IUCN Red List of Threatened Species 2020: E.T136933A92248451. https://dx.doi.org/10.2305/IUCN.UK.2020-2.RLTS.T136933A92248451.en

Krause, M. A., & Beran, M. J. (2020). Words matter: Reflections on language projects with chimpanzees and their implications. *American Journal of Primatology*, *82*(10), e23187. https://doi.org/https://doi.org/10.1002/ajp.23187

Kuhl, P. K. (2000). A new view of language acquisition. *Proceedings of the National Academy of Sciences of the United States of America*, *97*(22), 11850–11857. https://doi.org/10.1073/pnas.97.22.11850

Lameira, A. R. (2017). Bidding evidence for primate vocal learning and the cultural substrates for speech evolution. *Neuroscience & Biobehavioral Reviews*, *83*, 429–439. https://doi.org/https://doi.org/10.1016/j.neubiorev.2017.09.021

Laporte, M. N. C., & Zuberbühler, K. (2010). Vocal greeting behaviour in wild chimpanzee females. *Animal Behaviour*, *80*(3), 467–473. https://doi.org/https://doi.org/10.1016/j.anbehav.2010.06.005

Lattenkamp, E. Z., & Vernes, S. C. (2018). Vocal learning: a language-relevant trait in need of a broad cross-species approach. *Current Opinion in Behavioral Sciences*, *21*, 209–215. https://doi.org/https://doi.org/10.1016/j.cobeha.2018.04.007

Lattenkamp, E. Z., Vernes, S. C., & Wiegrebe, L. (2018). Volitional control of social vocalisations and vocal usage learning in bats. *Journal of Experimental Biology*, *221*(14), jeb180729. https://doi.org/10.1242/jeb.180729

Lemasson, A., Gandon, E., & Hausberger, M. (2010). Attention to elders' voice in non-human primates. *Biology Letters*, *6*(3), 328. https://doi.org/10.1098/rsbl.2009.0875

Lemasson, A., Ouattara, K., Petit, E. J., & Zuberbühler, K. (2011). Social learning of vocal structure in a nonhuman primate? *BMC Evolutionary Biology*, *11*(1), 362. https://doi.org/10.1186/1471-2148-11-362

León, J., Thiriau, C., Bodin, C., Crockford, C., & Zuberbühler, K. (2022). Acquisition of predator knowledge from alarm calls via one-trial social learning in monkeys. *IScience*, *25*, 104853. https://doi.org/https://doi.org/10.1016/j.isci.2022.104853

León, J., Thiriau, C., Crockford, C., & Zuberbühler, K. (2022). *https://osf.io/y2gvc/.*

Leroux, M., & Townsend, S. W. (2020). Call combinations in great apes and the evolution of syntax. *Animal Behavior and Cognition*, *7*(2), 131–139.

Li, J., Smithwick, Q., & Chu, D. (2022). Holobricks: modular coarse integral holographic displays. *Light: Science & Applications*, *11*(1), 57. https://doi.org/10.1038/s41377-022-00742-7

Liebal, K., & Call, J. (2012). The origins of non-human primates' manual gestures. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *367*(1585), 118–128. https://doi.org/10.1098/rstb.2011.0044

Liebal, K., Waller, B. M., Burrows, A. M., & Slocombe, K. E. (2014). Primate communication: A multimodal approach. In *Primate communication: A multimodal approach.* Cambridge University Press.

Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, *68*(4), 619–640.

https://doi.org/10.1139/z90-092

Luchkina, E., & Waxman, S. (2021). Acquiring verbal reference: The interplay of cognitive, linguistic, and general learning capacities. *Infant Behavior and Development*, *65*, 101624. https://doi.org/https://doi.org/10.1016/j.infbeh.2021.101624

Magrath, R. D., Haff, T. M., Fallow, P. M., & Radford, A. N. (2015). Eavesdropping on heterospecific alarm calls: from mechanisms to consequences. *Biological Reviews*, *90*(2), 560–586. https://doi.org/https://doi.org/10.1111/brv.12122

Manser, M. B. (2001). The acoustic structure of suricates' alarm calls varies with predator type and the level of response urgency. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *268*(1483), 2315–2324. https://doi.org/10.1098/rspb.2001.1773

Manser, M. B., Bell, M. B., & Fletcher, L. B. (2001). The information that receivers extract from alarm calls in suricates. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *268*(1484), 2485–2491. https://doi.org/10.1098/rspb.2001.1772

Masataka, N., & Fujita, K. (1989). Vocal Learning of Japanese and Rhesus Monkeys. *Behaviour*, *109*(3–4), 191–199. https://doi.org/https://doi.org/10.1163/156853989X00222

McCowan, B., Franceschini, N. V, & Vicino, G. A. (2001). Age differences and developmental trends in alarm peep responses by squirrel monkeys (Saimiri sciureus). *American Journal of Primatology*, *53*(1), 19–31. https://doi.org/https://doi.org/10.1002/1098-2345(200101)53:1<19::AID-AJP2>3.0.CO;2-#

McCullagh, P., & Nelder, J. A. (1989). *Generalized linear models* (Second). Chapman & Hall/CRC.

McGraw, W. (1998). Comparative locomotion and habitat use of six monkeys in the Tai Forest, Ivory Coast. *American Journal of Physical Anthropology*, *105*(4), 493–510. https://doi.org/https://doi.org/10.1002/(SICI)1096-8644(199804)105:4<493::AID-AJPA7>3.0.CO;2-P

McGraw, W., & Bshary, R. (2002). Association of Terrestrial Mangabeys (Cercocebus atys) with Arboreal Monkeys: Experimental Evidence for the Effects of Reduced Ground

Predator Pressure on Habitat Use. *International Journal of Primatology*, *23*(2), 311–325. https://doi.org/10.1023/A:1013883528244

McGraw, W. S., Zuberbühler, K., & Noë, R. (2007). *Monkeys of the Taï Forest: an African primate community* (Vol. 51). Cambridge University Press.

McGraw, W., & Zuberbühler, K. (2007). The monkeys of the Taï forest: an introduction. In Klaus Zuberbühler, R. Noë, & W. S. McGraw (Eds.), *Monkeys of the Taï Forest: An African Primate Community* (pp. 1–48). Cambridge University Press. https://doi.org/DOI: 10.1017/CBO9780511542121.002

McGraw, W., Zuberbühler, K., & Noë, R. (2007). *Monkeys of the Tai Forest*. Cambridge University Press. https://doi.org/10.1017/CBO9780511542121

Meno, W., Coss, R. G., & Perry, S. (2013a). Development of Snake-Directed Antipredator Behavior by Wild White-faced Capuchin Monkeys: I. Snake-Species Discrimination. *American Journal of Primatology*, *75*(3), 281–291. https://doi.org/https://doi.org/10.1002/ajp.22106

Meno, W., Coss, R. G., & Perry, S. (2013b). Development of Snake-Directed Antipredator Behavior by Wild White-Faced Capuchin Monkeys: II. Influence of the Social Environment. *American Journal of Primatology*, *75*(3), 292–300. https://doi.org/https://doi.org/10.1002/ajp.22109

Mery, F., & Burns, J. G. (2010). Behavioural plasticity: an interaction between evolution and experience. *Evolutionary Ecology*, *24*(3), 571–583. https://doi.org/10.1007/s10682-009-9336-y

Meyer, D., Hodges, J. K., Rinaldi, D., Wijaya, A., Roos, C., & Hammerschmidt, K. (2012). Acoustic structure of male loud-calls support molecular phylogeny of Sumatran and Javanese leaf monkeys (genus Presbytis). *BMC Evolutionary Biology*, *12*(1), 16.

Mielke, A., Crockford, C., & Wittig, R. M. (2019). Snake alarm calls as a public good in sooty mangabeys. *Animal Behaviour*, *158*, 201–209. https://doi.org/https://doi.org/10.1016/j.anbehav.2019.10.001

Mielke, A., & Zuberbühler, K. (2013). A method for automated individual, species and call type recognition in free-ranging animals. *Animal Behaviour*, *86*(2), 475–482. https://doi.org/https://doi.org/10.1016/j.anbehav.2013.04.017

Mineka, S. (1992). *Evolutionary Memories, Emotional Processing, and the Emotional Disorders* (D. L. B. T.-P. of L. and M. Medin (ed.); Vol. 28, pp. 161–206). Academic Press. https://doi.org/https://doi.org/10.1016/S0079-7421(08)60490-9

Mineka, S., & Cook, M. (1988). Social learning and the acquisition of snake fear in monkeys. In *Social learning: Psychological and biological perspectives.* (pp. 51–73). Lawrence Erlbaum Associates, Inc.

Mineka, S., & Cook, M. (1993). Mechanisms involved in the observational conditioning of fear. In *Journal of Experimental Psychology: General* (Vol. 122, Issue 1, pp. 23–38). American Psychological Association. https://doi.org/10.1037/0096-3445.122.1.23

Mittermeier, R., Wilson, D., & Rylands, A. B. (2013). *Handbook of the Mammals of the World: 3. Primates*. Lynx Edicions. https://books.google.com.co/books?id=P0-rMQEACAAJ

Mohamad Nor, N., & Rashid, R. A. (2018). A review of theoretical perspectives on language learning and acquisition. *Kasetsart Journal of Social Sciences*, *39*(1), 161–167. https://doi.org/https://doi.org/10.1016/j.kjss.2017.12.012

Mohr, T., Van de Waal, E., Zuberbühler, K., & Mercier, S. (2022). *https://osf.io/mjywg/.*

Morse, D. H. (1977). Feeding Behavior and Predator Avoidance in Heterospecific Groups. *BioScience*, *27*(5), 332–339. https://doi.org/10.2307/1297632

Munn, C. A. (1986). Birds that ‘cry wolf.’ *Nature*, *319*(6049), 143–145. https://doi.org/10.1038/319143a0

Newman, J. D., & Symmes, D. (1974). Vocal pathology in socially deprived monkeys. *Developmental Psychobiology*, *7*(4), 351–358. https://doi.org/https://doi.org/10.1002/dev.420070412

Oates, J. F., Whitesides, G. H., Davies, A. G., Waterman, P. G., Green, S. M., Dasilva, G. L., & Mole, S. (1990). Determinants of Variation in Tropical Forest Primate Biomass: New Evidence from West Africa. *Ecology*, *71*(1), 328–343. https://doi.org/10.2307/1940272

Oda, R. (1998). The responses of Verreaux’s sifakas to anti-predator alarm calls given by sympatric ring-tailed lemurs. *Folia Primatologica; International Journal of Primatology*, *69*(6), 357–360. https://doi.org/10.1159/000021651

Oda, R., & Masataka, N. (1996). Interspecific Responses of Ringtailed Lemurs to Playback of Antipredator Alarm Calls Given by Verreaux’s Sifakas. *Ethology*, *102*(3), 441–453. https://doi.org/https://doi.org/10.1111/j.1439-0310.1996.tb01138.x

Öhman, A. (2009). Of snakes and faces: An evolutionary perspective on the psychology of fear. *Scandinavian Journal of Psychology*, *50*(6), 543–552. https://doi.org/https://doi.org/10.1111/j.1467-9450.2009.00784.x

Ohman, A., & Mineka, S. (2001). Fears, phobias, and preparedness: toward an evolved module of fear and fear learning. *Psychological Review*, *108*(3), 483–522. https://doi.org/10.1037/0033-295x.108.3.483

Oliveira, L. C., & Dietz, J. M. (2011). Predation risk and the interspecific association of two Brazilian Atlantic forest primates in Cabruca agroforest. *American Journal of Primatology*, *73*(9), 852–860. https://doi.org/10.1002/ajp.20952

Olsson, A., & Phelps, E. A. (2007). Social learning of fear. *Nature Neuroscience*, *10*(9), 1095–1102. https://doi.org/10.1038/nn1968

Ouattara, K., Lemasson, A., & Zuberbühler, K. (2009a). Anti-predator strategies of free-ranging Campbell’s monkeys. *Behaviour*, *146*(12), 1687–1708. https://doi.org/10.1163/000579509X12469533725585

Ouattara, K., Lemasson, A., & Zuberbühler, K. (2009b). Campbell’s monkeys concatenate vocalizations into context-specific call sequences. In *PNAS Proceedings of the National Academy of Sciences of the United States of America* (Vol. 106, Issue 51, pp. 22026–22031). National Academy of Sciences. https://doi.org/10.1073/pnas.0908118106

Owren, M. J., Dieter, J. A., Seyfarth, R. M., & Cheney, D. L. (1992). “Food” Calls Produced by Adult Female Rhesus (Macaca mulatta) and Japanese (M. fuscata) Macaques, Their Normally-Raised Offspring, and Offspring Cross-Fostered between Species. *Behaviour*, *120*(3/4), 218–231. http://www.jstor.org/stable/4535009

Owren, M. J., Dieter, J. A., Seyfarth, R. M., & Cheney, D. L. (1993). Vocalizations of rhesus (Macaca mulatta) and Japanese (M. Fuscata) macaques cross-fostered between species show evidence of only limited modification. *Developmental Psychobiology*, *26*(7), 389–406. https://doi.org/https://doi.org/10.1002/dev.420260703

Owren, M. J., & Rendall, D. (1997). *An Affect-Conditioning Model of Nonhuman Primate Vocal Signaling BT - Communication* (D. H. Owings, M. D. Beecher, & N. S. Thompson (eds.); pp. 299–346). Springer US. https://doi.org/10.1007/978-1-4899-1745-4_10

Owren, M. J., & Rendall, D. (2001). Sound on the rebound: Bringing form and function back to the forefront in understanding nonhuman primate vocal signaling. *Evolutionary Anthropology: Issues, News, and Reviews*, *10*(2), 58–71. https://doi.org/https://doi.org/10.1002/evan.1014

Peake, T. M., & Mcgregor, P. K. (2004). Information and aggression in fishes. *Animal Learning & Behavior*, *32*(1), 114–121. https://doi.org/10.3758/BF03196012

Penner, J., Fruteau, C., Range, F., & Rodel, M. (2008). Finding a needle in a haystack: new methods of locating and working with rhinoceros vipers (Bitis rhinoceros). *Herpetological Review*, *39*(3), 310.

Pepperberg, I. M. (2010). Vocal learning in Grey parrots: A brief review of perception, production, and cross-species comparisons. *Brain and Language*, *115*(1), 81–91. https://doi.org/https://doi.org/10.1016/j.bandl.2009.11.002

Pepperberg, I. M. (2017). Animal language studies: What happened? *Psychonomic Bulletin & Review*, *24*(1), 181–185. https://doi.org/10.3758/s13423-016-1101-y

Perry, S., Panger, M., Rose, L. M., Baker, M., Gros-Louis, J., Jack, K., Mackinnon, K. C., Manson, J., Fedigan, L., & Pyle, K. (2003). Traditions in wild white-faced capuchin monkeys. In *The Biology of Traditions* (pp. 391–425). Cambridge University Press. https://doi.org/10.1017/CBO9780511584022.015

Pessoa, D. M. A., Maia, R., de Albuquerque Ajuz, R. C., De Moraes, P. Z. P. M. R., Spyrides, M. H. C., & Pessoa, V. F. (2014). The adaptive value of primate color vision for predator detection. *American Journal of Primatology*, *76*(8), 721–729. https://doi.org/10.1002/ajp.22264

Pika, S., & Liebal, K. (2006). Differences and similarties between the natural gestural communication of the great apes and human children. In *The Evolution of Language* (pp. 267–274). WORLD SCIENTIFIC. https://doi.org/doi:10.1142/9789812774262_0034

Pika, S., Liebal, K., & Tomasello, M. (2003). Gestural communication in young gorillas (Gorilla gorilla): gestural repertoire, learning, and use. *American Journal of Primatology*, *60*(3), 95–111. https://doi.org/10.1002/ajp.10097

Poole, J. H., Tyack, P. L., Stoeger-Horwath, A. S., & Watwood, S. (2005). Elephants are capable of vocal learning. *Nature*, *434*(7032), 455–456. https://doi.org/10.1038/434455a

Potvin, D. A., Ratnayake, C. P., Radford, A. N., & Magrath, R. D. (2018). Birds Learn Socially to Recognize Heterospecific Alarm Calls by Acoustic Association. *Current Biology*, *28*(16), 2632-2637.e4. https://doi.org/https://doi.org/10.1016/j.cub.2018.06.013

Pozzi, L., Gamba, M., & Giacoma, C. (2013). Artificial Neural Networks: A New Tool for Studying Lemur Vocal Communication. In J. Masters, M. Gamba, & F. Génin (Eds.), *Leaping Ahead: Advances in Prosimian Biology* (pp. 305–313). Springer New York. https://doi.org/10.1007/978-1-4614-4511-1_34

Pozzi, L., Hodgson, J. A., Burrell, A. S., Sterner, K. N., Raaum, R. L., & Disotell, T. R. (2014). Primate phylogenetic relationships and divergence dates inferred from complete mitochondrial genomes. *Molecular Phylogenetics and Evolution*, *75*, 165–183. https://doi.org/10.1016/j.ympev.2014.02.023

Price, T., Ndiaye, O., Hammerschmidt, K., & Fischer, J. (2014). Limited geographic variation in the acoustic structure of and responses to adult male alarm barks of African green monkeys. *Behavioral Ecology and Sociobiology*, *68*(5), 815–825. https://doi.org/10.1007/s00265-014-1694-y

Price, T., Wadewitz, P., Cheney, D., Seyfarth, R., Hammerschmidt, K., & Fischer, J. (2015). Vervets revisited: A quantitative analysis of alarm call structure and context specificity. *Scientific Reports*, *5*, 13220. https://doi.org/10.1038/srep13220

Quam, R. M., Ramsier, M. A., Fay, R. R., & Popper, A. N. (2017). *Primate hearing and communication*. Springer.

Quintero, F., Touitou, S., Magris, M., & Zuberbühler, K. (2022a). An audience effect in sooty mangabey alarm calling. *Front Psychol*, *13*. https://doi.org/10.3389/fpsyg.2022.816744

Quintero, F., Touitou, S., Magris, M., & Zuberbühler, K. (2022b). The Evolution of Food Calls: Vocal Behaviour of Sooty Mangabeys in the Presence of Food . In *Frontiers in Psychology* (Vol. 13). https://www.frontiersin.org/articles/10.3389/fpsyg.2022.897318

R Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

Ramakrishnan, U., & Coss, R. G. (2000). Recognition of heterospecific alarm vocalization by Bonnet Macaques (Macaca radiata). In *Journal of Comparative Psychology* (Vol. 114, Issue 1, pp. 3–12). American Psychological Association. https://doi.org/10.1037/0735-7036.114.1.3

Ramakrishnan, U., Coss, R. G., Schank, J., Dharawat, A., & Kim, S. (2005). Snake Species Discrimination by Wild Bonnet Macaques (Macaca radiata). *Ethology*, *111*(4), 337–356. https://doi.org/10.1111/j.1439-0310.2004.01063.x

Range, F., & Fischer, J. (2004). Vocal Repertoire of Sooty Mangabeys (Cercocebus torquatus atys) in the Tai National Park. *Ethology*, *110*(4), 301–321. https://doi.org/10.1111/j.1439-0310.2004.00973.x

Range, F., & Noë, R. (2002). Familiarity and dominance relations among female sooty mangabeys in the Taï National Park. *American Journal of Primatology*, *56*(3), 137–153. https://doi.org/https://doi.org/10.1002/ajp.1070

Rapaport, L. G., & Brown, G. R. (2008). Social influences on foraging behavior in young nonhuman primates: Learning what, where, and how to eat. *Evolutionary Anthropology: Issues, News, and Reviews*, *17*(4), 189–201. https://doi.org/https://doi.org/10.1002/evan.20180

Rendall, D., Owren, M. J., & Ryan, M. J. (2009). What do animal signals mean? *Animal Behaviour*, *78*(2), 233–240. https://doi.org/https://doi.org/10.1016/j.anbehav.2009.06.007

Rescorla, L. A. (1980). Overextension in early language development. *Journal of Child*

Language, *7*(2), 321–335. https://doi.org/DOI: 10.1017/S0305000900002658

Rescorla, R. A., & Wagner, A. (1972). A theory of Pavlovian conditioning: Variations in the effectiveness of reinforcement and nonreinforcement. In A. Black & P. W (Eds.), *Classical Conditioning II: Current Research and Theory: Vol. Vol. 2* (pp. 64–69). Appleton-Century-Crofts.

Ridgway, S., Carder, D., Jeffries, M., & Todd, M. (2012). Spontaneous human speech mimicry by a cetacean. *Current Biology*, *22*(20), R860–R861. https://doi.org/10.1016/j.cub.2012.08.044

Rödel, M., & Mahsberg, D. (2000). Vorläufige Liste der Schlangen des Taï-Nationalparks / Elfenbeinküste und angrenzender Gebiete. *Salamandra*, *36*, 25–38.

Romano, D., Donati, E., Benelli, G., & Stefanini, C. (2019). A review on animal–robot interaction: from bio-hybrid organisms to mixed societies. *Biological Cybernetics*, *113*(3), 201–225. https://doi.org/10.1007/s00422-018-0787-5

Rosati, A. G., Machanda, Z. P., & Slocombe, K. E. (2022). Cognition in the wild: understanding animal thought in its natural context. *Current Opinion in Behavioral Sciences*, *47*, 101210. https://doi.org/https://doi.org/10.1016/j.cobeha.2022.101210

Roupe, S., Pistorio, A., & Wang, X. (2003). Vocal plasticity induced by auditory deprivation in the common marmoset. *Program No. 627.7 2003 Abstract Viewer and Itinerary Planner. Society for Neuroscience Online*.

Schel, A. M., Machanda, Z., Townsend, S. W., Zuberbühler, K., & Slocombe, K. E. (2013). Chimpanzee food calls are directed at specific individuals. *Animal Behaviour*, *86*(5), 955–965. https://doi.org/https://doi.org/10.1016/j.anbehav.2013.08.013

Schel, A. M., Townsend, S. W., Machanda, Z., Zuberbühler, K., & Slocombe, K. E. (2013). Chimpanzee Alarm Call Production Meets Key Criteria for Intentionality. *PLOS ONE*, *8*(10), e76674. https://doi.org/10.1371/journal.pone.0076674

Schel, A. M., & Zuberbühler, K. (2009). Responses to leopards are independent of experience in Guereza colobus monkeys. *Behaviour*, *146*(12), 1709–1737. https://doi.org/https://doi.org/10.1163/000579509X12483520922007

Schrago, C. G., & Russo, C. A. M. (2003). Timing the Origin of New World Monkeys. *Molecular Biology and Evolution*, *20*(10), 1620–1625. https://doi.org/10.1093/molbev/msg172

Schuppli, C., Meulman, E. J. M., Forss, S. I. F., Aprilinayati, F., van Noordwijk, M. A., & van Schaik, C. P. (2016). Observational social learning and socially induced practice of routine skills in immature wild orang-utans. *Animal Behaviour*, *119*, 87–98. https://doi.org/https://doi.org/10.1016/j.anbehav.2016.06.014

Searcy, W. A., & Nowicki, S. (2010). The Evolution of Animal Communication: Reliability and Deception in Signaling Systems. In *Reliability and Deception in Signaling Systems*. Princeton University Press. https://doi.org/doi:10.1515/9781400835720

Seidenberg, M. S. (1997). Language Acquisition and Use: Learning and Applying Probabilistic Constraints. *Science*, *275*(5306), 1599–1603. https://doi.org/10.1126/science.275.5306.1599

Seiler, M., Schwitzer, C., Gamba, M., & Holderied, M. W. (2013). Interspecific Semantic Alarm Call Recognition in the Solitary Sahamalaza Sportive Lemur, Lepilemur sahamalazensis. *PLoS ONE*, *8*(6), e67397. https://doi.org/10.1371/journal.pone.0067397

Seppänen, J.-T., Forsman, J. T., Mönkkönen, M., & Thomson, R. L. (2007). Social information use is a process across time, space, and ecology, reaching heterospecifics. *Ecology*, *88*(7), 1622–1633. https://doi.org/10.1890/06-1757.1

Seyfarth, R. M., & Cheney, D. L. (1980). The Ontogeny of Vervet Monkey Alarm Calling Behavior: A Preliminary Report. *Zeitschrift Für Tierpsychologie*, *54*(1), 37–56. https://doi.org/10.1111/j.1439-0310.1980.tb01062.x

Seyfarth, R. M., & Cheney, D. L. (1986). Vocal development in vervet monkeys. *Animal Behaviour*, *34*(6), 1640–1658. https://doi.org/https://doi.org/10.1016/S0003-3472(86)80252-4

Seyfarth, R. M., & Cheney, D. L. (1997). Some general features of vocal development in nonhuman primates. In C. T. Snowdon & M. Hausberger (Eds.), *Social Influences on Vocal Development* (pp. 249–273). Cambridge University Press. https://doi.org/DOI: 10.1017/CBO9780511758843.013

Seyfarth, R. M., Cheney, D. L., & Marler, P. (1980). Vervet monkey alarm calls: semantic communication in a free-ranging primate. *Animal Behaviour*, *28*(4), 1070–1094.

Seyfarth, R, & Cheney, D. (2010). Production, usage, and comprehension in animal vocalizations. *Brain and Language*, *115*(1), 92–100. https://doi.org/https://doi.org/10.1016/j.bandl.2009.10.003

Seyfarth, R, Cheney, D., Bergman, T., Fischer, J., Zuberbühler, K., & Hammerschmidt, K. (2010). The central importance of information in studies of animal communication. *Animal Behaviour*, *80*(1), 3–8. https://doi.org/https://doi.org/10.1016/j.anbehav.2010.04.012

Seyfarth, R, Cheney, D., & Marler, P. (1980). Monkey responses to three different alarm calls: evidence of predator classification and semantic communication. *Science*, *210*(4471), 801–803.

Seyfarth, R, & Cheney, D. (1990). The assessment by vervet monkeys of their own and another species' alarm calls. *Animal Behaviour*, *40*(4), 754–764. https://doi.org/https://doi.org/10.1016/S0003-3472(05)80704-3

Shannon, C. E. (1948). A Mathematical Theory of Communication. *Bell System Technical Journal*, *27*(3), 379–423. https://doi.org/https://doi.org/10.1002/j.1538-7305.1948.tb01338.x

Sheldon, B. C., Kruuk, L. E. B., & Alberts, S. C. (2022). The expanding value of long-term studies of individuals in the wild. *Nature Ecology & Evolution*. https://doi.org/10.1038/s41559-022-01940-7

Shibasaki, M., & Kawai, N. (2009). Rapid detection of snakes by Japanese monkeys (Macaca fuscata): An evolutionarily predisposed visual system. In *Journal of Comparative Psychology* (Vol. 123, pp. 131–135). American Psychological Association. https://doi.org/10.1037/a0015095

Shultz, S, & Thomsett, S. (2007). Interactions between African crowned eagles and their prey community. In Klaus Zuberbühler, R. Noë, & W. S. McGraw (Eds.), *Monkeys of the Taï Forest: An African Primate Community* (pp. 171–193). Cambridge University Press. https://doi.org/DOI: 10.1017/CBO9780511542121.008

Shultz, S, Noë, R., McGraw, W. S., & Dunbar, R. I. M. (2004). A community-level evaluation of the impact of prey behavioural and ecological characteristics on predator diet composition. *Proceedings. Biological Sciences*, *271*(1540), 725–732. https://doi.org/10.1098/rspb.2003.2626

Simmons, J. P., Nelson, L. D., & Simonsohn, U. (2011). False-Positive Psychology: Undisclosed Flexibility in Data Collection and Analysis Allows Presenting Anything as Significant. *Psychological Science*, *22*(11), 1359–1366. https://doi.org/10.1177/0956797611417632

Slater, P. J. B. (2006). *Animal Communication: Vocal Learning* (K. B. T.-E. of L. & L. (Second E. Brown (ed.); pp. 291–294). Elsevier. https://doi.org/https://doi.org/10.1016/B0-08-044854-2/00824-5

Slocombe, K E, & Zuberbühler, K. (2005). Functionally Referential Communication in a Chimpanzee. *Current Biology*, *15*(19), 1779–1784. https://doi.org/https://doi.org/10.1016/j.cub.2005.08.068

Slocombe, K E, & Zuberbühler, K. (2007). Chimpanzees modify recruitment screams as a function of audience composition. *Proceedings of the National Academy of Sciences*, *104*(43), 17228 LP – 17233. https://doi.org/10.1073/pnas.0706741104

Slocombe, K E, Waller, B. M., & Liebal, K. (2011). The language void: the need for multimodality in primate communication research. *Animal Behaviour*, *81*(5), 919–924. https://doi.org/https://doi.org/10.1016/j.anbehav.2011.02.002

Smid, S. C., McNeish, D., Miočević, M., & van de Schoot, R. (2020). Bayesian Versus Frequentist Estimation for Structural Equation Models in Small Sample Contexts: A Systematic Review. *Structural Equation Modeling: A Multidisciplinary Journal*, *27*(1), 131–161. https://doi.org/10.1080/10705511.2019.1577140

Snowdon, C. T. B. T.-A. in the S. of B. (2009). Chapter 7 Plasticity of Communication in Nonhuman Primates. In *Advances in the Study of Behavior* (Vol. 40, pp. 239–276). Academic Press. https://doi.org/https://doi.org/10.1016/S0065-3454(09)40007-X

Stansbury, A. L., & Janik, V. M. (2019). Formant Modification through Vocal Production Learning in Gray Seals. *Current Biology*, *29*(13), 2244-2249.e4.

https://doi.org/10.1016/j.cub.2019.05.071

Stauffer, R. L., Walker, A., Ryder, O. A., Lyons-Weiler, M., & Hedges, S. B. (2001). Human and Ape Molecular Clocks and Constraints on Paleontological Hypotheses. *Journal of Heredity*, *92*(6), 469–474. https://doi.org/10.1093/jhered/92.6.469

Stensland, E., Angerbjörn, A., & Berggren, P. (2003). Mixed species groups in mammals. *Mammal Review*, *33*(3-4), 205–223. https://doi.org/https://doi.org/10.1046/j.1365-2907.2003.00022.x

Stephan, C., & Zuberbühler, K. (2008). Predation increases acoustic complexity in primate alarm calls. *Biology Letters*, *4*(6), 641–644. https://doi.org/10.1098/rsbl.2008.0488

Stephan, C., & Zuberbühler, K. (2014). Predation affects alarm call usage in female Diana monkeys (Cercopithecus diana diana). *Behavioral Ecology and Sociobiology*, *68*(2), 321–331. https://doi.org/10.1007/s00265-013-1647-x

Stephan, C., & Zuberbühler, K. (2021). *Alarm Calling and Kinship BT - Encyclopedia of Evolutionary Psychological Science* (T. K. Shackelford & V. A. Weekes-Shackelford (eds.); pp. 163–171). Springer International Publishing. https://doi.org/10.1007/978-3-319-19650-3_1512

Stevenson, M. (1973). Notes on pregnancy in the Sooty mangabey Cercocebus atys. *International Zoo Yearbook*, *13*(1), 134–135. https://doi.org/https://doi.org/10.1111/j.1748-1090.1973.tb02126.x

Stoeger, A. S., Mietchen, D., Oh, S., de Silva, S., Herbst, C. T., Kwon, S., & Fitch, W. T. (2012). An Asian Elephant Imitates Human Speech. *Current Biology*, *22*(22), 2144–2148. https://doi.org/10.1016/j.cub.2012.09.022

Struhsaker, T. T. (1967). Ecology of Vervet Monkeys (Cercopithecus Aethiops) in The Masai-Amboseli Game Reserve, Kenya. *Ecology*, *48*(6), 891–904. https://doi.org/https://doi.org/10.2307/1934531

Sugiura, H. (1998). Matching of acoustic features during the vocal exchange of coo calls by Japanese macaques. *Animal Behaviour*, *55*(3), 673–687. https://doi.org/https://doi.org/10.1006/anbe.1997.0602

Takahashi, D. Y., Liao, D. A., & Ghazanfar, A. A. (2017). Vocal Learning via Social Reinforcement by Infant Marmoset Monkeys. *Current Biology*, *27*(12), 1844-1852.e6. https://doi.org/10.1016/j.cub.2017.05.004

Talmage-Riggs, G., Winter, P., Ploog, D., & Mayer, W. (1972). Effect of deafening on the vocal behavior of the squirrel monkey (Saimiri sciureus). *Folia Primatologica; International Journal of Primatology*, *17*(5), 404–420. https://doi.org/10.1159/000155458

Team, J. (2020). *JASP (Version 0.14.1)*. https://jasp-stats.org/

Thinh, V. N., Hallam, C., Roos, C., & Hammerschmidt, K. (2011). Concordance between vocal and genetic diversity in crested gibbons. *BMC Evolutionary Biology*, *11*(1), 36. https://doi.org/10.1186/1471-2148-11-36

Thornton, A., & Clutton-Brock, T. (2011). Social learning and the development of individual and group behaviour in mammal societies. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*(1567), 978–987. https://doi.org/10.1098/rstb.2010.0312

Tomasello, M. (2010). *Why we cooperate*. Boston Review Books.

Tomasello, M, & Call, J. (1994). Social cognition of monkeys and apes. *American Journal of Physical Anthropology*, *37*(S19), 273–305. https://doi.org/https://doi.org/10.1002/ajpa.1330370610

Tomasello, M. (2008). *Origins of Human Communication*. MIT press.

Townsend, S. W., & Manser, M. B. (2013). Functionally Referential Communication in Mammals: The Past, Present and the Future. *Ethology*, *119*(1), 1–11. https://doi.org/https://doi.org/10.1111/eth.12015

Trape, J.-F., Trape, S., & Chirio, L. (2012). *Lézards, crocodiles et tortues d'Afrique occidentale et du Sahara*. IRD éditions.

Urbani, B. (2017). Humans as Primate Predators. In *The International Encyclopedia of Primatology* (pp. 1–3). https://doi.org/https://doi.org/10.1002/9781119179313.wbprim0258

Valente, D., De Gregorio, C., Torti, V., Miaretsoa, L., Friard, O., Randrianarison, R. M., Giacoma, C., & Gamba, M. (2019). Finding Meanings in Low Dimensional Structures: Stochastic Neighbor Embedding Applied to the Analysis of Indri indri Vocal Repertoire. *Animals : An Open Access Journal from MDPI*, *9*(5). https://doi.org/10.3390/ani9050243

van Doorn, J., van den Bergh, D., Böhm, U., Dablander, F., Derks, K., Draws, T., Etz, A., Evans, N. J., Gronau, Q. F., Haaf, J. M., Hinne, M., Kucharský, Š., Ly, A., Marsman, M., Matzke, D., Gupta, A. R. K. N., Sarafoglou, A., Stefan, A., Voelkel, J. G., & Wagenmakers, E.-J. (2021). The JASP guidelines for conducting and reporting a Bayesian analysis. *Psychonomic Bulletin & Review*, *28*(3), 813–826. https://doi.org/10.3758/s13423-020-01798-5

van Schaik, C. P., van Noordwijk, M. A., Warsono, B., & Sutriono, E. (1983). Party size and early detection of predators in sumatran forest primates. *Primates*, *24*(2), 211–221. https://doi.org/10.1007/BF02381083

Vernes, S. C., & Wilkinson, G. S. (2020). Behaviour, biology and evolution of vocal learning in bats. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *375*(1789), 20190061. https://doi.org/10.1098/rstb.2019.0061

Verzani, J. (2004). *Using R for introductory statistics* (1st ed.). Chapman and Hall/CRC. https://doi.org/https://doi.org/10.4324/9780203499894

Wadewitz, P., Hammerschmidt, K., Battaglia, D., Witt, A., Wolf, F., & Fischer, J. (2015). Characterizing vocal repertoires - Hard vs. Soft classification approaches. *PLoS ONE*, *10*(4). https://doi.org/10.1371/journal.pone.0125785

Watson, S. K., Townsend, S. W., Schel, A. M., Wilke, C., Wallace, E. K., Cheng, L., West, V., & Slocombe, K. E. (2015). Vocal Learning in the Functionally Referential Food Grunts of Chimpanzees. *Current Biology*, *25*(4), 495–499. https://doi.org/https://doi.org/10.1016/j.cub.2014.12.032

Wegdell, F., Hammerschmidt, K., & Fischer, J. (2019). Conserved alarm calls but rapid auditory learning in monkey responses to novel flying objects. *Nature Ecology & Evolution*, *3*(7), 1039–1042. https://doi.org/10.1038/s41559-019-0903-5

Weiss, L., Brandl, P., & Frynta, D. (2015). Fear reactions to snakes in naïve mouse lemurs and pig-tailed macaques. *Primates*, *56*(3), 279–284. https://doi.org/10.1007/s10329-015-0473-3

Wheeler, B. C. (2009). Monkeys crying wolf? Tufted capuchin monkeys use anti-predator calls to usurp resources from conspecifics. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1669), 3013–3018. https://doi.org/10.1098/rspb.2009.0544

Wheeler, B. C., Fahy, M., & Tiddi, B. (2019). Experimental evidence for heterospecific alarm signal recognition via associative learning in wild capuchin monkeys. *Animal Cognition*, *22*(5), 687–695. https://doi.org/10.1007/s10071-019-01264-3

Wheeler, B. C., & Fischer, J. (2012). Functionally referential signals: A promising paradigm whose time has passed. *Evolutionary Anthropology: Issues, News, and Reviews*, *21*(5), 195–205. https://doi.org/https://doi.org/10.1002/evan.21319

Wheeler, B. C., & Hammerschmidt, K. (2013). Proximate factors underpinning receiver responses to deceptive false alarm calls in wild tufted capuchin monkeys: is it counterdeception? *American Journal of Primatology*, *75*(7), 715–725. https://doi.org/10.1002/ajp.22097

White, D. J. (2004). Influences of social learning on mate-choice decisions. *Animal Learning & Behavior*, *32*(1), 105–113. https://doi.org/10.3758/BF03196011

Whiten, A., & van de Waal, E. (2018). The pervasive role of social learning in primate lifetime development. *Behavioral Ecology and Sociobiology*, *72*(5), 80. https://doi.org/10.1007/s00265-018-2489-3

Whitesides, G. H. (1989). Interspecific associations of Diana monkeys, Cercopithecus diana, in Sierra Leone, West Africa: biological significance or chance? *Animal Behaviour*, *37*, 760–776. https://doi.org/https://doi.org/10.1016/0003-3472(89)90062-6

Wich, S. A., & Sterck, E. H. M. (2003). Possible audience effect in Thomas langurs (Primates; Presbytis thomasi): an experimental study on male loud calls in response to a tiger model. *American Journal of Primatology*, *60*(4), 155–159. https://doi.org/10.1002/ajp.10102

Winter, P., Handley, P., Ploog, D., & Schott, D. (1973). Ontogeny of squirrel monkey calls under normal conditions and under acoustic isolation. *Behaviour*, *47*(3), 230–239.

https://doi.org/10.1163/156853973x00085

Wittig, R. M. (2018). 40 years of research at the Taï Chimpanzee Project. *Pan Africa News*, *25*(2), 16–18.

Wrangham, R. W., & Cheney, D. L. (1985). Predation rates and social-structure in primates. *American Journal of Primatology*, *8*(4), 372.

Zhang, Y. S., & Ghazanfar, A. A. (2018). Vocal development through morphological computation. *PLOS Biology*, *16*(2), e2003933. https://doi.org/10.1371/journal.pbio.2003933

Zuberbühler, K. (2000a). Interspecies semantic communication in two forest primates. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *267*(1444), 713–718. https://doi.org/10.1098/rspb.2000.1061

Zuberbühler, K. (2000b). Causal cognition in a non-human primate: field playback experiments with Diana monkeys. *Cognition*, *76*(3), 195–207. https://doi.org/10.1016/s0010-0277(00)00079-2

Zuberbühler, K. (2001). Predator-specific alarm calls in Campbell's monkeys, Cercopithecus campbelli. *Behavioral Ecology and Sociobiology*, *50*(5), 414–422.

Zuberbühler, K. (2003a). Natural semanticity in wild primates. In *Animal social complexity: Intelligence, culture, and individualized societies.* (pp. 362–367). Harvard University Press.

Zuberbühler, K. (2003b). Referential signaling in non-human primates: Cognitive precursors and limitations for the evolution of language. In *Advances in the study of behavior, Vol 33.* (pp. 265–307). Elsevier Academic Press. https://doi.org/10.1016/S0065-3454(03)33006-2

Zuberbühler, K. (2007). Monkey alarm calls. In Klaus Zuberbühler, R. Noë, & W. S. McGraw (Eds.), *Monkeys of the Taï Forest: An African Primate Community* (pp. 194–220). Cambridge University Press. https://doi.org/DOI: 10.1017/CBO9780511542121.009

Zuberbühler, K, & Jenny, D. (2002). Leopard predation and primate evolution. *Journal of Human Evolution*, *43*(6), 873–886.

https://doi.org/https://doi.org/10.1006/jhev.2002.0605

Zuberbühler, K, & Jenny, D. (2007). Interaction between leopard and monkeys. In Klaus Zuberbühler, R. Noë, & W. S. McGraw (Eds.), *Monkeys of the Taï Forest: An African Primate Community* (pp. 133–154). Cambridge University Press. https://doi.org/DOI: 10.1017/CBO9780511542121.006

Zuberbühler, K, Jenny, D., & Bshary, R. (1999). The Predator Deterrence Function of Primate Alarm Calls. *Ethology*, *105*(6), 477–490. https://doi.org/10.1046/j.1439-0310.1999.00396.x

Zuberbühler, K, Noë, R., & Seyfarth, R. M. (1997). Diana monkey long-distance calls: messages for conspecifics and predators. *Animal Behaviour*, *53*(3), 589–604.

Zuberbühler, K. (2000). Causal knowledge of predators' behaviour in wild Diana monkeys. *Animal Behaviour*, *59*(1), 209–220. https://doi.org/https://doi.org/10.1006/anbe.1999.1296

Zuberbühler, K. (2009). Survivor Signals: The Biology and Psychology of Animal Alarm Calling. *Advances in the Study of Behavior*, *40*, 277–322. https://doi.org/https://doi.org/10.1016/S0065-3454(09)40008-1

Zuberbühler, K, & Lemasson, A. (2014). *Primate Communication: Meaning from Strings of Calls BT - Language and Recursion* (F. Lowenthal & L. Lefebvre (eds.); pp. 115–125). Springer New York. https://doi.org/10.1007/978-1-4614-9414-0_9

Zuberbühler, K, León, J., Deshpande, A., & Quintero, F. (2022). Socially scripted vocal learning in primates. *Current Opinion in Behavioral Sciences*, *46*, 101153. https://doi.org/https://doi.org/10.1016/j.cobeha.2022.101153

4.12 Chapter 4: Appendix

Methods S4.1 Natural predator encounter rates.

We determined the natural predator encounter rates between August to October 2019 (N = 47 days). It was often not possible to see the actual predator, so we inferred encounter rates from alarm calls. We considered events as independent if they were separated by at least one hour. JL and two field assistants (PK and LB) took the data with a perfect interrater reliability of Cohen’s kappa = 1 for calling events classification (Table S4.1).

Methods S4.2 Role of experimenters.

For each model presentation, we strategically placed a chimeric model on the forest floor, behind a log or bush, prior to a subject's arrival. Once the model was detected we broadcasted either snake or leopard alarm calls. Three experimenters were involved during each trial who used Garmin Rino 655 Handheld GPS devices to communicate with each other. These devices transmitted their position in real time and also worked as radios, allowing experimenters to track each other's movements without visual contact. We collected data under the following conditions.

Baseline: Experimenter 1 followed and filmed the focal subject before (~30 s), during, and after detection of the model (~30 s or as soon as possible). As soon distance and visibility were adequate, Experimenter 2, in coordination via radio with the other experimenters, placed the chimeric model on the anticipated path and, once the subject detected the model, covered the model with a camouflage net pulled with a fishing line to avoid detection by other individuals. Experimenter 3 focused on the nearby group members.

Experiments: During the presentation trials (first model presentations), Experimenters 1 and 2 operated in the same way as in the baseline condition. Experimenter 3 hid the speaker behind a buttress root at a distance of ~10 m from the model. As soon as the subject detected the chimeric model, Experimenter 1 instructed Experimenter 3 to immediately play back either snake or leopard alarms. This was then followed by assessment trials (second model presentations), with Experimenters 1, 2 and 3 playing the same roles as in the baseline condition. For Experiment 2 (retest trials), all three experimenters played the same role as in the baseline condition.

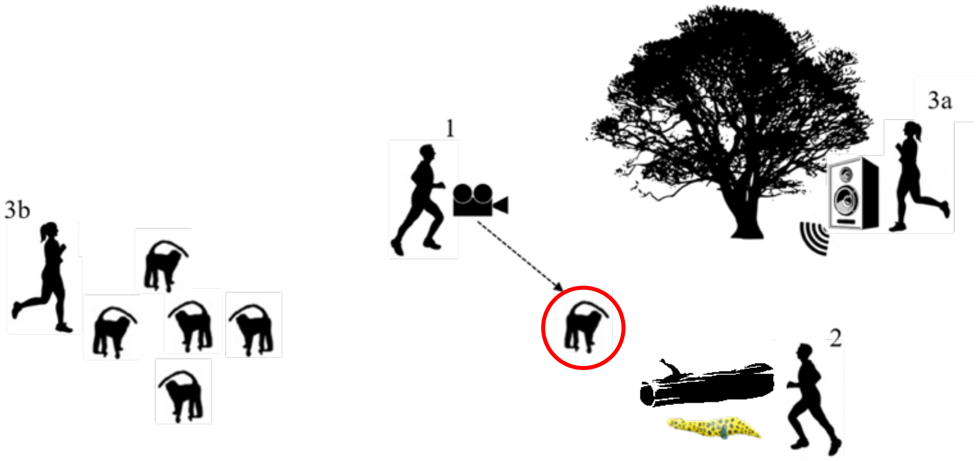

Figure S4.1 Set-up for the experiments. Experimenter 1 followed and filmed the focal subject (on the red circle). Experimenter 2 hid the chimeric model on the subject path in a location (e.g., behind a fallen trunk). During presentation trials, Experimenter 3 operated the speaker (3a), while in baseline, assessment and retest trials, focused on nearby group members (3b).

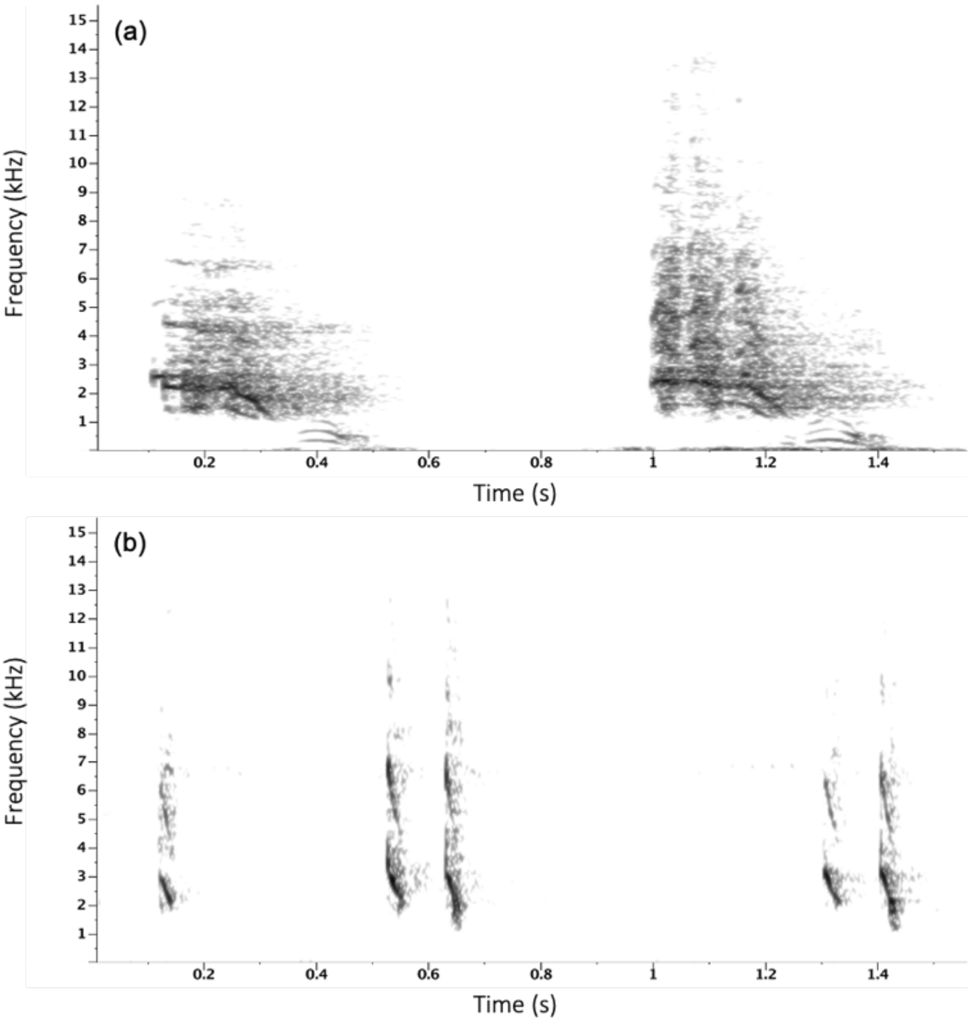

Figure S4.2 Spectrograms of (a) leopard alarm calls and (b) snake alarm calls from an adult female produced with Raven (V 1.4) and the following settings: 512 FFT, Hann window, 75% overlap, 22.05 kHz sampling frequency.

Table S4.1 Natural occurrences of sooty mangabey alarm calling events.

	Alarm Call Type		
	Snake	**Leopard**	**Eagle**
Alarm calling events	19	7	60
Calling events/week (±SE)	2.83 (0.07)	1.04 (0.06)	8.94 (0.19)

Table S4.2 Behavioural responses in baseline condition (N=19). Age group: young juveniles (YJ: 1–3 years), old juveniles (OJ: 3–5 years); adults (A: > 5 years). Audience: yes (Y), not (N). Snake and leopard antipredator behaviour and move > 10 m are binary responses.

				Responses			
Subject (ID trial)	Age group	Model type	Audience	Snake[a]	N pauses	Leopard[a]	Move > 10 m
IM (Con.5)	YJ	Fabric	Y	1	1		
KD (Con.7)	YJ	Fabric	Y	1	2		
JF (Con.8)	YJ	Fabric	N		2		
TC (Con.12)	YJ	Fabric	N	1[Voc]	1		
EM (Con.2)	YJ	Paint	Y		1		
KA (Con.4)	YJ	Paint	N		0	1	1
ME (Con.10)	OJ	Fabric	Y		1	1[Voc]	
MK (Con.11)	OJ	Fabric	Y		1	1[Voc]	1
TZ (Con.9)	OJ	Fabric	Y	1	1		
ND (Con.17)	OJ	Paint	N		2		
HO (Con.6)	OJ	Paint	N		1		
PE (Con.3)	OJ	Paint	N	1	0		
LU (Con.1)	OJ	Paint	N		0	1[Voc]	1
SR (Con.I)[b]	A	Fabric	Y		2		
MM (Con.II)[b]	A	Fabric	Y		2		
AN (Con.III)[b]	A	Paint	N		0		
BO (Con.IV)[b]	A	Paint	N		2		
ST (Con.V)[b]	A	Paint	Y		1		
BB (Con.VI)[b]	A	Fabric	Y		2		

[a] Snake antipredator behaviour: subject stays and scans the forest floor, approaches and inspects, jumps aside, stands bipedally and/or emits snake alarm calls. Leopard antipredator behaviour: subject escapes climbing into a tree, flees and/or emits leopard alarm calls; binary

[Voc] Vocal response

[b] Adults were excluded from subsequent experiments as they consistently ignored the chimeric models

Table S4.3 Behavioural responses in assessment trials (N=26). Age group: young juveniles (YJ: 1–3 years), old juveniles (OJ: 3–5 years); adults (A: > 5 years). Audience: yes (Y), not (N). Snake and leopard antipredator behaviour and move > 10 m are binary responses.

					Responses			
Subject (ID trial)	Playback stimuli	Age group	Model type	Audience	Snake[a]	N pauses	Leopard[a]	Move > 10 m
FI (Exp.12)	Snake	YJ	Fabric	Y	1	3		
HU (Exp.21)	Snake	YJ	Fabric	Y	1	0		
EM (Exp.8)	Snake	YJ	Fabric	N	1^{Voc}	3		
PA (Exp.15)	Snake	YJ	Fabric	N	1^{Voc}	5		
IR (Exp.16)	Snake	YJ	Paint	Y		1		
CA (Exp.3)	Snake	YJ	Paint	N		4		1
BA (Exp.9)	Snake	OJ	Fabric	Y	1	4		
MO (Exp.11)	Snake	OJ	Fabric	Y	1^{Voc}	1		
LO (Exp.19)	Snake	OJ	Fabric	N	1	0		
VI (Exp.18)	Snake	OJ	Fabric	N		3		
AG (Exp.23)	Snake	OJ	Paint	Y	1	2		
NA (Exp.6)	Snake	OJ	Paint	N		5		
NI (Exp.4)	Snake	OJ	Paint	N	1^{Voc}	0		
CH (Exp.14)	Leopard	YJ	Fabric	Y	1	3		
OS (Exp.22)	Leopard	YJ	Fabric	Y		1	1	1
SK (Exp.10)	Leopard	YJ	Fabric	Y		2	1^{Voc}	1
TO (Exp.26)	*Leopard*	*YJ*	*Paint*	*N*	.	.	.	.
AT (Exp.13)	Leopard	YJ	Fabric	N		1		1
MA (Exp.7)	Leopard	YJ	Fabric	N		0	1	1
BR (Exp.24)	Leopard	YJ	Paint	Y		0		
JU (Exp.20)	Leopard	OJ	Fabric	Y		0		
SO (Exp.25)	Leopard	OJ	Fabric	N		0	1	1
LA (Exp.17)	Leopard	OJ	Paint	Y		1		
MC (Exp.2)	Leopard	OJ	Paint	Y		2		1
DA (Exp.5)	Leopard	OJ	Paint	N		2		1
SA (Exp.1)	Leopard	OJ	Paint	N		0		

TO (Exp.26) trial was aborted

[a] Snake antipredator behaviour: subject stays and scans the forest floor, approaches and inspects, jumps aside, stands bipedally and/or emits snake alarm calls. Leopard antipredator behaviour: subject escapes climbing into a tree, flees and/or emits leopard alarm calls; binary

^{Voc} Vocal response

Table S4.4 Description of call providers (N=24) used for playback stimuli during N=26 presentation trials in Experiment 1. Age-sex classes: Adult Female (AF), Adult Male (AM), Subadult Male (SAM), Juvenile Female (JF), Juvenile Male (JM).

Call provider subject	Age-sex class	Playback stimuli	Subject (ID trial)
MIC	AM	Snake	FI (Exp.12)
ODI	AF	Snake	HU (Exp.21)
JOH	AF	Snake	EM (Exp.8)
FIJ	AF	Snake	PA (Exp.15)
CEC	AF	Snake	IR (Exp.16)
NIN	AF	Snake	CA (Exp.3)
EST	AF	Snake	BA (Exp.9)
BOB	SAM	Snake	MO (Exp.11)
TAR	AM	Snake	LO (Exp.19)
ERI	AF	Snake	VI (Exp.18)
ELI	JF	Snake	AG (Exp.23)
MOC	AM	Snake	NA (Exp.6)
SAM	JM	Snake	NI (Exp.4)
LAM	AF	Leopard	CH (Exp.14)
MON	AF	Leopard	OS (Exp.22)
BON	AM	Leopard	SK (Exp.10)
MAR	*AF*	*Leopard*	*TO (Exp.26)*
SAN	SAM	Leopard	AT (Exp.13)
HIL	AF	Leopard	MA (Exp.7)
TAT	AF	Leopard	BR (Exp.24)
ERI	AF	Leopard	JU (Exp.20)
BEN	AM	Leopard	SO (Exp.25)
HIL	AF	Leopard	LA (Exp.17)
JAC	AM	Leopard	MC (Exp.2)
SCR	AM	Leopard	DA (Exp.5)
PHA	AM	Leopard	SA (Exp.1)

TO (Exp.26) trial was aborted

Table S4.5 Influence of predictor variables on behavioural responses following the assessment trials.

Predictor variable	Estimates	SE	*z*	*P*
a. Snake antipredator behaviour				
Intercept	−0.68	0.99	[a]	[a]
Playback Stimulus (Leopard)	−3.29	1.16	−2.82	0.004**
Juvenile Age (Young)	−0.05	0.95	−0.06	0.95
Audience (Yes)	1.03	0.99	1.04	0.29
Model Type (Fabric)	1.73	1.04	1.66	0.09
b. Number of pauses				
Intercept	0.83	0.3	[a]	[a]
Playback Stimulus (Leopard)	−0.86	0.34	−2.51	0.011*
Juvenile Age (Young)	0.27	0.31	0.88	0.37
Audience (Yes)	−0.14	0.3	−0.47	0.63
Model Type (Fabric)	−0.06	0.31	−0.19	0.84
c. Leopard antipredator behaviour				
Intercept	−5.57	2.13	[a]	[a]
Playback Stimulus (Leopard)	2.99	1.57	1.9	0.05
Juvenile Age (Young)	0.54	1.15	0.47	0.63
Audience (Yes)	−0.36	1.09	−0.33	0.74
Model (Fabric)	2.31	1.58	1.46	0.14
d. Move >10 m				
Intercept	−2.19	1.13	[a]	[a]
Playback Stimulus (Leopard)	2.8	1.1	2.53	0.011*
Juvenile Age (Young)	1.07	0.99	1.08	0.27
Audience (Yes)	−1.46	1	−1.46	0.14
Model (Fabric)	−0.06	0.95	−0.073	0.94

[a] Omitted given that there is no interpretable result. () denote the variable level that reflects the estimate when tested against the alternative level: Leopard v Snake, Young v Old, Audience-Yes v No, Fabric v Paint.

* *P* < 0.05 and ** *P* < 0.01 following Bonferroni correction

In all four models, the interaction between type of played-back alarm call and juveniles' age group was not significant and was therefore removed (estimates are given with respect to leopard alarm calls and young juveniles, GLM for *Viper antipredator behaviour*: estimate = 0.27, SE = 1.48, $z = 0.18$, $P = 0.85$; GLM for *Number of pauses*: estimate = 0.16, SE = 0.7, $z = 0.23$, $P = 0.81$; GLM for *Leopard antipredator behaviour*: estimate = 0.86, SE = 1.54, $z = 0.56$, $P = 0.57$; GLM for *Move >10 m*: estimate = 0.31, SE = 1.36, $z = 0.23$, $P = 0.81$).

Table S4.6 Bayesian and frequentist binomial tests on subjects' behavioural responses during control condition and retest trials and their vocal response during assessment trials analysed with. Bayes factors (BF_{10}) < 3 are weak evidence, BF_{10} = 3–10 are moderate evidence and BF_{10} > 10 are strong evidence for the alternative H_1 relative to the null hypothesis H0.

	Bayesian binomial	**Binomial**
	Bayes factor (BF_{10})	*(z) P*
Control condition		
Adults ignoring the model	18.14	*(-2.15)* 0.015*
Pre-existing predator notion towards the model	1.49	*(-1.11)* 0.13
Innate bias for one of the two predator categories	0.3	*(0.66)* 0.74
Assessment trials (Exp 1.)		
Effect on subjects' vocal response:		
Playback Stimulus	10.5	*(-1.86)* 0.031*
Age	0.7	*(0)* 0.5
Audience	0.7	*(0)* 0.5
Model type	1.9	*(-0.88)* 0.18
Retest trials (Exp. 2)		
Long-term association (subjects exhibiting same response in assessment and retest trials)	18.51	*(-2.3)* 0.01*

* $P < 0.05$

Table S4.7 Behavioural responses in retest trials in function of the time interval between assessment and retest trials (N=11). Age group: young juveniles (YJ: 1–3 years), old juveniles (OJ: 3–5 years).

Subject (ID trial)	Playback stimuli	Age	Assessment trial*	Retest trial*	Long-term association	Days interval between trials
LO (EXP.19)	*Snake*	*OJ*	*1*	.	.	*498*
AG (EXP.23)	Snake	OJ	1	1	1	534
OS (EXP.22)	Leopard	YJ	1	1[a]	1	541
SO (EXP.25)	Leopard	OJ	1	Ignores	0	565
VI (EXP.18)	Snake	OJ	Ignores	Ignores	1	568
HU (EXP.21)	Snake	YJ	1	1	1	574
MA (EXP.7)	Leopard	YJ	1	1	1	594
MO (EXP.11)	Snake	OJ	1^{Voc}	1^{Voc}	1	606
CA (EXP.3)	Snake	YJ	Ignores	Ignores	1	663
DA (EXP.5)	Leopard	OJ	1	1	1	672
NA (EXP.6)	Snake	OJ	Ignores	Ignores	1	718

* Corresponding responses to the playback which the focal heard during presentation trials are scored with 1

[a] Subject first response is leopard-type and later shows a snake-type response

^{Voc} Vocal response

LO (Exp.19) retest trial was aborted

Chapter 5: General Discussion

5.1 Summary of findings

In the first empirical chapter, I examined the development of alarm call behaviour in mangabeys. I used focal animal samples to record data on the stimuli that elicited alarm calls by the focal subject during natural predator encounters. I also exposed subjects of three age groups (young juveniles, old juveniles, adults) to playbacks of leopard, and eagle alarm calls given either by other group members or by sympatric Diana monkeys. Moreover, I also presented conspecific snake alarm calls and Diana monkey tree loud calls (a non-predatory signal). Align with my predictions, young juveniles (1–2 years old) showed less appropriate locomotor and vocal responses than adults and engaged in more social referencing than older individuals, across conditions. Old juveniles (2–4 years old) already showed responses that did not differ significantly from adults. Adults differed from the juveniles insofar as they were particularly sensitive to others' alarm calls and in their alarm calling. In sum, these results suggest that mangabeys classified species and objects from the environment around them into broad categories from an early age and that their call comprehension becomes entrenched during the first 2 years of life, while competent alarm call usage does not appear until about 4 years of age. Moreover, as predicted, conspecific leopard alarms elicited the strongest overall responses in all age classes, highlighting the importance of leopard predation pressure in primates' anti-predator behaviour. Finally, contrary to my predictions, there were no clear differences in learning between predatory and non-predatory Diana monkey loud calls nor of con- and heterospecific alarm call signal meaning. Thus, these results suggest socially learned alarm call comprehension during juvenile stage, with escape responses diversifying into predator specificity with age and call comprehension preceding appropriate usage but no difference between learning their own or other species' alarm calls. Finally, primates, like most animals, inhabit ecosystems with multiple sources of information, including non-predatory heterospecifics. However, very few studies have approached the development of primate alarm calls by simultaneously considering both con- and heterospecific signals available to individuals (Fichtel, 2008; Hauser, 1988). Hence, this study is particularly valuable to understand the ontogeny of primate alarm call behaviour.

In the second empirical chapter, I provided one of the few empirical tests of Seyfarth &

Cheney's vocal development model by studying the ontogeny of snake antipredator behaviour. I systematically exposed young juveniles, old juveniles and adults to different snake models of dangerous vipers and not-venomous colubrids. As predicted, young individuals perceived all snakes as dangerous and were less proficient to recognize viper models as predators than adults. Moreover, young individuals engaged in more social referencing than adults, suggesting that they relied on more experienced individuals about how to best respond to snakes. On the other hand, adults responded faster to vipers than colubrids and never alarm called to them. Altogether, these results corroborated Seyfarth and Cheney's model: snake-predator learning departs from an over-generalized response to a wide variety of species, including some non-threatening ones, that is winnowed down, probably via social learning and individual experience, into a response directed toward specific dangerous species. Moreover, I compared and discussed this pruning process in the anti-predator behaviours of vervet monkeys and mangabeys and suggested that vocal production appears to develop in species-specific ways, with some species alarm calling from early on and others refraining from call production until cognitively competent. Finally, I elaborated on how these findings support theories that state that snakes as predators have played a central role in the evolution of primate cognition (Isbell, 2006, 2009).

In the third empirical chapter, I addressed the question of how primates learn to classify the world around them. I conducted a field experiment to test the role of social learning during this classification process. I exposed subjects to a novel, chimeric predator model with snake- and leopard-like visual features. During baseline presentations, we found that juveniles (but not adults) did not consistently assign the chimera to any familiar predator class, suggesting plausibility judgments in experienced adults. In subsequent experimental trials with 26 juveniles of another mangabeys group, we exposed half of our subjects to the chimera in conjunction with playbacks of conspecific leopard alarms while the other half heard conspecific snake alarms. We then tested each subject on the same day and found that response patterns corresponded to the predator alarm calls they heard during the playback trial, suggesting that they attended to others' alarm calls to classify the model as either belonging to the snake or leopard category. Nearly two years after the first experiment, we exposed 10 of the same individuals to the same chimera model for a second time, and found that 9 of 10 subjects continued to show the same anti-predator response as they did two years ago, indicating long-term retention of socially learned predator categorisation from one single predator experience. These results showed the presence of a meaning-driven, highly-efficient social learning mechanism that enables primates to acquire and retain ecological knowledge in very effective ways from one-time experiences.

In conclusion, the three studies presented here have as their central theme the development of vocal communication and the role of social learning in communicative competence in non-human primates, using sooty mangabeys as a model system. Overall, these results contribute to the growing body of evidence for primate vocal flexibility in the call usage and comprehension domains and highlight the central role of social learning and auditory experience in call comprehension and the development of primate communicative competence. My work also provides evidence supporting the presence of a highly-efficient social learning mechanism that enables primates to acquire and retain ecological knowledge in very effective ways from one-time experiences. More broadly, these findings have direct evolutionary implications for human language, including questions about fast-mapping and language evolution and acquisition. Moreover, our current understanding of non-human primate vocal communication in ecologically relevant settings is largely based on research conducted on apes and a few monkey species, and very little is known about the communication and cognition capacities of several primate species, such as sooty mangabeys. Thus, this thesis is of great value as it helps to fill this knowledge gap and expand our comprehension of the vocal communication and cognition of an important group of catarrhines. Finally, these studies are in line with the view that human cognition has deep roots in the primate lineage, in this case by demonstrating how non-human primates acquire and develop vocal communicative competence.

In the next sections, I attempt to provide an update on the different models of development of vocal communication in non-human primates and build up on the importance of social learning in the acquisition and moulding of primate communicative competence. Finally, I discuss the flaws and strengths of the experiments here presented and consider future research in non-human primate communication, behaviour and cognition that potentially would shed light to our understanding on the evolution of human language.

5.2 Social learning and vocal communication in primates

Primates use vocalizations to communicate with one another for different purposes, from coordinating group movement to alerting group members to predators (Cheney & Seyfarth, 2018). Classical behaviourist vision is based on the affect-conditioning model (Owren & Rendall, 1997), which suggests that non-human primate vocalizations are hard-wired and only represent the internal states of the callers (Owren & Rendall, 2001). However, In order for vocalizations to function as signals, group members must be able to recognize these vocalizations as being produced by a particular individual. Despite the vocal production limitation exhibited by non-human primates, evidence of vocal individual recognition is abundant in the literature (Carlson et al., 2020). Therefore, there must be a higher degree of cognitive control from the listener compared to the vocal production ability of callers (Seyfarth & Cheney, 2010; Snowdon, 2009). This contrast illustrates the marked disparity among vocal production, usage, and comprehension in non-human primates, where vocal production and usage are highly constrained (particularly the former one) and vocal comprehension is flexible, open-ended, and cognitively rich (Seyfarth & Cheney, 2010).

If the capacity of listeners to process signals differs greatly from the competence of callers' vocal production learning, then it is also possible that all domains of vocal communication do not necessarily have evolved under the same mechanisms and selective pressures. In line with this argument, a recent review of communicative acts in primates proposes a novel classification of gestural and vocal signals (Fröhlich & van Schaik, 2020). This new classification scheme suggests distinguishing between innate signals that evolved through natural selection and invented signals that are learned during ontogeny. Although this review mainly focuses on gestures, the suggestion that elements of some signals may have mixed origins can easily apply to vocalizations. Thus, it is entirely possible that the processes of vocal development and learning, which refers to the ability to acquire and learn vocalizations through age and experience, respectively, could have evolved under different ontogeny and learning mechanisms. Additionally, recent research on vervet monkeys has also suggested a new classification for primate call repertoires based on differences in the amount of production and cognitive control over each call type (Deshpande, 2021).

Based on this theoretical framework, I suggest that, due to differences in selection pressure and anatomical limitations, the vocal production, usage and comprehension of the different primate call types may have different underlying –innate and learned– mechanisms driving their acquisition and development.

Vocal production: innate vs learning mechanisms

Vocal production learning refers to the ability to learn to selectively produce new vocalizations after exposure to model sounds. For example, humans can learn new words through experience. Studies of humans and songbirds serve as the foundation for the traditional theory of vocal production learning. Depending on the species, the animal uses auditory information from a model sound to create copies of varying degrees of fidelity. Learning new sounds from an auditory input is also known from other groups of birds and mammals, such as parrots (Bradbury & Balsby, 2016; Pepperberg, 2010), hummingbirds (Araya-Salas & Wright, 2013; Johnson & Clark, 2020, 2022), bats (Lattenkamp et al., 2018; Vernes & Wilkinson, 2020), pinnipeds (Stansbury & Janik, 2019), cetaceans (King & Janik, 2013; Ridgway et al., 2012) and elephants (Poole et al., 2005; Stoeger et al., 2012). Among non-human primates, limited vocal production learning has been demonstrated in the contact and food calls of some platyrrhines, such as cotton-top tamarins (Egnor et al., 2006) and common marmosets (Takahashi et al., 2017), and in some catarrhines (Lemasson et al., 2011; Sugiura, 1998), including apes (Watson et al., 2015). Likewise, chimpanzees victim of aggression modify the acoustic structure of their screams depending on the composition of the by-standing audience, probably to solicit support (Slocombe & Zuberbühler, 2007). On the other hand, studies on the vocalizations of African green monkeys (*Chlorocebus*) revealed that alarm calls of closely related species and subspecies are highly conserved in their acoustic structure (Price et al., 2014, 2015).

While vocal production in non-human primates is primarily innate, slight, but meaningful, changes in the acoustic structure of their calls seem to involve limited learning. These modifications occur mainly in the amplitude and temporal features of their vocalizations (Brumm et al., 2004; Egnor et al., 2006; Egnor & Hauser, 2006), with spectral changes being less common (Fischer et al., 2004; Hotchkin et al., 2013; Snowdon, 2009). Moreover, it seems that calls given during both affiliative and agonistic social interactions (e.g., contact, food and distress calls) can experience more acoustic modifications than other call types, such as alarm calls. Social calls not only facilitate interactions between individuals, which are highly dynamic but also are relatively free from specific biological functions compared to alarm calls. Overall, it seems that limited plasticity in the call structure of non-human primate vocalizations is mostly regulated by physical maturation, with narrow production learning occurring mostly in calls involved in social contexts.

Vocal usage: innate vs learning mechanisms

Vocal usage learning comprises the adjustment of usage in relation to experience. Here, there is much more evidence of learning involved in the communication process. Many non-human primates use their vocalizations in a range of contexts, suggesting that there is not a one-to-one strict mapping between a call and how or when it is used. In vervet monkeys, adult males produce leopard alarms (or alarm barks) during encounters with terrestrial predators as well as during intra- and intergroup aggressions (Price et al., 2015). Importantly, these contexts share key similarities, i.e., heightened arousal and potential danger on the ground. Moreover, even if vervet infants appear to have a general concept of when and to what give specific alarm calls, learning seems to be essential in the pruning process by which infants focus their anti-predator and alarm call behaviour toward a small number of dangerous predators (Seyfarth & Cheney, 1986). Furthermore, adult Japanese macaques living in a visually restricted habitat produced more contact calls compared to adults in a more open habitat (Koda et al., 2008). Interestingly, this difference in call rate emerged and increased developmentally, suggesting vocal usage learning.

A typical example of vocal usage learning occurs when individuals produce (or decide to not produce) their calls as a function of the audience composition. There are several examples of audience effects on call usage (and inhibition) across different call types in non-human primates. Chimpanzee vocal usage of food (Schel, Machanda, et al., 2013), alarm (Schel, Townsend, et al., 2013), and distress calls (Fedurek et al., 2015) meet some key criteria for intentionality. The decision of whether to call or not is influenced by the caller's own experience and can be extended even to heterospecific audiences, such as predators. Diana monkeys give alarm calls in response to leopards to deter them from attacking, while remaining silent when detecting a group of chimpanzees, which could use the alarm calls to localize and attack the monkeys (Zuberbühler et al., 1999).

Overall, vocal usage is more variable and plastic compared to vocal production. Although young non-human primates appear to use calls in generally appropriate contexts from an early age, there is substantial evidence that their appropriate vocal usage is acquired through learning processes that start occurring during their early stages of life and refine throughout their maturation. Vocal usage of most call types seems to be refined via learning. Even calls that are tightly coupled with the internal states of the caller (i.e., screams) undergo changes in their usage via experience and learning due to the influence of external factors, such as audience composition. Finally, for alarm calls, which are linked to anti-predatory behaviour, natural selection has likely favoured a combination of some degree of predisposition, and efficient social learning or alternative more general learning mechanisms to produce optimal anti-predatory behavioural strategies.

Vocal comprehension: innate vs learning mechanisms

Vocal comprehension learning encompasses the ability to associate a sound with its source and to understand what the sound predicts. In contrast to production and usage learning, vocal comprehension learning is open-ended and extremely rapid. There is abundant evidence of plasticity in this vocal domain with differences in life history affecting the comprehension of acoustic signals, even from heterospecifics and artificial sound sources. Recent field experiments have shown that monkeys can acquire predator knowledge by learning threat-acoustic associations from a variety of sounds, such as alarm calls (Deshpande et al., 2022; León, Thiriau, Bodin, et al., 2022), heterospecific calls (e.g., rooster crow; Wheeler et al. 2019), and even artificial sounds (e.g., drone sound; Wegdell et al. 2019). Particularly, it seems that conspecific alarm calls serve as vehicles for rapid and highly efficient one-trail social learning (Deshpande et al., 2022; León, Thiriau, Bodin, et al., 2022).

Some of the most compelling evidence from non-human primate vocal comprehension learning comes from studies of heterospecific communication. Different primate species learn to respond appropriately to the alarm calls of other species (including primates, mammals and birds), reacting to heterospecific alarm calls as strongly as to the actual predators (Cheney & Seyfarth, 1985; Fichtel, 2008; Hauser, 1988; Oda & Masataka, 1996; Zuberbühler, 2000a). Moreover, monkeys can extract causal knowledge of predators' behaviour from heterospecific alarm calls. Diana monkeys whose home range overlaps with the one of a chimpanzee community were more likely to respond to chimpanzee leopard alarm calls than peripheral groups, indicating between-group differences in semantic knowledge (Zuberbühler, 2000).

Additionally, Rhesus monkeys are able to discriminate between different individuals' screams, which suggests some kind of comprehension learning about the connection between the individual identity of group members and their screams' acoustic features (Fugate et al., 2008). Furthermore, cross-fostering experiments in Rhesus and Japanese macaques showed that foster mothers reacted faster to play and food calls of their foster infant than they did to playbacks of calls of conspecific infants. This result indicates that foster mothers have learned the individually distinctive features of these social calls of their foster infants and react appropriately to them (Owren et al., 1992; Seyfarth & Cheney, 1997).

Overall, non-human primates are remarkably flexible in their ability to ascertain sound-source associations and to act on well-founded predictions that are based on acoustic signals from both their own species and heterospecifics. Moreover, it seems that open-ended vocal comprehension learning occurs in most call types present in primates' vocal repertoire, and is driven by learning mechanisms, with social learning playing a key role in the acquisition of sound comprehension competence. Furthermore, rapid and efficient learning is clearly adaptive in the predation context, this is probably why some monkey species show one-trial social learning from alarm calls. Whether rapid social learning of vocal comprehension occurs in call types produced in other contexts remains a topic of future research.

There is a clear distinction in the role that learning mechanisms play in the production, usage and comprehension of non-human primates' different call types. To shed light on the evolution and ontogeny of primate vocal learning, I suggest focusing on potential ancestral independence in the development of voice output, call usage and auditory perception of the different call types in non-human primates. Comparison of the different mechanisms that may mediate vocal learning in various call types (e.g., social, alarm, copulation and distress calls, among others) of different species is essential to this endeavour.

Although non-human primates do not have the vocal production learning abilities present in songbirds or some cetaceans and bats species, they still show impressive and sophisticated auditory usage and comprehension learning capacities. We can extract two main conclusions from this discrepancy. First, when talking about vocal learning, the continuity between non-human primate communication and human language may rely on the capacity of listeners to process signals rather than on the vocal production abilities of callers (Fischer, 2017). Second, limiting factors in language evolution are likely to be found in the fundamental differences between non-human primate vocal production and human speech, while the control over usage and processing of acoustic signals shows striking similarities between vocal learning in non-human primates and speech –evidencing some of the biological roots of human language. In conjunction, cognitive capacities of listeners overcome vocal production abilities of callers and vocal production, usage and comprehension learning seems to be ancestral independent in non-human primates (Fischer & Hammerschmidt, 2020).

Social learning and vocal development

Research efforts devoted to the ontogenetic development of no-human primates have clearly shown that social learning typically influences primates' lifetimes across multiple domains (reviewed in Whiten and van de Waal 2018). Alternation and integration of social and asocial learning are fundamental in the acquisition of vocal communication competence. Moreover, call variants seem to develop and refine in function of an animal's experience with the relevant external factors, which is likely to be socially learned by observing and interacting with others. Here, I suggest that social learning influences the acquisition of alarm call behaviour competence in non-human primates in a model of three main phases: the first step is an over-generalised and quasi-silent acquisition phase, where infants mostly learn from primary attachment figures, typically the mother; in the second step, young individuals start to discriminate different stimuli and classify them into broad categories. This is a selective learning phase when knowledge is acquired from other group members and sympatric heterospecifics; finally, in the third step, after developing cognitive competence, primates direct species-specific anti-predator behaviours, including active alarm calling behaviour, to dangerous predators. This third phase comprises learning from novel social environments generated by the migration of individuals outside the group and new social and ecological learning circumstances for migrant, usually mature, individuals. The idea of a three-phase scheme of social learning in the ontogenetic development of no-human primates is not novel (Whiten & van de Waal, 2018). Rather, I have only briefly integrated this three-step social learning view into the development of vocal communication in non-human primates.

5.3 Study limits

Here, I have shown that different elements of the communicative competence of sooty mangabeys arise and refine during juvenile stage and are mediated by social learning and experience, i.e., competent alarm call behaviour towards con- and heterospecific signals, snake-specific discrimination and snake anti-predator behaviour (alarm calling) towards dangerous vipers, but also that they can acquire predator knowledge from alarm calls via one-trial social learning, communicate this knowledge subsequently to others and retain it in the long-term. However, all three studies here presented face limitations due to the nature of the experimental designs.

First, low sample size is a common problem in animal cognition research, especially in experimental procedures in the wild, and these studies are no exception (particularly the second and third empirical chapters). This issue can potentially have an impact on statistical analyses and limit the capacity to draw deeper conclusions. Second, due to logistical constraints (e.g., low number of infants and their dependency to their mothers), I did not determine the exact age at which infants start to display their species-specific alarm calling behaviour. This information is crucial to have a complete picture of the ontogeny of sooty mangabey alarm calling behaviour. Third, all animal models that I used during experiments were stationary, and studies in vervet monkeys and wild jackdaws (*Corvus monedula*) have shown that the animacy of the objects influences subjects' responses (Deshpande et al., 2022; Greggor et al., 2022). Thus, experiments with mobile predator models could help to understand how knowledge about objects' animacy combines with predator knowledge and information acquired via social learning. Fourth, I used a limited spectrum of animal models: vipers and colubrid snakes and chimeric models with both snake and leopard features. It would be of great interest to conduct experiments using other predator models, such as crowned eagles and pythons, which are confirmed primates' predators (Jaffe & Isbell, 2010; Khamcha & Sukumal, 2009; Shultz & Thomsett, 2007; Struhsaker, 1967). Moreover, the use of a wider range of chimera models, varying both in shape and colour patterns, or even of 'unnatural' models (e.g., random objects) would have been convenient to enrich the conclusions of this research. Despite these limitations, all the experimental procedures here can be used as a reference point for upcoming research that could replicate and enhance these experimental designs. Finally, and acknowledging the flaws described above, this thesis adds to our understanding of primate cognition, vocal communication and social learning

5.4 Future research directions

This thesis illustrates the value of combining direct long-term behavioural observations with novel field experiments to understand how free-ranging primates communicate using vocal signals. Now, I will briefly discuss what I consider possible future research directions on primate vocal communication.

First, to test which socioecology and cognitive features may shape species-specific vocal development, it is necessary to conduct future comparative field studies that determine the exact age at which infants of different primate species start to display their species-specific alarm calling behaviour. Field studies on immature of different primate species have shown an important variance in the age at which juveniles begin to consistently produce alarm calls in response to threats: I found that the development of adult-like responses to alarm calls in sooty mangabeys (24 months old) is in between the ages that have been reported for Verreaux's sifakas, squirrel monkeys, vervet monkeys and chacma baboons (6–12 months old; Fichtel, 2008; Fischer et al., 2000; McCowan et al., 2001; Seyfarth & Cheney, 1980, 1986) and chimpanzees (80 months old; Dezecache et al. 2019). This suggests that further research on the ontogeny of alarm call comprehension across taxonomic groups of primates could shed light on the cognitive division between prosimians, monkeys, apes and, ultimately, humans (Amici et al., 2010; Tomasello, 2010; Tomasello & Call, 1994).

The use of animal models has been proven to be very useful to elicit anti-predator responses in animals, including primates (Adams & Kitchen, 2020; Arnold et al., 2008). I propose to extend this approach to three, not necessarily mutually exclusive, lines of research. First, as shown in the third empirical chapter, the use of chimeric models, combining stimuli that already are meaningful (e.g., snake shape, leopard coat), provides a unique opportunity to study the cognitive and communicative abilities of free-ranging primates. Thus, I encourage the use of chimeric models that ‘equally’ combine features of different predators to test different aspects of primate anti-predator behaviour. Second, two- and three-dimensional holograms as animated stimuli have the advantage of being highly controlled, offering standardization and repeatability, and allowing researchers to test how specific cues influence perception (Chouinard-Thuly et al., 2017; Li et al., 2022). However, due to its limitations outside laboratory conditions, the suitable use of these technologies still raises several technical questions. Third, live demonstration provides a more realistic, natural, interactive context in animal experiments (Abdai et al., 2022). Thus, artificial models (i.e., robots) can be used to manipulate subjects in a unique way, allowing us to study motion and social perception in non-human species, with potential implications in our understanding of the evolution of cooperative behaviour and communication (Romano et al., 2019). Finally, each of these three lines of research involves different and specific technological challenges, particularly when applied in field research, where conditions can be more erratic and difficult to control.

Additionally, communication systems are an emergent product of interactions among individuals. These systems are based on signals subject to different temporal dynamics ranging from changes over evolutionary time –to have consistent meanings to senders and receivers– to shorter timescales and faster modifications –like the development of dialects and cultural transmission–. Thus, improving our understanding of the social and temporal dynamics of primate vocal communication is essential to make inferences about the evolution and dynamics of collective behaviours, such as human language. However, detailed analyses of the extent and temporal dynamics of such changes across the different call types of a species remain limited. Moreover, until recent years, most classification methods used in bioacoustics analyses were traditionally carried out manually, which presents significant technical and conceptual disadvantages. Combining recent advances in computational bioacoustics and machine learning algorithms for acoustic feature analysis and classification of large datasets can overcome such shortfalls. Nowadays, there is evidence that datasets with a higher number of acoustic features, instead of factors, and fuzzy clustering algorithms provide better clustering results (Wadewitz et al., 2015). This is because it is hard to capture all the acoustic variance using hard classification approaches as most call types are graded. Moreover, methods for automatic classification, like unsupervised Artificial Neural Networks (ANNs), which require few *a priori* assumptions reduce the degree of subjectivity in the classification procedure while increasing replicability (Mielke & Zuberbühler, 2013; Pozzi et al., 2013). Likewise, variations of stochastic neighbour embedding (SNE) models improve bioacoustics data visualization in a remarkable way (Valente et al., 2019). Furthermore, algorithms for measuring similarity that can be applied to call classification, such as Dynamic Time Warping (DTW) processes, should be favoured because they allow comparisons between different datasets (Gamba et al., 2015). Overall, these new techniques provide an effective and robust approach to automatic call classification, which unravels information contained in vocal signals, enables to process large datasets, reduces human bias in the classification process, and, therefore, allows replications and comparisons between different datasets. Therefore, projects that combine novel bioacoustics and computational tools and that aim to explore how and to what extent the social environment affects the acoustic structure and usage of the different call types of free-living primates in the short-, medium- and long-term would advance the state-of-the-art of primate vocal communication.

Finally, studies that replicate classic research and, even better, monitor individuals in the long-term allow analyses of variation and the study of processes rather than simply states or events (Sheldon et al., 2022). It is true that the habituation of wild primates to human observers is extremely time-consuming and a major financial commitment. However, field experiments in long-term studied wild primate populations are indispensable to evaluate the extent of variation and temporal change in how social, ecological and evolutionary processes operate and shape primate communication.

In conclusion, leading research on animal communication and cognition requires the study of dynamic, social, multi-scale and interdependent behaviours, and the combination of behavioural observations, field experiments, emerging technologies and long-term studies. This interdisciplinary research has an enormous potential to revolutionise our understanding of primate communication and human language.

5.5 Conclusion

Social learning is a key component of sooty mangabeys' vocal communication, particularly in the acquisition and development of communicative competence. Results presented here support the notion that non-human primates have limited vocal production learning in contrast to their extraordinary signal processing abilities. Thus, the latter is where we should look for any continuity between non-human primate communication and human language (Fischer, 2017). Furthermore, it is clear that to some extent the communicative capacities of non-human primates are socially learned, which is also essential for language acquisition in humans. These results suggest that the neural underpinnings of the cognitive system responsible for processing vocal signals and socially learn about them—both of which are present in human language—evolved gradually within the primate evolutionary lineage, with roots at least as far back as the last common ancestor of catarrhines and humans, which lived around 23–25 million years ago (Schrago & Russo, 2003; Stauffer et al., 2001). Moreover, these studies empirically confirmed Seyfarth and Cheney's maturational model (Seyfarth & Cheney, 1980, 1986), an influential, but largely untested, model of primate anti-predator vocal development. The value of studying primates in ecologically relevant settings and species that had previously received less attention in the field of communication, such as sooty mangabeys, is also demonstrated by the research presented here. In the coming years, emerging technologies and novel field experiments should enhance bioacoustics analyses and animal communication and cognition research. Furthermore, I reiterate the importance of establishing new long-term field studies and the continuity of the ongoing ones to study how social and ecological processes have operated in the evolution of animal communication in natural populations, and the extent of variation and temporal change in these processes. Altogether, this integrative approach will continue to help us better comprehend the major transition from non-linguistic to linguistic communication that has occurred in human evolution. In other words, comparative research on animal communication and human language has never been this promising and fascinating.

5.6 References

Abdai, J., Uccheddu, S., Gácsi, M., & Miklósi, Á. (2022). Exploring the advantages of using artificial agents to investigate animacy perception in cats and dogs. *Bioinspiration & Biomimetics*, *17*(6). https://doi.org/10.1088/1748-3190/ac93d9

Abrams, P. A. (2001). Predator-Prey Interactions. In C. W. Fox, D. A. Roff, & D. J. Fairbairn (Eds.), *Evolutionary Ecology: Concepts and Case Studies* (p. 0). Oxford University Press. https://doi.org/10.1093/oso/9780195131543.003.0028

Adams, D. B., & Kitchen, D. M. (2020). Model vs. playback experiments: The impact of sensory mode on predator-specific escape responses in saki monkeys. *Ethology*, *126*(5), 563–575. https://doi.org/https://doi.org/10.1111/eth.13008

Altmann, J. (1974). Observational Study of Behavior: Sampling Methods. *Behaviour*, *49*(3/4), 227–267. http://www.jstor.org/stable/4533591

Amici, F., Aureli, F., & Call, J. (2010). Monkeys and apes: are their cognitive skills really so different? *American Journal of Physical Anthropology*, *143*(2), 188–197. https://doi.org/10.1002/ajpa.21305

Araya-Salas, M., & Wright, T. (2013). Open-ended song learning in a hummingbird. *Biology Letters*, *9*(5), 20130625. https://doi.org/10.1098/rsbl.2013.0625

Arnold, K., Pohlner, Y., & Zuberbühler, K. (2008). A forest monkey's alarm call series to predator models. *Behavioral Ecology and Sociobiology*, *62*(4), 549–559. https://doi.org/10.1007/s00265-007-0479-y

Arnold, K., & Zuberbühler, K. (2006). Semantic combinations in primate calls. *Nature*, *441*(7091), 303.

Audacity Team. (2020). *Audacity: Free Audio Editor and Recorder* (2.2.2).

Baldwin, D. A., & Moses, L. J. (1996). The Ontogeny of Social Information Gathering. *Child Development*, *67*(5), 1915–1939. https://doi.org/10.2307/1131601

Barros, M., Boere, V., Mello, E. L., & Tomaz, C. (2002). Reactions to Potential Predators in Captive-Born Marmosets (Callithrix penicillata). *International Journal of Primatology*, *23*(2), 443–454. https://doi.org/10.1023/A:1013899931878

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software; Vol 1, Issue 1 (2015)* . https://doi.org/10.18637/jss.v067.i01

Bergman, T. J., Beehner, J. C., Painter, M. C., & Gustison, M. L. (2019). The speech-like properties of nonhuman primate vocalizations. *Animal Behaviour*, *151*, 229–237. https://doi.org/https://doi.org/10.1016/j.anbehav.2019.02.015

Bidner, L. R. (2014). Primates on the Menu: Direct and Indirect Effects of Predation on Primate Communities. *International Journal of Primatology*, *35*(6), 1164–1177. https://doi.org/10.1007/s10764-014-9797-x

Boesch, C., & Boesch-Achermann, H. (2000). *The chimpanzees of the Taï forest : behavioural ecology and evolution*. Oxford : Oxford university press. http://lib.ugent.be/catalog/rug01:000534901

Boesch, C., & Boesch, H. (1989). Hunting behavior of wild chimpanzees in the Taï National Park. *American Journal of Physical Anthropology*, *78*(4), 547–573. https://doi.org/https://doi.org/10.1002/ajpa.1330780410

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., & White, J.-S. S. (2009). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution*, *24*(3), 127–135. https://doi.org/10.1016/j.tree.2008.10.008

Borrow, N. (2014). *Field Guide to Birds of Western Africa*. Bloomsbury Publishing.

Bradbury, J. W., & Balsby, T. J. S. (2016). The functions of vocal learning in parrots. *Behavioral Ecology and Sociobiology*, *70*(3), 293–312. https://doi.org/10.1007/s00265-

016-2068-4

Brodbeck, D. R., Burack, O. R., & Shettleworth, S. J. (1992). One-trial associative memory in black-capped chickadees. *Journal of Experimental Psychology: Animal Behavior Processes*, *18*, 12–21. https://doi.org/10.1037/0097-7403.18.1.12

Brumm, H., Voss, K., Köllmer, I., & Todt, D. (2004). Acoustic communication in noise: regulation of call characteristics in a New World monkey. *The Journal of Experimental Biology*, *207*(Pt 3), 443–448. https://doi.org/10.1242/jeb.00768

Bshary, R., & Noë, R. (1997). Red colobus and Diana monkeys provide mutual protection against predators. *Animal Behaviour*, *54*(6), 1461–1474. https://doi.org/https://doi.org/10.1006/anbe.1997.0553

Carlson, N. V, Kelly, E. M., & Couzin, I. (2020). Individual vocal recognition across taxa: a review of the literature and a look into the future. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *375*(1802), 20190479. https://doi.org/10.1098/rstb.2019.0479

Cäsar, C., & Zuberbühler, K. (2012). Referential alarm calling behaviour in New World primates. *Current Zoology*, *58*(5), 680–697. https://doi.org/10.1093/czoolo/58.5.680

Castro, N. A., & Snowdon, C. T. (2000). Development of Vocal Responses in Infant Cotton-Top Tamarins. *Behaviour*, *137*(5), 629–646. http://www.jstor.org/stable/4535727

Center for Conservation Bioacoustics. (2014). Raven Pro: Interactive Sound Analysis Software. In *Ithaca, NY: The Cornell Lab of Ornithology.* (1.5).

Cheney, D. L., & Seyfarth, R. M. (1985). Social and non-social knowledge in vervet monkeys. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences*, *308*(1135), 187–201. https://doi.org/10.1098/rstb.1985.0019

Cheney, D, & Seyfarth, R. (2018). Flexible usage and social function in primate vocalizations. *Proceedings of the National Academy of Sciences*, *115*(9), 1974–1979. https://doi.org/10.1073/pnas.1717572115

Cheney, DL, & Seyfarth, R. (1990). How monkeys see the world: Inside the mind of another species. In *How monkeys see the world: Inside the mind of another species.* University of

Chicago Press.

Chippaux, J.-P. (2006). *Les serpents d'Afrique occidentale et centrale*. IRD éditions.

Chomsky, N. (1965). *Aspects of the Theory of Syntax*. MIT press.

Chomsky, N. (2017). Language architecture and its import for evolution. *Neuroscience & Biobehavioral Reviews*, *81*, 295–300. https://doi.org/https://doi.org/10.1016/j.neubiorev.2017.01.053

Chouinard-Thuly, L., Gierszewski, S., Rosenthal, G. G., Reader, S. M., Rieucau, G., Woo, K. L., Gerlai, R., Tedore, C., Ingley, S. J., Stowers, J. R., Frommen, J. G., Dolins, F. L., & Witte, K. (2017). Technical and conceptual considerations for using animated stimuli in studies of animal behavior. *Current Zoology*, *63*(1), 5–19. https://doi.org/10.1093/cz/zow104

Chow, C. P., Mitchell, J. F., & Miller, C. T. (2015). Vocal turn-taking in a non-human primate is learned during ontogeny. *Proceedings. Biological Sciences*, *282*(1807), 20150069. https://doi.org/10.1098/rspb.2015.0069

Clark, E. (2003). *First language acquisition*. Cambridge University Press.

Clarke, E., Reichard, U. H., & Zuberbühler, K. (2006). The syntax and meaning of wild gibbon songs. *PloS One*, *1*(1), e73.

Clay, Z., & Zuberbühler, K. (2011). Bonobos Extract Meaning from Call Sequences. *PLoS ONE*, *6*(4), e18786. https://doi.org/10.1371/journal.pone.0018786

Cook, M., & Mineka, S. (1990). Selective associations in the observational conditioning of fear in rhesus monkeys. *Journal of Experimental Psychology. Animal Behavior Processes*, *16*(4), 372–389.

Coss, R. G., McCowan, B., & Ramakrishnan, U. (2007). Threat-Related Acoustical Differences in Alarm Calls by Wild Bonnet Macaques (Macaca radiata) Elicited by Python and Leopard Models. *Ethology*, *113*(4), 352–367. https://doi.org/https://doi.org/10.1111/j.1439-0310.2007.01336.x

Coss, R. G., & Ramakrishnan, U. (2000). Perceptual Aspects of Leopard Recognition by Wild

Bonnet Macaques (Macaca radiata). *Behaviour*, *137*(3), 315–335. http://www.jstor.org/stable/4535708

Coss, R. G., Ramakrishnan, U., & Schank, J. (2005). Recognition of partially concealed leopards by wild bonnet macaques (Macaca radiata): The role of the spotted coat. *Behavioural Processes*, *68*(2), 145–163. https://doi.org/https://doi.org/10.1016/j.beproc.2004.12.004

Crockford, C, & Boesch, C. (2005). Call combinations in wild chimpanzees. *Behaviour*, *142*, 397–421.

Crockford, C, Wittig, R. M., Mundry, R., & Zuberbühler, K. (2012). Wild Chimpanzees Inform Ignorant Group Members of Danger. *Current Biology*, *22*(2), 142–146. https://doi.org/https://doi.org/10.1016/j.cub.2011.11.053

Crockford, C, Wittig, R. M., & Zuberbühler, K. (2015). An intentional vocalization draws others' attention: a playback experiment with wild chimpanzees. *Animal Cognition*, *18*(3), 581–591. https://doi.org/10.1007/s10071-014-0827-z

Crockford, C, Wittig, R. M., & Zuberbühler, K. (2017). Vocalizing in chimpanzees is influenced by social-cognitive processes. *Science Advances*, *3*(11), e1701742. https://doi.org/10.1126/sciadv.1701742

Curio, E. (1976). *The ethology of predation* (Vol. 7). Springer Science & Business Media.

Curio, E., Ernst, U., & Vieth, W. (1978). Cultural Transmission of Enemy Recognition: One Function of Mobbing. *Science*, *202*(4370), 899 LP – 901. https://doi.org/10.1126/science.202.4370.899

Davenport, T. R. B., Stanley, W. T., Sargis, E. J., De Luca, D. W., Mpunga, N. E., Machaga, S. J., & Olson, L. E. (2006). A New Genus of African Monkey, Rungwecebus: Morphology, Ecology, and Molecular Phylogenetics. *Science*, *312*(5778), 1378–1381. https://doi.org/10.1126/science.1125631

de Boer, B. (2005). Evolution of Speech and Its Acquisition. *Adaptive Behavior*, *13*(4), 281–292. https://doi.org/10.1177/105971230501300405

Deshpande, A. (2021). *Social learning and flexibility in vocal communication of wild vervet* *monkeys* [Université de Neuchâtel]. https://unine.swisscovery.slsp.ch/permalink/41SLSP_UNE/b1j16q/alma991009764729505517%0A

Deshpande, A., Van Boekholt, B., & Zuberbuhler, K. (2022). Preliminary evidence for one-trial social learning of vervet monkey alarm calling. *Royal Society Open Science*, *9*(8), 210560. https://doi.org/10.1098/rsos.210560

Dezecache, G., Crockford, C., & Zuberbühler, K. (2019). The development of communication in alarm contexts in wild chimpanzees. *Behavioral Ecology and Sociobiology*, *73*(8), 104. https://doi.org/10.1007/s00265-019-2716-6

Di Bitetti, M., & Wheeler, B. (2017). The vocal repertoire of the black horned capuchin monkey (Cebus [Sapajus] nigritus): an acoustic and contextual analysis. In M. Kowalewski & L. Oklander (Eds.), *Primatology in Argentina* (Vol. 2, pp. 171–199). Sociedad Argentina para el Estudio de los Mamíferos, Buenos Aires.

Ducheminsky, N., Henzi, S. P., & Barrett, L. (2014). Responses of vervet monkeys in large troops to terrestrial and aerial predator alarm calls. *Behavioral Ecology*, *25*(6), 1474–1484. https://doi.org/10.1093/beheco/aru151

Edwards, M. C., Ford, C., Hoy, J. M., FitzGibbon, S., & Murray, P. J. (2021). How to train your wildlife: A review of predator avoidance training. *Applied Animal Behaviour Science*, *234*, 105170. https://doi.org/https://doi.org/10.1016/j.applanim.2020.105170

Egnor, S. E. R., & Hauser, M. D. (2004). A paradox in the evolution of primate vocal learning. *Trends in Neurosciences*, *27*(11), 649–654. https://doi.org/https://doi.org/10.1016/j.tins.2004.08.009

Egnor, S. E. R., & Hauser, M. D. (2006). Noise-induced vocal modulation in cotton-top tamarins (Saguinus oedipus). *American Journal of Primatology*, *68*(12), 1183–1190. https://doi.org/10.1002/ajp.20317

Egnor, S. E. R., Iguina, C. G., & Hauser, M. D. (2006). Perturbation of auditory feedback causes systematic perturbation in vocal structure in adult cotton-top tamarins. *The Journal of Experimental Biology*, *209*(Pt 18), 3652–3663. https://doi.org/10.1242/jeb.02420

Eisenberg, J. F. (1976). Communication mechanisms and social integration in the black spider monkey, Ateles fusciceps robustus, and related species. *Smithson. Contrib. to Zool.*, 1–108. https://doi.org/doi:10.5479/si.00810282.213

Elowson, A. M., Snowdon, C. T., & Sweet, C. J. (1992). Ontogeny of trill and J-call vocalizations in the pygmy marmoset, Cebuella pygmaea. *Animal Behaviour*, *43*(5), 703–715. https://doi.org/https://doi.org/10.1016/S0003-3472(05)80195-2

Engqvist, L. (2005). The mistreatment of covariate interaction terms in linear model analyses of behavioural and evolutionary ecology studies. *Animal Behaviour*, *70*(4), 967–971. https://doi.org/https://doi.org/10.1016/j.anbehav.2005.01.016

Ernst, R., & Rödel, M. (2002). A new Atheris species (Serpentes: Viperidae), from Taï National Park, Ivory Coast. *Herpetological Journal*, *12*, 55–61.

Etting, S. F., Isbell, L. A., & Grote, M. N. (2014). Factors increasing snake detection and perceived threat in captive rhesus macaques (Macaca mulatta). *American Journal of Primatology*, *76*(2), 135–145. https://doi.org/10.1002/ajp.22216

Evans, A., & Tomasello, M. (1986). Evidence for social referencing in young chimpanzees (Pan troglodytes). *Folia Primatologica; International Journal of Primatology*, *47*(1), 49–54. https://doi.org/10.1159/000156263

Fedurek, P., & Slocombe, K. E. (2011). Primate vocal communication: a useful tool for understanding human speech and language evolution? *Human Biology*, *83*(2), 153–173. https://doi.org/10.3378/027.083.0202

Fedurek, P., Slocombe, K. E., & Zuberbühler, K. (2015). Chimpanzees communicate to two different audiences during aggressive interactions. *Animal Behaviour*, *110*, 21–28. https://doi.org/https://doi.org/10.1016/j.anbehav.2015.09.010

Feise, R. J. (2002). Do multiple outcome measures require p-value adjustment? *BMC Medical Research Methodology*, *2*, 8. https://doi.org/10.1186/1471-2288-2-8

Fichtel, C. (2004). Reciprocal recognition of sifaka (Propithecus verreauxi verreauxi) and redfronted lemur (Eulemur fulvus rufus) alarm calls. *Animal Cognition*, *7*(1), 45–52. https://doi.org/10.1007/s10071-003-0180-0

Fichtel, C. (2008). Ontogeny of conspecific and heterospecific alarm call recognition in wild Verreaux's sifakas (Propithecus verreauxi verreauxi). *American Journal of Primatology*, *70*(2), 127–135. https://doi.org/https://doi.org/10.1002/ajp.20464

Fichtel, C. (2020). Monkey Alarm Calling: It Ain't all Referential, or is It? *Animal Behavior and Cognition*, *7*, 101–107.

Fichtel, C., & Kappeler, P. M. (2002). Anti-Predator Behavior of Group-Living Malagasy Primates: Mixed Evidence for a Referential Alarm Call System. *Behavioral Ecology and Sociobiology*, *51*(3), 262–275. http://www.jstor.org/stable/4602047

Fichtel, C., & Kappeler, P. M. (2011). Variation in the Meaning of Alarm Calls in Verreaux's and Coquerel's Sifakas (Propithecus verreauxi, P. coquereli). *International Journal of Primatology*, *32*(2), 346–361. https://doi.org/10.1007/s10764-010-9472-9

Fischer, J. (2017). Primate vocal production and the riddle of language evolution. *Psychonomic Bulletin & Review*, *24*(1), 72–78. https://doi.org/10.3758/s13423-016-1076-8

Fischer, J, & Hammerschmidt, K. (2020). Towards a new taxonomy of primate vocal production learning. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *375*(1789), 20190045. https://doi.org/10.1098/rstb.2019.0045

Fischer, J, Metz, M., Cheney, D., & Seyfarth, R. (2001). Baboon responses to graded bark variants. *Animal Behaviour*, *61*(5), 925–931. https://doi.org/https://doi.org/10.1006/anbe.2000.1687

Fischer, J, & Price, T. (2017). Meaning, intention, and inference in primate vocal communication. *Neuroscience & Biobehavioral Reviews*, *82*, 22–31. https://doi.org/https://doi.org/10.1016/j.neubiorev.2016.10.014

Fischer, J. (2020). Nonhuman primate alarm calls then and now. *Animal Behavior and Cognition*, *7*.

Fischer, J. (2021). Primate Vocal Communication and the Evolution of Speech. *Current Directions in Psychological Science*, *30*(1), 55–60. https://doi.org/10.1177/0963721420979580

Fischer, J, Cheney, D. L., & Seyfarth, R. M. (2000). Development of infant baboons' responses to graded bark variants. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *267*(1459), 2317–2321. https://doi.org/10.1098/rspb.2000.1285

Fischer, J, & Hammerschmidt, K. (2001). Functional referents and acoustic similarity revisited: the case of Barbary macaque alarm calls. *Animal Cognition*, *4*(1), 29–35. https://doi.org/10.1007/s100710100093

Fischer, J, Kitchen, D. M., Seyfarth, R. M., & Cheney, D. L. (2004). Baboon loud calls advertise male quality: acoustic features and their relation to rank, age, and exhaustion. *Behavioral Ecology and Sociobiology*, *56*(2), 140–148. https://doi.org/10.1007/s00265-003-0739-4

Foerster, S. (2008). Two incidents of venomous snakebite on juvenile blue and Sykes monkeys (Cercopithecus mitis stuhlmanni and C. m. albogularis). *Primates*, *49*(4), 300–303. https://doi.org/10.1007/s10329-008-0098-x

Friard, O., & Gamba, M. (2016). BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. *Methods in Ecology and Evolution*, *7*(11), 1325–1330. https://doi.org/10.1111/2041-210X.12584

Fröhlich, M., & van Schaik, C. P. (2020). Must all signals be evolved? A proposal for a new classification of communicative acts. *WIREs Cognitive Science*, *11*(4), e1527. https://doi.org/https://doi.org/10.1002/wcs.1527

Fugate, J. M. B., Gouzoules, H., & Nygaard, L. C. (2008). Recognition of rhesus macaque (Macaca mulatta) noisy screams: evidence from conspecifics and human listeners. *American Journal of Primatology*, *70*(6), 594–604. https://doi.org/https://doi.org/10.1002/ajp.20533

Galat, G., & Galat-Luong, A. (1985). La communauté de primates diurnes de la forêt de Taï, Côte-d'Ivoire. *Revue d'écologie (Terre Vie)*, *40*, 3–32.

Galef, B. G., & Giraldeau, L.-A. (2001). Social influences on foraging in vertebrates: causal mechanisms and adaptive functions. *Animal Behaviour*, *61*(1), 3–15. https://doi.org/https://doi.org/10.1006/anbe.2000.1557

Galef, B. G., & Laland, K. N. (2005). Social learning in animals: empirical studies and theoretical models. *Bioscience*, *55*(6), 489–499.

Gamba, M., Friard, O., Riondato, I., Righini, R., Colombo, C., Miaretsoa, L., Torti, V., Nadhurou, B., & Giacoma, C. (2015). Comparative analysis of the vocal repertoire of Eulemur: a dynamic time warping approach. *International Journal of Primatology*, *36*(5), 894–910.

Garcia, J., Kimeldorf, D. J., & Koelling, R. A. (1955). Conditioned aversion to saccharin resulting from exposure to gamma radiation. In *Science* (Vol. 122, pp. 157–158). American Assn for the Advancement of Science. https://doi.org/10.1126/science.122.3179.1089

Gautier-Hion, A., Quris, R., & Gautier, J.-P. (1983). Monospecific vs polyspecific life: A comparative study of foraging and antipredatory tactics in a community of Cercopithecus monkeys. *Behavioral Ecology and Sociobiology*, *12*(4), 325–335. https://doi.org/10.1007/BF00302901

Gelman, A., & Su, Y.-S. (2020). *arm: Data analysis using regression and multilevel/hierarchical models* (R package version 1.11-1). https://cran.r-project.org/package=arm

Genovart, M., Negre, N., Tavecchia, G., Bistuer, A., Parpal, L., & Oro, D. (2010). The young, the weak and the sick: evidence of natural selection by predation. *PloS One*, *5*(3), e9774. https://doi.org/10.1371/journal.pone.0009774

Genty, E., Breuer, T., Hobaiter, C., & Byrne, R. W. (2009). Gestural communication of the gorilla (Gorilla gorilla): repertoire, intentionality and possible origins. *Animal Cognition*, *12*(3), 527–546. https://doi.org/10.1007/s10071-009-0213-4

Ghazanfar, A. A., Liao, D. A., & Takahashi, D. Y. (2019). Volition and learning in primate vocal behaviour. *Animal Behaviour*, *151*, 239–247. https://doi.org/https://doi.org/10.1016/j.anbehav.2019.01.021

Gill, S. A., & Bierema, A. M.-K. (2013). On the Meaning of Alarm Calls: A Review of Functional Reference in Avian Alarm Calling. *Ethology*, *119*(6), 449–461. https://doi.org/https://doi.org/10.1111/eth.12097

Girard-Buttoz, C., Zaccarella, E., Bortolato, T., Friederici, A. D., Wittig, R. M., & Crockford, C. (2022). Chimpanzees produce diverse vocal sequences with ordered and recombinatorial properties. *Communications Biology*, *5*(1), 410. https://doi.org/10.1038/s42003-022-03350-8

Goodale, E., Beauchamp, G., Magrath, R. D., Nieh, J. C., & Ruxton, G. D. (2010). Interspecific information transfer influences animal community structure. *Trends in Ecology & Evolution*, *25*(6), 354–361. https://doi.org/10.1016/j.tree.2010.01.002

Goris, R. C. (2011). Infrared Organs of Snakes: An Integral Part of Vision. *Journal of Herpetology*, *45*(1), 2–14. https://doi.org/10.1670/10-238.1

Greene, H. W. (1997). *Snakes: the evolution of mystery in nature*. Univ of California Press.

Greggor, A. L., McIvor, G. E., Clayton, N. S., & Thornton, A. (2022). Wild jackdaws are wary of objects that violate expectations of animacy. *Royal Society Open Science*, *5*(10), 181070. https://doi.org/10.1098/rsos.181070

Griffin, A. (2004). Social learning about predators: a review and prospectus. *Animal Learning & Behavior*, *32*(1), 131–140. https://doi.org/10.3758/BF03196014

Grubb, P., Butynski, T. M., Oates, J. F., Bearder, S. K., Disotell, T. R., Groves, C. P., & Struhsaker, T. T. (2003). Assessment of the Diversity of African Primates. *International Journal of Primatology*, *24*(6), 1301–1357. https://doi.org/10.1023/B:IJOP.0000005994.86792.b9

Gursky, S. (2003). Predation Experiments on Infant Spectral Tarsiers (Tarsius spectrum). *Folia Primatologica*, *74*(5–6), 272–284. https://doi.org/https://doi.org/10.1159/000073314

Gust, D. A. (1994). A brief report on the social behavior of the crested mangabey (Cercocebus galeritus galeritus) with a comparison to the sooty mangabey (C. torquatus atys). *Primates*, *35*(3), 375–383. https://doi.org/10.1007/BF02382734

Gust, D. A., Busse, C. D., & Gordon, T. P. (1990). Reproductive parameters in the sooty mangabey (Cercocebus torquatus atys). *American Journal of Primatology*, *22*(4), 241–250. https://doi.org/10.1002/ajp.1350220404

Gust, D. A., & Gordon, T. P. (1993). Conflict resolution in sooty mangabeys. *Animal*

Behaviour, *46*(4), 685–694. https://doi.org/https://doi.org/10.1006/anbe.1993.1245

Haff, T. M., & Magrath, R. D. (2013). To call or not to call: parents assess the vulnerability of their young before warning them about predators. *Biology Letters*, *9*(6), 20130745. https://doi.org/10.1098/rsbl.2013.0745

Hammerschmidt, K., & Fischer, J. (2008). Constraints in Primate Vocal Production. In *Evolution of Communicative Flexibility*. The MIT Press. https://doi.org/10.7551/mitpress/9780262151214.003.0005

Hammerschmidt, K., Freudenstein, T., & Jürgens, U. (2001). Vocal Development in Squirrel Monkeys. *Behaviour*, *138*(9), 1179–1204. http://www.jstor.org/stable/4535882

Hammerschmidt, K., Newman, J. D., Champoux, M., & Suomi, S. J. (2000). Changes In Rhesus Macaque 'Coo' Vocalizations during Early Development. *Ethology*, *106*(10), 873–886. https://doi.org/https://doi.org/10.1046/j.1439-0310.2000.00611.x

Harvey, P. H., & Clutton-Brock, T. H. (1985). Life History Variation in Primates. *Evolution*, *39*(3), 559–581. https://doi.org/10.2307/2408653

Hauser, M. D. (1988). How Infant Vervet Monkeys Learn To Recognize Starling Alarm Calls: the Role of Experience. *Behaviour*, *105*(3–4), 187–201. https://doi.org/https://doi.org/10.1163/156853988X00016

Hauser, M. D. (1989). Ontogenetic changes in the comprehension and production of vervet monkey (Cercopithecus aethiops) vocalizations. *Journal of Comparative Psychology*, *103*(2), 149–158. https://doi.org/10.1037/0735-7036.103.2.149

Hauser, M. D., Chomsky, N., & Fitch, W. T. (2002). The Faculty of Language: What Is It, Who Has It, and How Did It Evolve? *Science*, *298*(5598), 1569–1579. https://doi.org/10.1126/science.298.5598.1569

Hayes, C. (1951). The ape in our house. In *The ape in our house*. Harper.

Headland, T. N., & Greene, H. W. (2011). Hunter–gatherers and other primates as prey, predators, and competitors of snakes. *Proceedings of the National Academy of Sciences*, *108*(52), E1470–E1474. https://doi.org/10.1073/pnas.1115116108

Heyes, C., & Galef Jr, B. (1996). *Social learning in animals: the roots of culture*. Elsevier.

Heymann, E. W., & Buchanan-Smith, H. M. (2000). The behavioural ecology of mixed-species troops of callitrichine primates. *Biological Reviews of the Cambridge Philosophical Society*, *75*(2), 169–190. https://doi.org/10.1017/s0006323199005460

Hollén, L. I., Clutton-Brock, T., & Manser, M. B. (2008). Ontogenetic Changes in Alarm-Call Production and Usage in Meerkats (Suricata suricatta): Adaptations or Constraints? *Behavioral Ecology and Sociobiology*, *62*(5), 821–829. http://www.jstor.org/stable/25511757

Höner, O. P., Leumann, L., & Noë, R. (1997). Dyadic associations of red Colobus and diana monkey groups in the Taï National Park, Ivory Coast. *Primates*, *38*(3), 281–291. https://doi.org/10.1007/BF02381615

Hotchkin, C. F., Parks, S. E., & Weiss, D. J. (2013). Vocal modifications in primates: Effects of noise and behavioral context on vocalization structure. *Proceedings of Meetings on Acoustics. Acoustical Society of America*, *19*. https://doi.org/10.1121/1.4799257

Isbell, L. A. (1994). Predation on primates: Ecological patterns and evolutionary consequences. *Evolutionary Anthropology: Issues, News, and Reviews*, *3*(2), 61–71. https://doi.org/10.1002/evan.1360030207

Isbell, L. A. (2006). Snakes as agents of evolutionary change in primate brains. *Journal of Human Evolution*, *51*(1), 1–35. https://doi.org/https://doi.org/10.1016/j.jhevol.2005.12.012

Isbell, L. A. (2009). *The Fruit, the Tree, and the Serpent*. Harvard University Press. https://doi.org/10.2307/j.ctvjnrvj0

Jaffe, K. . E., & Isbell, L. (2010). The Guenons: Polyspecific associations in sociological perspective. In C. J. Campbell, A. Fuentes, K. C. MacKinnon, S. K. Bearder, & R. Stumpf (Eds.), *Primates in Perspective* (pp. 277–300). Oxford University Press.

Janik, V. M., & Slater, P. J. B. (2000). The different roles of social learning in vocal communication. *Animal Behaviour*, *60*(1), 1–11. https://doi.org/https://doi.org/10.1006/anbe.2000.1410

Janson, C. H., & van Schaik, C. P. (1993). Ecological risk aversion in juvenile primates: slow and steady wins the race. In M. E. Pereira & L. A. Fairbanks (Eds.), *Juvenile primates: life history, development, and behavior* (pp. 57–74). Oxford Univ. Press.

Jeffreys, H. (1939). *The theory of probability* (1st ed.). Oxford University Press.

Johnson, K. E., & Clark, C. J. (2020). Ontogeny of vocal learning in a hummingbird. *Animal Behaviour*, *167*, 139–150. https://doi.org/https://doi.org/10.1016/j.anbehav.2020.07.010

Johnson, K. E., & Clark, C. J. (2022). Costa's hummingbird has an extended sensitive phase of vocal learning. *Animal Behaviour*, *188*, 75–84. https://doi.org/https://doi.org/10.1016/j.anbehav.2022.04.001

Kaminski, J., Call, J., & Fischer, J. (2004). Word learning in a domestic dog: evidence for "fast mapping". *Science (New York, N.Y.)*, *304*(5677), 1682–1683. https://doi.org/10.1126/science.1097859

Kawai, N., & He, H. (2016). Breaking Snake Camouflage: Humans Detect Snakes More Accurately than Other Animals under Less Discernible Visual Conditions. *PLOS ONE*, *11*(10), e0164342. https://doi.org/10.1371/journal.pone.0164342

Kawai, N., & Koda, H. (2016). Japanese monkeys (Macaca fuscata) quickly detect snakes but not spiders: Evolutionary origins of fear-relevant animals. In *Journal of Comparative Psychology* (Vol. 130, pp. 299–303). American Psychological Association. https://doi.org/10.1037/com0000032

Keen, S. C., Cole, E. F., Sheehan, M. J., & Sheldon, B. C. (2020). Social learning of acoustic anti-predator cues occurs between wild bird species. *Proceedings of the Royal Society B: Biological Sciences*, *287*(1920), 20192513. https://doi.org/10.1098/rspb.2019.2513

Kelley, J. L., & Magurran, A. E. (2003). Learned predator recognition and antipredator responses in fishes. *Fish and Fisheries*, *4*(3), 216–226. https://doi.org/https://doi.org/10.1046/j.1467-2979.2003.00126.x

Kellogg, W. N., & Kellogg, L. A. (1933). The ape and the child: a study of environmental influence upon early behavior. In *The ape and the child: a study of environmental influence upon early behavior.* Whittlesey House.

Kendal, R. L., Coolen, I., van Bergen, Y., & Laland, K. N. B. T.-A. in the S. of B. (2005). *Trade-Offs in the Adaptive Use of Social and Asocial Learning* (Vol. 35, pp. 333–379). Academic Press. https://doi.org/https://doi.org/10.1016/S0065-3454(05)35008-X

Khamcha, D., & Sukumal, N. (2009). Burmese python (Python molurus) predation on a pig-tailed macaque (Macaca nemestrina) in Khao Yai National Park. *Hamadryad*, *34*, 176–178. https://doi.org/10.13140/2.1.3857.7449

King, S. L., & Janik, V. M. (2013). Bottlenose dolphins can use learned vocal labels to address each other. *Proceedings of the National Academy of Sciences*, *110*(32), 13216–13221. https://doi.org/10.1073/pnas.1304459110

Kingdon, J. (2015). *The Kingdon field guide to African mammals*. Bloomsbury Publishing.

Kirchhof, J., & Hammerschmidt, K. (2006). Functionally Referential Alarm Calls in Tamarins (Saguinus fuscicollis and Saguinus mystax) – Evidence from Playback Experiments. *Ethology*, *112*(4), 346–354. https://doi.org/https://doi.org/10.1111/j.1439-0310.2006.01165.x

Koda, H., Shimooka, Y., & Sugiura, H. (2008). Effects of caller activity and habitat visibility on contact call rate of wild Japanese macaques (Macaca fuscata). *American Journal of Primatology*, *70*(11), 1055–1063. https://doi.org/10.1002/ajp.20597

Koné, I., McGraw, S., Gonedelé Bi, S., & Barrie, A. (2020). *Cercocebus atys*. The IUCN Red List of Threatened Species 2020: E.T136933A92248451. https://dx.doi.org/10.2305/IUCN.UK.2020-2.RLTS.T136933A92248451.en

Krause, M. A., & Beran, M. J. (2020). Words matter: Reflections on language projects with chimpanzees and their implications. *American Journal of Primatology*, *82*(10), e23187. https://doi.org/https://doi.org/10.1002/ajp.23187

Kuhl, P. K. (2000). A new view of language acquisition. *Proceedings of the National Academy of Sciences of the United States of America*, *97*(22), 11850–11857. https://doi.org/10.1073/pnas.97.22.11850

Lameira, A. R. (2017). Bidding evidence for primate vocal learning and the cultural substrates for speech evolution. *Neuroscience & Biobehavioral Reviews*, *83*, 429–439.

https://doi.org/https://doi.org/10.1016/j.neubiorev.2017.09.021

Laporte, M. N. C., & Zuberbühler, K. (2010). Vocal greeting behaviour in wild chimpanzee females. *Animal Behaviour*, *80*(3), 467–473. https://doi.org/https://doi.org/10.1016/j.anbehav.2010.06.005

Lattenkamp, E. Z., & Vernes, S. C. (2018). Vocal learning: a language-relevant trait in need of a broad cross-species approach. *Current Opinion in Behavioral Sciences*, *21*, 209–215. https://doi.org/https://doi.org/10.1016/j.cobeha.2018.04.007

Lattenkamp, E. Z., Vernes, S. C., & Wiegrebe, L. (2018). Volitional control of social vocalisations and vocal usage learning in bats. *Journal of Experimental Biology*, *221*(14), jeb180729. https://doi.org/10.1242/jeb.180729

Lemasson, A., Gandon, E., & Hausberger, M. (2010). Attention to elders' voice in non-human primates. *Biology Letters*, *6*(3), 328. https://doi.org/10.1098/rsbl.2009.0875

Lemasson, A., Ouattara, K., Petit, E. J., & Zuberbühler, K. (2011). Social learning of vocal structure in a nonhuman primate? *BMC Evolutionary Biology*, *11*(1), 362. https://doi.org/10.1186/1471-2148-11-362

León, J., Thiriau, C., Bodin, C., Crockford, C., & Zuberbühler, K. (2022). Acquisition of predator knowledge from alarm calls via one-trial social learning in monkeys. *IScience*, *25*, 104853. https://doi.org/https://doi.org/10.1016/j.isci.2022.104853

León, J., Thiriau, C., Crockford, C., & Zuberbühler, K. (2022). *https://osf.io/y2gvc/.*

Leroux, M., & Townsend, S. W. (2020). Call combinations in great apes and the evolution of syntax. *Animal Behavior and Cognition*, *7*(2), 131–139.

Li, J., Smithwick, Q., & Chu, D. (2022). Holobricks: modular coarse integral holographic displays. *Light: Science & Applications*, *11*(1), 57. https://doi.org/10.1038/s41377-022-00742-7

Liebal, K., & Call, J. (2012). The origins of non-human primates' manual gestures. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *367*(1585), 118–128. https://doi.org/10.1098/rstb.2011.0044

Liebal, K., Waller, B. M., Burrows, A. M., & Slocombe, K. E. (2014). Primate communication: A multimodal approach. In *Primate communication: A multimodal approach.* Cambridge University Press.

Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, *68*(4), 619–640. https://doi.org/10.1139/z90-092

Luchkina, E., & Waxman, S. (2021). Acquiring verbal reference: The interplay of cognitive, linguistic, and general learning capacities. *Infant Behavior and Development*, *65*, 101624. https://doi.org/https://doi.org/10.1016/j.infbeh.2021.101624

Magrath, R. D., Haff, T. M., Fallow, P. M., & Radford, A. N. (2015). Eavesdropping on heterospecific alarm calls: from mechanisms to consequences. *Biological Reviews*, *90*(2), 560–586. https://doi.org/https://doi.org/10.1111/brv.12122

Manser, M. B. (2001). The acoustic structure of suricates' alarm calls varies with predator type and the level of response urgency. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *268*(1483), 2315–2324. https://doi.org/10.1098/rspb.2001.1773

Manser, M. B., Bell, M. B., & Fletcher, L. B. (2001). The information that receivers extract from alarm calls in suricates. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *268*(1484), 2485–2491. https://doi.org/10.1098/rspb.2001.1772

Masataka, N., & Fujita, K. (1989). Vocal Learning of Japanese and Rhesus Monkeys. *Behaviour*, *109*(3–4), 191–199. https://doi.org/https://doi.org/10.1163/156853989X00222

McCowan, B., Franceschini, N. V, & Vicino, G. A. (2001). Age differences and developmental trends in alarm peep responses by squirrel monkeys (Saimiri sciureus). *American Journal of Primatology*, *53*(1), 19–31. https://doi.org/https://doi.org/10.1002/1098-2345(200101)53:1<19::AID-AJP2>3.0.CO;2-#

McCullagh, P., & Nelder, J. A. (1989). *Generalized linear models* (Second). Chapman & Hall/CRC.

McGraw, W. (1998). Comparative locomotion and habitat use of six monkeys in the Tai Forest, Ivory Coast. *American Journal of Physical Anthropology*, *105*(4), 493–510. https://doi.org/https://doi.org/10.1002/(SICI)1096-8644(199804)105:4<493::AID-AJPA7>3.0.CO;2-P

McGraw, W., & Bshary, R. (2002). Association of Terrestrial Mangabeys (Cercocebus atys) with Arboreal Monkeys: Experimental Evidence for the Effects of Reduced Ground Predator Pressure on Habitat Use. *International Journal of Primatology*, *23*(2), 311–325. https://doi.org/10.1023/A:1013883528244

McGraw, W. S., Zuberbühler, K., & Noë, R. (2007). *Monkeys of the Taï Forest: an African primate community* (Vol. 51). Cambridge University Press.

McGraw, W., & Zuberbühler, K. (2007). The monkeys of the Taï forest: an introduction. In Klaus Zuberbühler, R. Noë, & W. S. McGraw (Eds.), *Monkeys of the Taï Forest: An African Primate Community* (pp. 1–48). Cambridge University Press. https://doi.org/DOI: 10.1017/CBO9780511542121.002

McGraw, W., Zuberbühler, K., & Noë, R. (2007). *Monkeys of the Tai Forest*. Cambridge University Press. https://doi.org/10.1017/CBO9780511542121

Meno, W., Coss, R. G., & Perry, S. (2013a). Development of Snake-Directed Antipredator Behavior by Wild White-faced Capuchin Monkeys: I. Snake-Species Discrimination. *American Journal of Primatology*, *75*(3), 281–291. https://doi.org/https://doi.org/10.1002/ajp.22106

Meno, W., Coss, R. G., & Perry, S. (2013b). Development of Snake-Directed Antipredator Behavior by Wild White-Faced Capuchin Monkeys: II. Influence of the Social Environment. *American Journal of Primatology*, *75*(3), 292–300. https://doi.org/https://doi.org/10.1002/ajp.22109

Mery, F., & Burns, J. G. (2010). Behavioural plasticity: an interaction between evolution and experience. *Evolutionary Ecology*, *24*(3), 571–583. https://doi.org/10.1007/s10682-009-9336-y

Meyer, D., Hodges, J. K., Rinaldi, D., Wijaya, A., Roos, C., & Hammerschmidt, K. (2012). Acoustic structure of male loud-calls support molecular phylogeny of Sumatran and Javanese leaf monkeys (genus Presbytis). *BMC Evolutionary Biology*, *12*(1), 16.

Mielke, A., Crockford, C., & Wittig, R. M. (2019). Snake alarm calls as a public good in sooty mangabeys. *Animal Behaviour*, *158*, 201–209. https://doi.org/https://doi.org/10.1016/j.anbehav.2019.10.001

Mielke, A., & Zuberbühler, K. (2013). A method for automated individual, species and call type recognition in free-ranging animals. *Animal Behaviour*, *86*(2), 475–482. https://doi.org/https://doi.org/10.1016/j.anbehav.2013.04.017

Mineka, S. (1992). *Evolutionary Memories, Emotional Processing, and the Emotional Disorders* (D. L. B. T.-P. of L. and M. Medin (ed.); Vol. 28, pp. 161–206). Academic Press. https://doi.org/https://doi.org/10.1016/S0079-7421(08)60490-9

Mineka, S., & Cook, M. (1988). Social learning and the acquisition of snake fear in monkeys. In *Social learning: Psychological and biological perspectives.* (pp. 51–73). Lawrence Erlbaum Associates, Inc.

Mineka, S., & Cook, M. (1993). Mechanisms involved in the observational conditioning of fear. In *Journal of Experimental Psychology: General* (Vol. 122, Issue 1, pp. 23–38). American Psychological Association. https://doi.org/10.1037/0096-3445.122.1.23

Mittermeier, R., Wilson, D., & Rylands, A. B. (2013). *Handbook of the Mammals of the World: 3. Primates*. Lynx Edicions. https://books.google.com.co/books?id=P0-rMQEACAAJ

Mohamad Nor, N., & Rashid, R. A. (2018). A review of theoretical perspectives on language learning and acquisition. *Kasetsart Journal of Social Sciences*, *39*(1), 161–167. https://doi.org/https://doi.org/10.1016/j.kjss.2017.12.012

Mohr, T., Van de Waal, E., Zuberbühler, K., & Mercier, S. (2022). *https://osf.io/mjywg/.*

Morse, D. H. (1977). Feeding Behavior and Predator Avoidance in Heterospecific Groups. *BioScience*, *27*(5), 332–339. https://doi.org/10.2307/1297632

Munn, C. A. (1986). Birds that 'cry wolf.' *Nature*, *319*(6049), 143–145. https://doi.org/10.1038/319143a0

Newman, J. D., & Symmes, D. (1974). Vocal pathology in socially deprived monkeys. *Developmental Psychobiology*, *7*(4), 351–358. https://doi.org/https://doi.org/10.1002/dev.420070412

Oates, J. F., Whitesides, G. H., Davies, A. G., Waterman, P. G., Green, S. M., Dasilva, G. L., & Mole, S. (1990). Determinants of Variation in Tropical Forest Primate Biomass: New Evidence from West Africa. *Ecology*, *71*(1), 328–343. https://doi.org/10.2307/1940272

Oda, R. (1998). The responses of Verreaux's sifakas to anti-predator alarm calls given by sympatric ring-tailed lemurs. *Folia Primatologica; International Journal of Primatology*, *69*(6), 357–360. https://doi.org/10.1159/000021651

Oda, R., & Masataka, N. (1996). Interspecific Responses of Ringtailed Lemurs to Playback of Antipredator Alarm Calls Given by Verreaux's Sifakas. *Ethology*, *102*(3), 441–453. https://doi.org/https://doi.org/10.1111/j.1439-0310.1996.tb01138.x

Öhman, A. (2009). Of snakes and faces: An evolutionary perspective on the psychology of fear. *Scandinavian Journal of Psychology*, *50*(6), 543–552. https://doi.org/https://doi.org/10.1111/j.1467-9450.2009.00784.x

Ohman, A., & Mineka, S. (2001). Fears, phobias, and preparedness: toward an evolved module of fear and fear learning. *Psychological Review*, *108*(3), 483–522. https://doi.org/10.1037/0033-295x.108.3.483

Oliveira, L. C., & Dietz, J. M. (2011). Predation risk and the interspecific association of two Brazilian Atlantic forest primates in Cabruca agroforest. *American Journal of Primatology*, *73*(9), 852–860. https://doi.org/10.1002/ajp.20952

Olsson, A., & Phelps, E. A. (2007). Social learning of fear. *Nature Neuroscience*, *10*(9), 1095–1102. https://doi.org/10.1038/nn1968

Ouattara, K., Lemasson, A., & Zuberbühler, K. (2009a). Anti-predator strategies of free-ranging Campbell's monkeys. *Behaviour*, *146*(12), 1687–1708. https://doi.org/10.1163/000579509X12469533725585

Ouattara, K., Lemasson, A., & Zuberbühler, K. (2009b). Campbell's monkeys concatenate vocalizations into context-specific call sequences. In *PNAS Proceedings of the National Academy of Sciences of the United States of America* (Vol. 106, Issue 51, pp. 22026–22031). National Academy of Sciences. https://doi.org/10.1073/pnas.0908118106

Owren, M. J., Dieter, J. A., Seyfarth, R. M., & Cheney, D. L. (1992). "Food" Calls Produced by Adult Female Rhesus (Macaca mulatta) and Japanese (M. fuscata) Macaques, Their Normally-Raised Offspring, and Offspring Cross-Fostered between Species. *Behaviour*, *120*(3/4), 218–231. http://www.jstor.org/stable/4535009

Owren, M. J., Dieter, J. A., Seyfarth, R. M., & Cheney, D. L. (1993). Vocalizations of rhesus (Macaca mulatta) and Japanese (M. Fuscata) macaques cross-fostered between species show evidence of only limited modification. *Developmental Psychobiology*, *26*(7), 389–406. https://doi.org/https://doi.org/10.1002/dev.420260703

Owren, M. J., & Rendall, D. (1997). *An Affect-Conditioning Model of Nonhuman Primate Vocal Signaling BT - Communication* (D. H. Owings, M. D. Beecher, & N. S. Thompson (eds.); pp. 299–346). Springer US. https://doi.org/10.1007/978-1-4899-1745-4_10

Owren, M. J., & Rendall, D. (2001). Sound on the rebound: Bringing form and function back to the forefront in understanding nonhuman primate vocal signaling. *Evolutionary Anthropology: Issues, News, and Reviews*, *10*(2), 58–71. https://doi.org/https://doi.org/10.1002/evan.1014

Peake, T. M., & Mcgregor, P. K. (2004). Information and aggression in fishes. *Animal Learning & Behavior*, *32*(1), 114–121. https://doi.org/10.3758/BF03196012

Penner, J., Fruteau, C., Range, F., & Rodel, M. (2008). Finding a needle in a haystack: new methods of locating and working with rhinoceros vipers (Bitis rhinoceros). *Herpetological Review*, *39*(3), 310.

Pepperberg, I. M. (2010). Vocal learning in Grey parrots: A brief review of perception, production, and cross-species comparisons. *Brain and Language*, *115*(1), 81–91. https://doi.org/https://doi.org/10.1016/j.bandl.2009.11.002

Pepperberg, I. M. (2017). Animal language studies: What happened? *Psychonomic Bulletin & Review*, *24*(1), 181–185. https://doi.org/10.3758/s13423-016-1101-y

Perry, S., Panger, M., Rose, L. M., Baker, M., Gros-Louis, J., Jack, K., Mackinnon, K. C., Manson, J., Fedigan, L., & Pyle, K. (2003). Traditions in wild white-faced capuchin monkeys. In *The Biology of Traditions* (pp. 391–425). Cambridge University Press. https://doi.org/10.1017/CBO9780511584022.015

Pessoa, D. M. A., Maia, R., de Albuquerque Ajuz, R. C., De Moraes, P. Z. P. M. R., Spyrides, M. H. C., & Pessoa, V. F. (2014). The adaptive value of primate color vision for predator detection. *American Journal of Primatology*, *76*(8), 721–729. https://doi.org/10.1002/ajp.22264

Pika, S., & Liebal, K. (2006). Differences and similarties between the natural gestural communication of the great apes and human children. In *The Evolution of Language* (pp. 267–274). WORLD SCIENTIFIC. https://doi.org/doi:10.1142/9789812774262_0034

Pika, S., Liebal, K., & Tomasello, M. (2003). Gestural communication in young gorillas (Gorilla gorilla): gestural repertoire, learning, and use. *American Journal of Primatology*, *60*(3), 95–111. https://doi.org/10.1002/ajp.10097

Poole, J. H., Tyack, P. L., Stoeger-Horwath, A. S., & Watwood, S. (2005). Elephants are capable of vocal learning. *Nature*, *434*(7032), 455–456. https://doi.org/10.1038/434455a

Potvin, D. A., Ratnayake, C. P., Radford, A. N., & Magrath, R. D. (2018). Birds Learn Socially to Recognize Heterospecific Alarm Calls by Acoustic Association. *Current Biology*, *28*(16), 2632-2637.e4. https://doi.org/https://doi.org/10.1016/j.cub.2018.06.013

Pozzi, L., Gamba, M., & Giacoma, C. (2013). Artificial Neural Networks: A New Tool for Studying Lemur Vocal Communication. In J. Masters, M. Gamba, & F. Génin (Eds.), *Leaping Ahead: Advances in Prosimian Biology* (pp. 305–313). Springer New York. https://doi.org/10.1007/978-1-4614-4511-1_34

Pozzi, L., Hodgson, J. A., Burrell, A. S., Sterner, K. N., Raaum, R. L., & Disotell, T. R. (2014). Primate phylogenetic relationships and divergence dates inferred from complete mitochondrial genomes. *Molecular Phylogenetics and Evolution*, *75*, 165–183. https://doi.org/10.1016/j.ympev.2014.02.023

Price, T., Ndiaye, O., Hammerschmidt, K., & Fischer, J. (2014). Limited geographic variation in the acoustic structure of and responses to adult male alarm barks of African green monkeys. *Behavioral Ecology and Sociobiology*, *68*(5), 815–825. https://doi.org/10.1007/s00265-014-1694-y

Price, T., Wadewitz, P., Cheney, D., Seyfarth, R., Hammerschmidt, K., & Fischer, J. (2015). Vervets revisited: A quantitative analysis of alarm call structure and context specificity.

Scientific Reports, *5*, 13220. https://doi.org/10.1038/srep13220

Quam, R. M., Ramsier, M. A., Fay, R. R., & Popper, A. N. (2017). *Primate hearing and communication*. Springer.

Quintero, F., Touitou, S., Magris, M., & Zuberbühler, K. (2022a). An audience effect in sooty mangabey alarm calling. *Front Psychol*, *13*. https://doi.org/10.3389/fpsyg.2022.816744

Quintero, F., Touitou, S., Magris, M., & Zuberbühler, K. (2022b). The Evolution of Food Calls: Vocal Behaviour of Sooty Mangabeys in the Presence of Food . In *Frontiers in Psychology* (Vol. 13). https://www.frontiersin.org/articles/10.3389/fpsyg.2022.897318

R Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

Ramakrishnan, U., & Coss, R. G. (2000). Recognition of heterospecific alarm vocalization by Bonnet Macaques (Macaca radiata). In *Journal of Comparative Psychology* (Vol. 114, Issue 1, pp. 3–12). American Psychological Association. https://doi.org/10.1037/0735-7036.114.1.3

Ramakrishnan, U., Coss, R. G., Schank, J., Dharawat, A., & Kim, S. (2005). Snake Species Discrimination by Wild Bonnet Macaques (Macaca radiata). *Ethology*, *111*(4), 337–356. https://doi.org/10.1111/j.1439-0310.2004.01063.x

Range, F., & Fischer, J. (2004). Vocal Repertoire of Sooty Mangabeys (Cercocebus torquatus atys) in the Tai National Park. *Ethology*, *110*(4), 301–321. https://doi.org/10.1111/j.1439-0310.2004.00973.x

Range, F., & Noë, R. (2002). Familiarity and dominance relations among female sooty mangabeys in the Taï National Park. *American Journal of Primatology*, *56*(3), 137–153. https://doi.org/https://doi.org/10.1002/ajp.1070

Rapaport, L. G., & Brown, G. R. (2008). Social influences on foraging behavior in young nonhuman primates: Learning what, where, and how to eat. *Evolutionary Anthropology: Issues, News, and Reviews*, *17*(4), 189–201. https://doi.org/https://doi.org/10.1002/evan.20180

Rendall, D., Owren, M. J., & Ryan, M. J. (2009). What do animal signals mean? *Animal*

Behaviour, *78*(2), 233–240. https://doi.org/https://doi.org/10.1016/j.anbehav.2009.06.007

Rescorla, L. A. (1980). Overextension in early language development. *Journal of Child Language*, *7*(2), 321–335. https://doi.org/DOI: 10.1017/S0305000900002658

Rescorla, R. A., & Wagner, A. (1972). A theory of Pavlovian conditioning: Variations in the effectiveness of reinforcement and nonreinforcement. In A. Black & P. W (Eds.), *Classical Conditioning II: Current Research and Theory: Vol. Vol. 2* (pp. 64–69). Appleton-Century-Crofts.

Ridgway, S., Carder, D., Jeffries, M., & Todd, M. (2012). Spontaneous human speech mimicry by a cetacean. *Current Biology*, *22*(20), R860–R861. https://doi.org/10.1016/j.cub.2012.08.044

Rödel, M., & Mahsberg, D. (2000). Vorläufige Liste der Schlangen des Taï-Nationalparks / Elfenbeinküste und angrenzender Gebiete. *Salamandra*, *36*, 25–38.

Romano, D., Donati, E., Benelli, G., & Stefanini, C. (2019). A review on animal–robot interaction: from bio-hybrid organisms to mixed societies. *Biological Cybernetics*, *113*(3), 201–225. https://doi.org/10.1007/s00422-018-0787-5

Rosati, A. G., Machanda, Z. P., & Slocombe, K. E. (2022). Cognition in the wild: understanding animal thought in its natural context. *Current Opinion in Behavioral Sciences*, *47*, 101210. https://doi.org/https://doi.org/10.1016/j.cobeha.2022.101210

Roupe, S., Pistorio, A., & Wang, X. (2003). Vocal plasticity induced by auditory deprivation in the common marmoset. *Program No. 627.7 2003 Abstract Viewer and Itinerary Planner. Society for Neuroscience Online*.

Schel, A. M., Machanda, Z., Townsend, S. W., Zuberbühler, K., & Slocombe, K. E. (2013). Chimpanzee food calls are directed at specific individuals. *Animal Behaviour*, *86*(5), 955–965. https://doi.org/https://doi.org/10.1016/j.anbehav.2013.08.013

Schel, A. M., Townsend, S. W., Machanda, Z., Zuberbühler, K., & Slocombe, K. E. (2013). Chimpanzee Alarm Call Production Meets Key Criteria for Intentionality. *PLOS ONE*, *8*(10), e76674. https://doi.org/10.1371/journal.pone.0076674

Schel, A. M., & Zuberbühler, K. (2009). Responses to leopards are independent of experience in Guereza colobus monkeys. *Behaviour*, *146*(12), 1709–1737. https://doi.org/https://doi.org/10.1163/000579509X12483520922007

Schrago, C. G., & Russo, C. A. M. (2003). Timing the Origin of New World Monkeys. *Molecular Biology and Evolution*, *20*(10), 1620–1625. https://doi.org/10.1093/molbev/msg172

Schuppli, C., Meulman, E. J. M., Forss, S. I. F., Aprilinayati, F., van Noordwijk, M. A., & van Schaik, C. P. (2016). Observational social learning and socially induced practice of routine skills in immature wild orang-utans. *Animal Behaviour*, *119*, 87–98. https://doi.org/https://doi.org/10.1016/j.anbehav.2016.06.014

Searcy, W. A., & Nowicki, S. (2010). The Evolution of Animal Communication: Reliability and Deception in Signaling Systems. In *Reliability and Deception in Signaling Systems*. Princeton University Press. https://doi.org/doi:10.1515/9781400835720

Seidenberg, M. S. (1997). Language Acquisition and Use: Learning and Applying Probabilistic Constraints. *Science*, *275*(5306), 1599–1603. https://doi.org/10.1126/science.275.5306.1599

Seiler, M., Schwitzer, C., Gamba, M., & Holderied, M. W. (2013). Interspecific Semantic Alarm Call Recognition in the Solitary Sahamalaza Sportive Lemur, Lepilemur sahamalazensis. *PLoS ONE*, *8*(6), e67397. https://doi.org/10.1371/journal.pone.0067397

Seppänen, J.-T., Forsman, J. T., Mönkkönen, M., & Thomson, R. L. (2007). Social information use is a process across time, space, and ecology, reaching heterospecifics. *Ecology*, *88*(7), 1622–1633. https://doi.org/10.1890/06-1757.1

Seyfarth, R. M., & Cheney, D. L. (1980). The Ontogeny of Vervet Monkey Alarm Calling Behavior: A Preliminary Report. *Zeitschrift Für Tierpsychologie*, *54*(1), 37–56. https://doi.org/10.1111/j.1439-0310.1980.tb01062.x

Seyfarth, R. M., & Cheney, D. L. (1986). Vocal development in vervet monkeys. *Animal Behaviour*, *34*(6), 1640–1658. https://doi.org/https://doi.org/10.1016/S0003-3472(86)80252-4

Seyfarth, R. M., & Cheney, D. L. (1997). Some general features of vocal development in nonhuman primates. In C. T. Snowdon & M. Hausberger (Eds.), *Social Influences on Vocal Development* (pp. 249–273). Cambridge University Press. https://doi.org/DOI: 10.1017/CBO9780511758843.013

Seyfarth, R. M., Cheney, D. L., & Marler, P. (1980). Vervet monkey alarm calls: semantic communication in a free-ranging primate. *Animal Behaviour*, *28*(4), 1070–1094.

Seyfarth, R, & Cheney, D. (2010). Production, usage, and comprehension in animal vocalizations. *Brain and Language*, *115*(1), 92–100. https://doi.org/https://doi.org/10.1016/j.bandl.2009.10.003

Seyfarth, R, Cheney, D., Bergman, T., Fischer, J., Zuberbühler, K., & Hammerschmidt, K. (2010). The central importance of information in studies of animal communication. *Animal Behaviour*, *80*(1), 3–8. https://doi.org/https://doi.org/10.1016/j.anbehav.2010.04.012

Seyfarth, R, Cheney, D., & Marler, P. (1980). Monkey responses to three different alarm calls: evidence of predator classification and semantic communication. *Science*, *210*(4471), 801–803.

Seyfarth, R, & Cheney, D. (1990). The assessment by vervet monkeys of their own and another species' alarm calls. *Animal Behaviour*, *40*(4), 754–764. https://doi.org/https://doi.org/10.1016/S0003-3472(05)80704-3

Shannon, C. E. (1948). A Mathematical Theory of Communication. *Bell System Technical Journal*, *27*(3), 379–423. https://doi.org/https://doi.org/10.1002/j.1538-7305.1948.tb01338.x

Sheldon, B. C., Kruuk, L. E. B., & Alberts, S. C. (2022). The expanding value of long-term studies of individuals in the wild. *Nature Ecology & Evolution*. https://doi.org/10.1038/s41559-022-01940-7

Shibasaki, M., & Kawai, N. (2009). Rapid detection of snakes by Japanese monkeys (Macaca fuscata): An evolutionarily predisposed visual system. In *Journal of Comparative Psychology* (Vol. 123, pp. 131–135). American Psychological Association. https://doi.org/10.1037/a0015095

Shultz, S, & Thomsett, S. (2007). Interactions between African crowned eagles and their prey community. In Klaus Zuberbühler, R. Noë, & W. S. McGraw (Eds.), *Monkeys of the Taï Forest: An African Primate Community* (pp. 171–193). Cambridge University Press. https://doi.org/DOI: 10.1017/CBO9780511542121.008

Shultz, S, Noë, R., McGraw, W. S., & Dunbar, R. I. M. (2004). A community-level evaluation of the impact of prey behavioural and ecological characteristics on predator diet composition. *Proceedings. Biological Sciences*, *271*(1540), 725–732. https://doi.org/10.1098/rspb.2003.2626

Simmons, J. P., Nelson, L. D., & Simonsohn, U. (2011). False-Positive Psychology: Undisclosed Flexibility in Data Collection and Analysis Allows Presenting Anything as Significant. *Psychological Science*, *22*(11), 1359–1366. https://doi.org/10.1177/0956797611417632

Slater, P. J. B. (2006). *Animal Communication: Vocal Learning* (K. B. T.-E. of L. & L. (Second E. Brown (ed.); pp. 291–294). Elsevier. https://doi.org/https://doi.org/10.1016/B0-08-044854-2/00824-5

Slocombe, K E, & Zuberbühler, K. (2005). Functionally Referential Communication in a Chimpanzee. *Current Biology*, *15*(19), 1779–1784. https://doi.org/https://doi.org/10.1016/j.cub.2005.08.068

Slocombe, K E, & Zuberbühler, K. (2007). Chimpanzees modify recruitment screams as a function of audience composition. *Proceedings of the National Academy of Sciences*, *104*(43), 17228 LP – 17233. https://doi.org/10.1073/pnas.0706741104

Slocombe, K E, Waller, B. M., & Liebal, K. (2011). The language void: the need for multimodality in primate communication research. *Animal Behaviour*, *81*(5), 919–924. https://doi.org/https://doi.org/10.1016/j.anbehav.2011.02.002

Smid, S. C., McNeish, D., Miočević, M., & van de Schoot, R. (2020). Bayesian Versus Frequentist Estimation for Structural Equation Models in Small Sample Contexts: A Systematic Review. *Structural Equation Modeling: A Multidisciplinary Journal*, *27*(1), 131–161. https://doi.org/10.1080/10705511.2019.1577140

Snowdon, C. T. B. T.-A. in the S. of B. (2009). Chapter 7 Plasticity of Communication in

Nonhuman Primates. In *Advances in the Study of Behavior* (Vol. 40, pp. 239–276). Academic Press. https://doi.org/https://doi.org/10.1016/S0065-3454(09)40007-X

Stansbury, A. L., & Janik, V. M. (2019). Formant Modification through Vocal Production Learning in Gray Seals. *Current Biology*, *29*(13), 2244-2249.e4. https://doi.org/10.1016/j.cub.2019.05.071

Stauffer, R. L., Walker, A., Ryder, O. A., Lyons-Weiler, M., & Hedges, S. B. (2001). Human and Ape Molecular Clocks and Constraints on Paleontological Hypotheses. *Journal of Heredity*, *92*(6), 469–474. https://doi.org/10.1093/jhered/92.6.469

Stensland, E., Angerbjörn, A., & Berggren, P. (2003). Mixed species groups in mammals. *Mammal Review*, *33*(3-4), 205–223. https://doi.org/https://doi.org/10.1046/j.1365-2907.2003.00022.x

Stephan, C., & Zuberbühler, K. (2008). Predation increases acoustic complexity in primate alarm calls. *Biology Letters*, *4*(6), 641–644. https://doi.org/10.1098/rsbl.2008.0488

Stephan, C., & Zuberbühler, K. (2014). Predation affects alarm call usage in female Diana monkeys (Cercopithecus diana diana). *Behavioral Ecology and Sociobiology*, *68*(2), 321–331. https://doi.org/10.1007/s00265-013-1647-x

Stephan, C., & Zuberbühler, K. (2021). *Alarm Calling and Kinship BT - Encyclopedia of Evolutionary Psychological Science* (T. K. Shackelford & V. A. Weekes-Shackelford (eds.); pp. 163–171). Springer International Publishing. https://doi.org/10.1007/978-3-319-19650-3_1512

Stevenson, M. (1973). Notes on pregnancy in the Sooty mangabey Cercocebus atys. *International Zoo Yearbook*, *13*(1), 134–135. https://doi.org/https://doi.org/10.1111/j.1748-1090.1973.tb02126.x

Stoeger, A. S., Mietchen, D., Oh, S., de Silva, S., Herbst, C. T., Kwon, S., & Fitch, W. T. (2012). An Asian Elephant Imitates Human Speech. *Current Biology*, *22*(22), 2144–2148. https://doi.org/10.1016/j.cub.2012.09.022

Struhsaker, T. T. (1967). Ecology of Vervet Monkeys (Cercopithecus Aethiops) in The Masai-Amboseli Game Reserve, Kenya. *Ecology*, *48*(6), 891–904.

https://doi.org/https://doi.org/10.2307/1934531

Sugiura, H. (1998). Matching of acoustic features during the vocal exchange of coo calls by Japanese macaques. *Animal Behaviour*, *55*(3), 673–687. https://doi.org/https://doi.org/10.1006/anbe.1997.0602

Takahashi, D. Y., Liao, D. A., & Ghazanfar, A. A. (2017). Vocal Learning via Social Reinforcement by Infant Marmoset Monkeys. *Current Biology*, *27*(12), 1844-1852.e6. https://doi.org/10.1016/j.cub.2017.05.004

Talmage-Riggs, G., Winter, P., Ploog, D., & Mayer, W. (1972). Effect of deafening on the vocal behavior of the squirrel monkey (Saimiri sciureus). *Folia Primatologica; International Journal of Primatology*, *17*(5), 404–420. https://doi.org/10.1159/000155458

Team, J. (2020). *JASP (Version 0.14.1)*. https://jasp-stats.org/

Thinh, V. N., Hallam, C., Roos, C., & Hammerschmidt, K. (2011). Concordance between vocal and genetic diversity in crested gibbons. *BMC Evolutionary Biology*, *11*(1), 36. https://doi.org/10.1186/1471-2148-11-36

Thornton, A., & Clutton-Brock, T. (2011). Social learning and the development of individual and group behaviour in mammal societies. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*(1567), 978–987. https://doi.org/10.1098/rstb.2010.0312

Tomasello, M. (2010). *Why we cooperate*. Boston Review Books.

Tomasello, M, & Call, J. (1994). Social cognition of monkeys and apes. *American Journal of Physical Anthropology*, *37*(S19), 273–305. https://doi.org/https://doi.org/10.1002/ajpa.1330370610

Tomasello, M. (2008). *Origins of Human Communication*. MIT press.

Townsend, S. W., & Manser, M. B. (2013). Functionally Referential Communication in Mammals: The Past, Present and the Future. *Ethology*, *119*(1), 1–11. https://doi.org/https://doi.org/10.1111/eth.12015

Trape, J.-F., Trape, S., & Chirio, L. (2012). *Lézards, crocodiles et tortues d'Afrique occidentale et du Sahara*. IRD éditions.

Urbani, B. (2017). Humans as Primate Predators. In *The International Encyclopedia of Primatology* (pp. 1–3). https://doi.org/https://doi.org/10.1002/9781119179313.wbprim0258

Valente, D., De Gregorio, C., Torti, V., Miaretsoa, L., Friard, O., Randrianarison, R. M., Giacoma, C., & Gamba, M. (2019). Finding Meanings in Low Dimensional Structures: Stochastic Neighbor Embedding Applied to the Analysis of Indri indri Vocal Repertoire. *Animals : An Open Access Journal from MDPI*, *9*(5). https://doi.org/10.3390/ani9050243

van Doorn, J., van den Bergh, D., Böhm, U., Dablander, F., Derks, K., Draws, T., Etz, A., Evans, N. J., Gronau, Q. F., Haaf, J. M., Hinne, M., Kucharský, Š., Ly, A., Marsman, M., Matzke, D., Gupta, A. R. K. N., Sarafoglou, A., Stefan, A., Voelkel, J. G., & Wagenmakers, E.-J. (2021). The JASP guidelines for conducting and reporting a Bayesian analysis. *Psychonomic Bulletin & Review*, *28*(3), 813–826. https://doi.org/10.3758/s13423-020-01798-5

van Schaik, C. P., van Noordwijk, M. A., Warsono, B., & Sutriono, E. (1983). Party size and early detection of predators in sumatran forest primates. *Primates*, *24*(2), 211–221. https://doi.org/10.1007/BF02381083

Vernes, S. C., & Wilkinson, G. S. (2020). Behaviour, biology and evolution of vocal learning in bats. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *375*(1789), 20190061. https://doi.org/10.1098/rstb.2019.0061

Verzani, J. (2004). *Using R for introductory statistics* (1st ed.). Chapman and Hall/CRC. https://doi.org/https://doi.org/10.4324/9780203499894

Wadewitz, P., Hammerschmidt, K., Battaglia, D., Witt, A., Wolf, F., & Fischer, J. (2015). Characterizing vocal repertoires - Hard vs. Soft classification approaches. *PLoS ONE*, *10*(4). https://doi.org/10.1371/journal.pone.0125785

Watson, S. K., Townsend, S. W., Schel, A. M., Wilke, C., Wallace, E. K., Cheng, L., West, V., & Slocombe, K. E. (2015). Vocal Learning in the Functionally Referential Food Grunts of Chimpanzees. *Current Biology*, *25*(4), 495–499.

https://doi.org/https://doi.org/10.1016/j.cub.2014.12.032

Wegdell, F., Hammerschmidt, K., & Fischer, J. (2019). Conserved alarm calls but rapid auditory learning in monkey responses to novel flying objects. *Nature Ecology & Evolution*, *3*(7), 1039–1042. https://doi.org/10.1038/s41559-019-0903-5

Weiss, L., Brandl, P., & Frynta, D. (2015). Fear reactions to snakes in naïve mouse lemurs and pig-tailed macaques. *Primates*, *56*(3), 279–284. https://doi.org/10.1007/s10329-015-0473-3

Wheeler, B. C. (2009). Monkeys crying wolf? Tufted capuchin monkeys use anti-predator calls to usurp resources from conspecifics. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1669), 3013–3018. https://doi.org/10.1098/rspb.2009.0544

Wheeler, B. C., Fahy, M., & Tiddi, B. (2019). Experimental evidence for heterospecific alarm signal recognition via associative learning in wild capuchin monkeys. *Animal Cognition*, *22*(5), 687–695. https://doi.org/10.1007/s10071-019-01264-3

Wheeler, B. C., & Fischer, J. (2012). Functionally referential signals: A promising paradigm whose time has passed. *Evolutionary Anthropology: Issues, News, and Reviews*, *21*(5), 195–205. https://doi.org/https://doi.org/10.1002/evan.21319

Wheeler, B. C., & Hammerschmidt, K. (2013). Proximate factors underpinning receiver responses to deceptive false alarm calls in wild tufted capuchin monkeys: is it counterdeception? *American Journal of Primatology*, *75*(7), 715–725. https://doi.org/10.1002/ajp.22097

White, D. J. (2004). Influences of social learning on mate-choice decisions. *Animal Learning & Behavior*, *32*(1), 105–113. https://doi.org/10.3758/BF03196011

Whiten, A., & van de Waal, E. (2018). The pervasive role of social learning in primate lifetime development. *Behavioral Ecology and Sociobiology*, *72*(5), 80. https://doi.org/10.1007/s00265-018-2489-3

Whitesides, G. H. (1989). Interspecific associations of Diana monkeys, Cercopithecus diana, in Sierra Leone, West Africa: biological significance or chance? *Animal Behaviour*, *37*, 760–776. https://doi.org/https://doi.org/10.1016/0003-3472(89)90062-6

Wich, S. A., & Sterck, E. H. M. (2003). Possible audience effect in Thomas langurs (Primates; Presbytis thomasi): an experimental study on male loud calls in response to a tiger model. *American Journal of Primatology*, *60*(4), 155–159. https://doi.org/10.1002/ajp.10102

Winter, P., Handley, P., Ploog, D., & Schott, D. (1973). Ontogeny of squirrel monkey calls under normal conditions and under acoustic isolation. *Behaviour*, *47*(3), 230–239. https://doi.org/10.1163/156853973x00085

Wittig, R. M. (2018). 40 years of research at the Taï Chimpanzee Project. *Pan Africa News*, *25*(2), 16–18.

Wrangham, R. W., & Cheney, D. L. (1985). Predation rates and social-structure in primates. *American Journal of Primatology*, *8*(4), 372.

Zhang, Y. S., & Ghazanfar, A. A. (2018). Vocal development through morphological computation. *PLOS Biology*, *16*(2), e2003933. https://doi.org/10.1371/journal.pbio.2003933

Zuberbühler, K. (2000a). Interspecies semantic communication in two forest primates. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *267*(1444), 713–718. https://doi.org/10.1098/rspb.2000.1061

Zuberbühler, K. (2000b). Causal cognition in a non-human primate: field playback experiments with Diana monkeys. *Cognition*, *76*(3), 195–207. https://doi.org/10.1016/s0010-0277(00)00079-2

Zuberbühler, K. (2001). Predator-specific alarm calls in Campbell’s monkeys, Cercopithecus campbelli. *Behavioral Ecology and Sociobiology*, *50*(5), 414–422.

Zuberbühler, K. (2003a). Natural semanticity in wild primates. In *Animal social complexity: Intelligence, culture, and individualized societies.* (pp. 362–367). Harvard University Press.

Zuberbühler, K. (2003b). Referential signaling in non-human primates: Cognitive precursors and limitations for the evolution of language. In *Advances in the study of behavior, Vol 33.* (pp. 265–307). Elsevier Academic Press. https://doi.org/10.1016/S0065-3454(03)33006-2

Zuberbühler, K. (2007). Monkey alarm calls. In Klaus Zuberbühler, R. Noë, & W. S. McGraw (Eds.), *Monkeys of the Taï Forest: An African Primate Community* (pp. 194–220). Cambridge University Press. https://doi.org/DOI: 10.1017/CBO9780511542121.009

Zuberbühler, K, & Jenny, D. (2002). Leopard predation and primate evolution. *Journal of Human Evolution*, *43*(6), 873–886. https://doi.org/https://doi.org/10.1006/jhev.2002.0605

Zuberbühler, K, & Jenny, D. (2007). Interaction between leopard and monkeys. In Klaus Zuberbühler, R. Noë, & W. S. McGraw (Eds.), *Monkeys of the Taï Forest: An African Primate Community* (pp. 133–154). Cambridge University Press. https://doi.org/DOI: 10.1017/CBO9780511542121.006

Zuberbühler, K, Jenny, D., & Bshary, R. (1999). The Predator Deterrence Function of Primate Alarm Calls. *Ethology*, *105*(6), 477–490. https://doi.org/10.1046/j.1439-0310.1999.00396.x

Zuberbühler, K, Noë, R., & Seyfarth, R. M. (1997). Diana monkey long-distance calls: messages for conspecifics and predators. *Animal Behaviour*, *53*(3), 589–604.

Zuberbühler, Klaus. (2000). Causal knowledge of predators' behaviour in wild Diana monkeys. *Animal Behaviour*, *59*(1), 209–220. https://doi.org/https://doi.org/10.1006/anbe.1999.1296

Zuberbühler, Klaus. (2009). Survivor Signals: The Biology and Psychology of Animal Alarm Calling. *Advances in the Study of Behavior*, *40*, 277–322. https://doi.org/https://doi.org/10.1016/S0065-3454(09)40008-1

Zuberbühler, Klaus, & Lemasson, A. (2014). *Primate Communication: Meaning from Strings of Calls BT - Language and Recursion* (F. Lowenthal & L. Lefebvre (eds.); pp. 115–125). Springer New York. https://doi.org/10.1007/978-1-4614-9414-0_9

Zuberbühler, Klaus, León, J., Deshpande, A., & Quintero, F. (2022). Socially scripted vocal learning in primates. *Current Opinion in Behavioral Sciences*, *46*, 101153. https://doi.org/https://doi.org/10.1016/j.cobeha.2022.101153

Annexe 1: Habitat-dependent intergroup hostility in Diana monkeys, *Cercopithecus diana*

Maxence Decellieres[1], Klaus Zuberbühler[1,2,3], Julián León[1,2,]

[1]Taï Monkey Project, Centre Suisse de Recherches Scientifiques, Abidjan, Cote d'Ivoire

[2]Institute of Biology, Department of Comparative Cognition, University of Neuchatel, Neuchâtel, Switzerland

3School of Psychology and Neuroscience, University of St Andrews, St Andrews, U.K.

Manuscript published in Animal Behaviour; DOI: https://doi.org/10.1016/j.anbehav.2021.06.001

Abstract

Territorial threat is costly and variable across contexts and behavioural flexibility is favoured to maximize any cost/benefit ratio. This is well illustrated in how animals react to familiar or unfamiliar outgroup members. In some situations, neighbours are better tolerated than strangers, resulting in a 'dear-enemy effect'; in other situations, the pattern is reversed, resulting in a 'nasty-neighbour effect'. Typically, the effects are species-specific traits, although both can also occur within the same species. Here, we investigated wild Diana monkeys of Taï Forest (Côte d'Ivoire) in their reactions to outgroup individuals using playbacks of both familiar and unfamiliar male alarm calls to eagles. We found that groups living in primary forest (high group density, high food availability and low predation pressure) followed a 'nasty neighbour' strategy whereas groups living in secondary forest (low group density, low resources and high predation risk) followed a 'dear enemy' strategy, suggesting that group density, predation pressure and food availability can impact how hostile behaviour is displayed in nonhuman primates. Our results confirm a high behavioural flexibility in primate relationships between conspecifics of different identities depending on ecological traits of the habitat.

Annexe 2: Socially scripted vocal learning in primates

Klaus Zuberbühler[1,2,3,4], Julián León[1,2], Adwait Deshpande[1,3], Fredy Quintero[1,2]

[1]Institute of Biology, University of Neuchatel, Neuchatel, Switzerland

[2]Taï Monkey Project, Centre Suisse de Recherches Scientifiques, Abidjan, Côte d'Ivoire

[3]Inkawu Vervet Project, South Africa

[4]School of Psychology and Neuroscience, University of St Andrews, St Andrews, Scotland (UK)

Manuscript published in Current Opinion in Behavioral Sciences; DOI:
https://doi.org/10.1016/j.cobeha.2022.101153

Abstract

Animal learning theory has been enormously influential in setting up laws of how individuals gradually learn associations and instrumentation by reinforcement. Yet, the theory rests on data collected from socially isolated laboratory animals, exposed to artificial cause–effect relations without visible agents. We review the primate vocal learning literature and find that animal learning theory performs poorly in accounting for real-life learning and evolutionarily relevant problem-solving. Instead, learning occurs when conspecifics act as event-causing agents, often without direct consequences for learners. We illustrate this with recent field studies, which suggest that the default mode of learning may not be through reinforcement and repeated trials but by acquiring scripts — mental representations of how events typically unfold. Becoming communicatively competent may be more about learning how events unfold than becoming conditioned to stimuli and responses.