

The alarm-calling system of adult male putty-nosed monkeys, *Cercopithecus nictitans martini*

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We investigated the calls of male putty-nosed monkeys produced in response to playbacks of leopard, *Panthera pardus*, growls and crowned eagle, *Stephanoaetus coronatus*, shrieks. Two call types, hacks and pyows were produced and both occurred within alarm-calling sequences regardless of the predator category simulated by the playbacks. Unlike previous studies of alarm calling in guenon monkeys, we therefore could not conclude that the alarm calls of putty-nosed males are functionally referential. There were, however, striking regularities in the patterning of the calls given in response to these stimuli and different call combinations were strongly associated with each of the two predator types. While we concluded that individual calls did not qualify as vehicles of semantic content, these males produced structurally unique call sequences that provided sufficient information for receivers to select appropriate antipredator responses.

Traditionally, animal vocal signal production has been viewed as dependent upon the motivational or affective state of the caller (e.g. Lancaster 1975; Morton 1982). A number of mammalian alarm-calling systems have been documented in which acoustically distinct alarm call types appear to encode information about the level of threat imposed by a predator according to its proximity or hunting tactics (e.g. Owings & Virginia 1978; Owings & Leger 1980). Alternatively, differences in the level of threat may be reflected in the number of notes in alarm calls (e.g. Blumstein 1995) or the length of the call (e.g. Le Roux et al. 2001). Such alarm-calling systems, known as response urgency systems, are common to species with similar escape strategies (e.g. bolting into a burrow) in the face of all predators (Macedonia & Evans 1993). Call types have only a probabilistic association with the eliciting stimulus and contextual information can be important in determining the responses of conspecifics (Leger et al. 1979).

Signal systems that show production specificity, discrete structure and context independence are collectively known as functionally referential systems (Evans 1997). A functionally referential alarm-calling system provides conspecific listeners with sufficient information about the eliciting stimulus to enable them to respond to alarm calls as though they had direct evidence of the presence of

the predator. While contextual information is unlikely to be redundant, it is not necessary for the selection of the appropriate antipredator response. The classic case of a functionally referential system is the alarm-calling system of vervet monkeys, *Chlorocebus aethiops*, which have several acoustically distinct alarm calls for leopards, eagles and pythons (Struhsaker 1967). They respond to these alarm calls by taking evasive action that is appropriate to the hunting tactics of the predator in question. They also respond appropriately to playbacks of alarm calls in the absence of any visual contextual cues and are relatively uninfluenced by other forms of contextual information (Seyfarth et al. 1980). Vervet alarm calls appear to be insensitive to the spatial location (Struhsaker 1967) and proximity of the predator (Cheney & Seyfarth 1990). Furthermore, each alarm call type is associated with a narrow range of stimuli thereby providing listeners with specific information (Seyfarth & Cheney 1980). These findings first raised the possibility that certain animal signals might designate external objects or events (Seyfarth et al. 1980; Cheney & Seyfarth 1990; Seyfarth & Cheney 1993).

Since then, several other primate alarm-calling systems have been identified as functionally referential. Like vervet monkeys, ringtailed lemurs, *Lemur catta*, Diana monkeys, *Cercopithecus diana*, and Campbell's monkeys, *Cercopithecus campbelli*, also produce acoustically distinct alarm calls to ground predators and large raptors regardless of the level of threat (Macedonia 1990; Pereira & Macedonia 1990; Zuberbühler 2000a, 2001). Two other lemur species, red-fronted lemurs, *Eulemur fulvus rufus*, and white sifakas,

Propithecus verreauxi verreauxi, have specific alarm calls for raptors but give a call associated with high arousal to ground predators and in social contexts (Fichtel & Kappeler 2002). By contrast, the alarm-calling system of captive black-and-white ruffed lemurs, *Varecia variagata variagata*, has low production specificity and does not elicit qualitatively different responses in playback experiments (Macedonia 1990). Macedonia & Evans (1993) suggested that the major selective force in the evolution of referential alarm-calling systems may be the incompatibility of antipredator responses required by different predator classes since, while ground-dwelling mammals can respond in only a single plane, arboreal species can respond in two planes. Ruffed lemurs, however, are relatively invulnerable to predators since their large body size deters raptors and their primarily arboreal lifestyle gives them an important advantage over ground predators.

Despite the apparent dichotomy in alarm-calling systems (referential versus affective) a number of authors have pointed out that this categorical distinction may, in fact, be a false one (e.g. Marler et al. 1992; Seyfarth & Cheney 2003). There is no reason to assume that a referential signal can have no affective component (Evans 1997; Manser et al. 2002) or that it cannot be based purely on affect if different degrees of arousal are routinely associated with different predator categories (Seyfarth & Cheney 2003).

Given the variability in the types and distribution of alarm-calling systems and the absence of any comprehensive model, it is necessary to carry out research on a wider range of species to understand the socioecological and psychological underpinnings of these phenomena. As yet, we do not know what psychological mechanisms drive alarm call production in the signaller. The evidence for monkeys suggests that call production is mediated by mental representations of predator classes (Cheney & Seyfarth 1990; Seyfarth & Cheney 1993; Zuberbühler et al. 1999a; Zuberbühler 2000a, b, c). However, data remain scant for primates and conclusions have been based on analyses of only the first few calls given in response to stimuli even though alarm calling can be prolonged in many species.

Putty-nosed monkeys are a West African guenon species that live in one-male groups with several adult females and dependent offspring. The males have a repertoire of three loud call types; 'booms', 'pyows' and 'hacks'. Booms are rare whereas pyows and hacks are frequently heard and have been interpreted as functioning primarily as calls used for intragroup cohesion and the maintenance of intergroup spacing (Gautier & Gautier-Hion 1977). There are also reports of pyows and hacks being used in a variety of contexts (e.g. falling trees, thunderclaps, aerial predators, the approach of humans), all of which can be characterized as having a disturbing effect on the group (Struhsaker 1970). Eckhardt & Zuberbühler (2004) concluded that pyows and hacks also function as alarm calls in *C. nictitans stampflii*.

We investigated the alarm-calling behaviour of wild putty-nosed monkeys living in the Gashaka Gumti National Park, Nigeria. Putty-nosed monkeys are primarily arboreal and spend much of their time in polyspecific associations with other primate species (Gautier-Hion &

Gautier 1974; Gautier & Gautier-Hion 1983) suggesting that predator pressure is high (e.g. Noë & Bshary 1997). Our primary aim was to discover whether this putty-nosed monkey population gives alarm calls to predators and whether they respond primarily to features of the stimulus, which might indicate predator type, or to the degree of threat perceived by the subjects. To distinguish between these two hypotheses we experimentally simulated the presence of a predator by playing back recordings of the vocalizations of crowned eagles, *Stephanoaetus coronatus*, and leopards, *Panthera pardus*. This method is a reliable way of simulating predator presence (Zuberbühler et al. 1997, 1999b; Zuberbühler 2000a, 2001). We manipulated (1) the predator category to vary the biological class and associated features of the stimulus, and (2) the distance between the subjects and the playback speaker in the horizontal plane to vary the degree of apparent threat imposed by the stimulus. We then examined the acoustic structure of the calls given in response to the stimuli and described the alarm call series in their entirety.

METHODS

Study Site and Subjects

The first author (K.A.) collected the data in the Gashaka Gumti National Park, Nigeria, between March and May 2003 and between December 2003 and May 2004. Permission for the research was provided by the Nigerian National Parks Service. A portion of the park is made up of lowland and montane rainforest, which supports a number of primate species including putty-nosed monkeys, mona monkeys, *Cercopithecus mona*, and black-and-white colobus monkeys, *Colobus guereza*. Putty-nosed monkeys are described as common and widespread (3–4 groups/km², A. Dunn, unpublished data). Crowned eagles are regularly observed within the study area and leopards are known to be present but at low densities (A. Dunn, unpublished data). All data were collected in the Kwano region of the park surrounding the Gashaka Primate Project research station (7°19'N, 11°35'E) within a 38-km² study area consisting primarily of semideciduous lowland rainforest and including small patches of lowland rainforest/Guinea savannah mosaic. For a more complete description of the site see Sommer et al. (2004). Putty-nosed monkey groups typically consist of 13–22 individuals comprising one adult male, six to nine adult females and several immatures (Gautier-Hion & Gautier 1974; K. Arnold, personal observation). None of the groups tested were habituated to the presence of humans. To avoid dependencies in the data, groups were selected for testing only if they were 1 km or more from a group previously tested with the same stimulus, thereby ensuring that no group was exposed to the same stimulus more than once. Group locations were recorded with a Magellan 330 GPS unit.

Experimental Protocols

Putty-nosed monkey groups were systematically searched for throughout the study area and located by

sight or by hearing their vocalizations from a distance. Once detected, the experimenter and field assistant positioned themselves 25–100 m from the group and out of sight. Variation within this range is likely to be perceptually salient since the acoustic structure of Campbell's monkey alarm calls differs in response to playbacks of predator vocalizations over a similar range (Zuberbühler 2001). All vocal behaviour was monitored for 30 min to ensure that the group was not aware of the presence of the experimenter and field assistant, and that no other disturbance, indicated by alert or alarm calls, had occurred prior to an experiment. If this condition was met, a NAGRA DSM speaker connected to a portable CD player was positioned 0–2 m from the ground, in preparation for broadcasting the playback stimulus, while the group was monitored. Recording of all vocalizations began 5 min before exposure to the playback stimulus and continued until all antipredator vocalizations had ceased. Playback stimuli were presented as natural series lasting 15 s and consisted of either leopard growls ($N=2$: purchased from the Natural Sound Archive, London, U.K.) or crowned eagle shrieks ($N=2$: recorded by K.Z. in the Tai National Park, Ivory Coast; eagle shrieks recorded at Tai are identical to those heard in the study area). Spectrograms depicting examples of these stimuli are published elsewhere (Zuberbühler 2000a). Vocalizations were recorded with a SONY DAT TCD-D8 professional Walkman (sampling rate 44.1 kHz) and a SENNHEISER K6-ME66 directional microphone. Trials were abandoned or discarded if the monkeys detected the experimenter, field assistant or equipment at any time before the end of the trial. The following contextual information was also recorded: (1) the distance between the speaker and the group male, later coded as 'close' (<50 m) or 'far' (>50 m), (2) the local density of the vegetation, coded as 'dense' (thick undergrowth, upper canopy not

visible) or 'open' (little undergrowth, several tree crowns visible), (3) the general illumination, coded as 'dark' (no shadows on the ground, sky heavily overcast or twilight) or 'light' (shadows visible, sky slightly overcast or full sunlight). Calls produced spontaneously were also recorded ad libitum throughout the day. The context of these naturally occurring calls was rarely identified.

Acoustic Analysis

All recordings of the vocal responses to playbacks were transferred to an APPLE G3 iBook via an iMIC line level audio to digital USB converter and digitized at 16 bits, 44.1 kHz, using CANARY 1.2.4 sound-editing software (Charif et al. 1995). Clipped recordings were resampled at appropriately reduced amplitude. Spectrographic representations of the calls were displayed with an analysis resolution of 341.95 Hz/512 points, and a grid resolution of 43.07 Hz/1024 points, 1.451 ms, 87.5% overlap, using a Hanning window function. We measured (1) the number of calls given in response to the stimulus, (2) the inter-call interval and (3) the total duration of the response series. We also calculated (4) the call rate over the whole response series. From the spectrograms (Fig. 1) we measured (5) the call duration, (6) the frequency of the most prominent spectral peak (dominant frequency, DF) at the onset, middle and end of the call and (7) the position of the peak frequency, and we calculated (8) the change in DF between the onset and end of the call (overall transition), (9) the change in DF between the onset and middle of the call (early transition), (10) the change in DF between the middle and end of the call (late transition), (11) the rate of change in DF between the onset and end of the call (overall transition rate), (12) the rate of change in DF between the onset and middle of the call (early

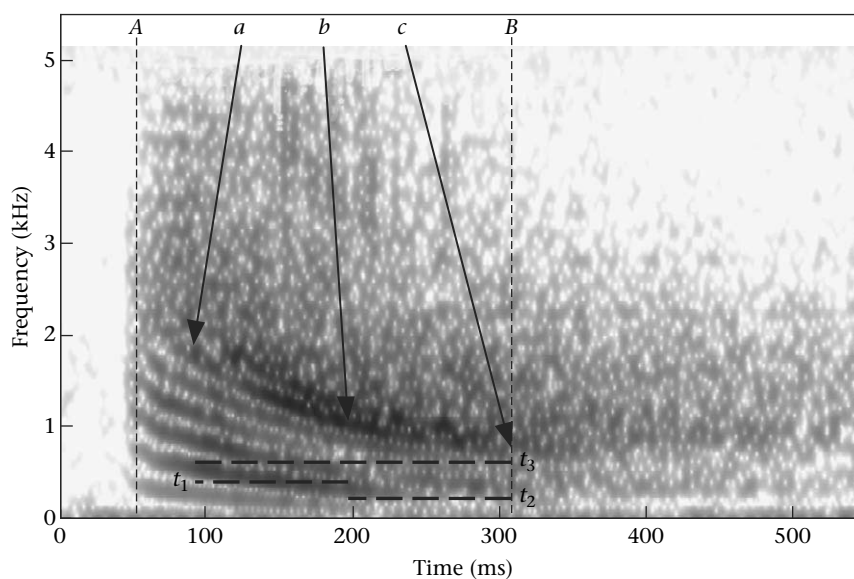


Figure 1. The acoustic parameters measured to describe male putty-nosed monkey alarm calls: call duration ($B-A$); dominant frequency at the onset, middle and end of the call (a , b , c); the overall transition ($c-a$); the early transition ($b-a$); the late transition ($c-b$). Calculations based on these measurements were: the overall transition rate ($((c-a)/t_1)$); the late transition rate ($((b-a)/t_2)$); the late transition rate ($((c-b)/t_3)$).

transition rate), and (13) the rate of change in DF between the middle and end of the call (late transition rate).

Male Loud Calls

Following Struhsaker (1970) we refer to male putty-nosed monkey loud call types as hacks and pyows. Booms were never produced in response to the experimental stimuli. Hacks are low-frequency tonal calls that can be characterized as having an abrupt onset, a duration of 18–68 ms and a major band of acoustic energy lying between 0.6 and 1.1 kHz (Fig. 2). Pyows are a more variable (Gautier & Gautier-Hion 1977), higher-frequency tonal call characterized by descending frequency modulation from around 2.5 to 0.6 kHz. Pyow calls vary in length from 28 to 289 ms. The transition in the dominant frequency between the onset and end of the call becomes more rapid with decreasing call length and shorter calls tend to be of higher frequency overall (Fig. 2). Although long and short pyow variants are easily distinguishable by ear, we consider them to lie at the extreme ends of a continuum of highly graded calls, with intermediate forms being the most commonly produced in the context of predation (long pyow, $N = 58$; intermediate pyow, $N = 84$; short pyow, $N = 55$).

Statistical Analysis

Before conducting statistical tests designed to distinguish call types, we selected 200 calls of sufficient spectrographic quality for analysis. We included a maximum of 10 calls produced in response to 36 playbacks resulting in a data set comprising 19 hacks, 19 long pyows, 18 intermediate pyows and seven short pyows given to leopard growls and 94 hacks, 10 long pyows, 23 intermediate pyows and 10 short pyows given in response to eagle shrieks. We then excluded those acoustic parameters that were highly correlated with one another. We regressed all parameters together and removed those parameters that exceeded a variance inflation factor of 10 indicating a high degree of multicollinearity (Belsley et al. 1980). We looked for outliers by producing standardized Z scores for all values and rejecting all cases in which at least one parameter had a Z score of greater than 3.29 (Tabachnick & Fidell 2001). We performed a K -means cluster analysis to confirm the presence of four call types corresponding to our own subjective

classification. K -means clustering seeks to partition the data set into a predefined number of groupings to minimize variability within clusters and maximize variability between clusters. The number of clusters is set a priori. We used analysis of variance tests to identify differences between seven uncorrelated acoustic properties of these four call types. Dunnett's T3 multiple comparisons post hoc tests were used to identify differences between the sample means. Multinomial logistic regression was used to identify the contextual variables that predict the category of response produced in experiments. Sequence categories with $N < 4$ are not included in the analysis. Probabilities associated with the results of Wilcoxon signed-ranks tests are exact. Statistical analyses were conducted with the statistical package SPSS 11.0. (SPSS Inc., Chicago, IL, U.S.A.). All tests were two tailed with a significance level set at 0.05.

RESULTS

Alarm Call Types

Male putty-nosed monkeys produced both hacks and pyows in response to predator stimuli. In addition, we identified long, intermediate and short variants of the pyow calls. A K -means cluster analysis performed on 200 selected calls resulted in an agreement with our original classification of call types in 83.0% of cases overall (hack = 112/113; long pyow = 20/29; intermediate pyow = 17/49; short pyow = 17/17). Most disagreement occurred within the highly variable intermediate-pyow category where intermediate pyows were classified as short pyows (18/41) and in the long-pyow category where long pyows were classified as intermediate pyows (7/29). We then compared these calls according to seven parameters (Fig. 3, Table 1). Each of the seven acoustic features varied significantly between call types. Post hoc tests showed that call duration, the dominant frequency at the end of the call and the late dominant frequency transition rate discriminated well between all call types. In addition, the early dominant frequency transition discriminated hacks from all pyow variants, peak frequency discriminated hacks and long pyows from intermediate and short pyow variants and the early dominant frequency transition rate discriminated between pyow variants and between long pyows and hacks (Table 2).

Hacks were elicited by the experimental acoustic stimuli and occurred during encounters with real eagles. Pyows

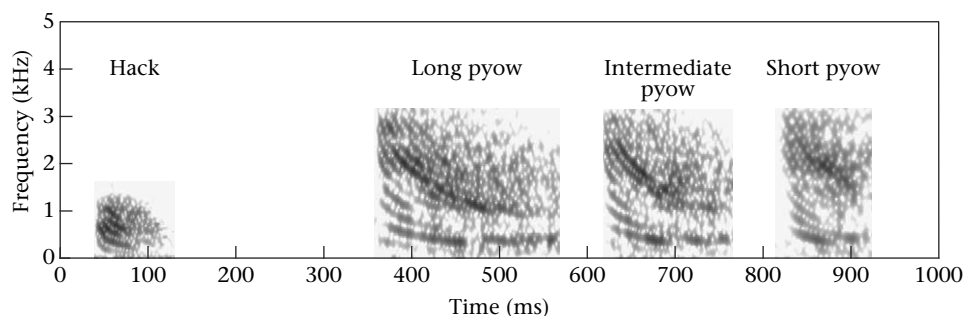


Figure 2. Spectrographic representations of male putty-nosed monkey call types.

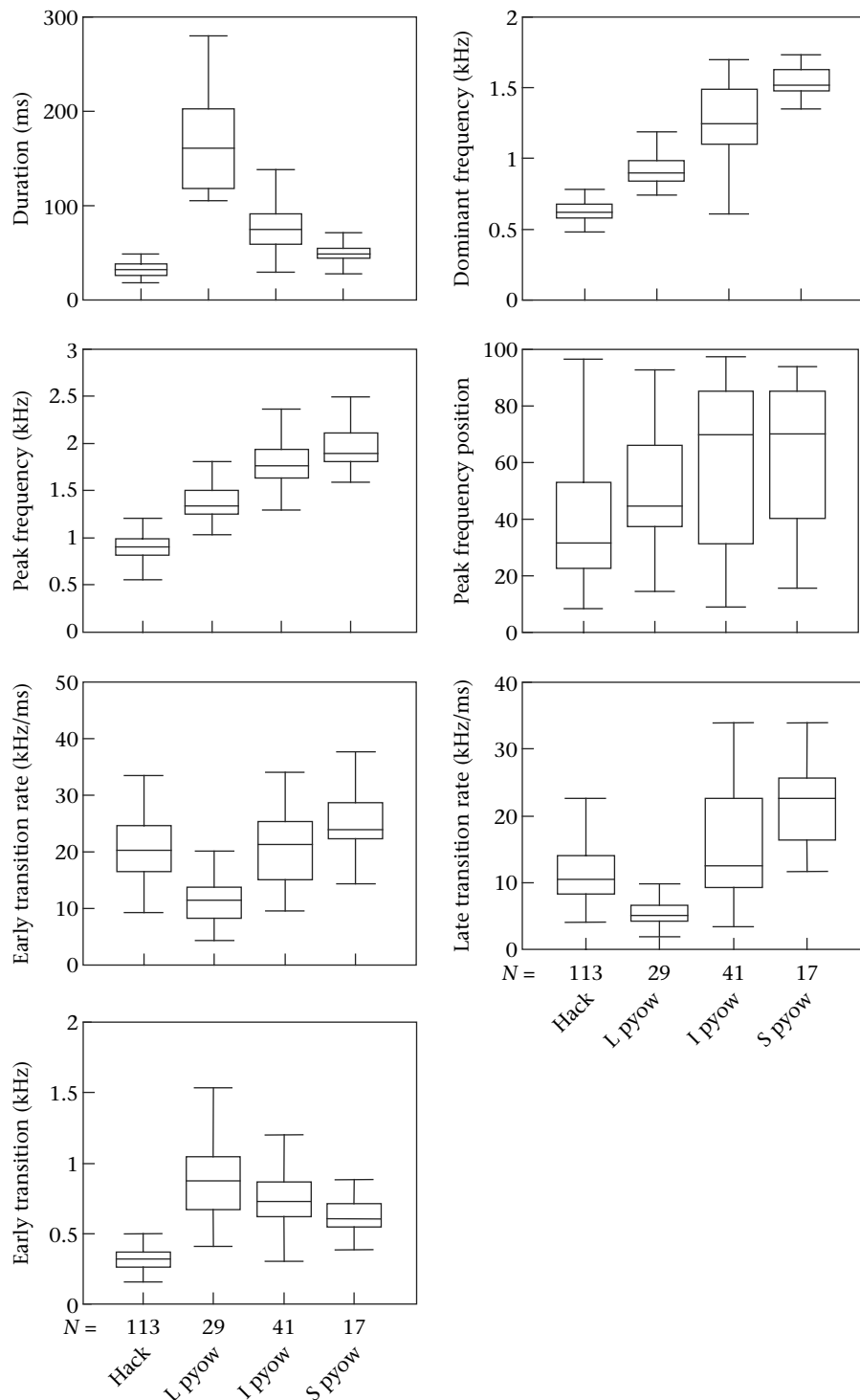


Figure 3. Box plots indicating the median, interquartile range and range for each of seven uncorrelated acoustic parameters describing male putty-nosed monkey call types. N = the number of data points representing each call type. L.pyow: long pyow; I.pyow: intermediate pyow; S.pyow: short pyow.

were elicited by the experimental acoustic stimuli and during encounters with real eagles and large mammals including humans. However, pyows were produced in response to both eagle and leopard stimuli. Long pyows were more likely to occur during the first phase of call series than the last whereas the reverse was true for short and intermediate pyows (Fig. 4). We demonstrated this

statistically by comparing the distribution of each of the pyow variants produced during the first and fourth quartiles for each alarm call series comprising at least four calls (long: $N = 23$, $\text{mean}_{1\text{st}} = 0.51$, $\text{mean}_{4\text{th}} = 0.07$; Wilcoxon signed-ranks test: $Z = -3.02$, $P < 0.001$; intermediate: $N = 18$, $\text{mean}_{1\text{st}} = 0.04$, $\text{mean}_{4\text{th}} = 0.38$; $Z = -3.12$, $P < 0.001$; short: $N = 14$, $\text{mean}_{1\text{st}} = 0.0$, $\text{mean}_{4\text{th}} = 0.50$;

Table 1. Analysis of variance of seven uncorrelated acoustic features of hacks ($N = 167$) and pyow variants (long, $N = 36$; intermediate, $N = 46$; short, $N = 16$)

Acoustic feature	Sum of squares	$F_{3,196}$	P
Duration	0.42	259.77	<0.001
Dominant frequency at end	20 925 877.70	250.92	<0.001
Peak frequency	36 257 404.70	222.78	<0.001
Peak frequency position	19 666.48	11.62	<0.001
Early transition	110 218 722.80	123.5	<0.001
Rate of early transition	2723.94	27.56	<0.001
Rate of late transition	3279.62	36.84	<0.001

$Z = -2.95$, $P = 0.001$). Our data suggest that the occurrence of each of the pyow variants within alarm call series is most likely to be determined by the position of the call within the alarm call series rather than any other factor such as predator type. We consider the transition from long pyows to progressively shorter pyows to be the result of increased calling effort during the production of long and uninterrupted call series (Notman & Rendall 2005). Long pyows sometimes occurred late in a series following a significant pause. On this basis we do not consider the pyow variants separately during the remainder of the paper.

Adult female putty-nosed monkeys and immatures of either sex produced only one call type, the chirp, in response to predator stimuli. Chirps varied in pitch but it was impossible to differentiate variants since individual callers could not be identified and the variation in pitch is likely to be influenced by factors such as body size. Consequently we do not consider them further.

Responses to Predator Stimuli Playbacks

General response characteristics

We conducted 49 trials in which leopard growls were presented and 34 trials in which eagle shrieks were presented to different groups. Whole group responses were recorded in 65% of leopard trials and in 79% of eagle trials. Adult male subjects produced loud calls in 39% (19/49) of leopard trials and in 59% (20/34) of eagle trials. Three leopard trials were discarded where we

Table 2. Dunnett's T3 multiple comparisons post hoc tests for differences between the sample means of hacks and pyow variants (long, L; intermediate, I; short, S)

Acoustic feature		L pyow	I pyow	S pyow
Duration	Hack	***	***	***
	L pyow		***	***
	I pyow			***
Dominant frequency at end	Hack	***	***	***
	L pyow		***	***
	I pyow			***
Peak frequency	Hack	***	***	***
	L pyow		***	***
	I pyow			NS
Peak frequency position	Hack	NS	***	**
	L pyow		NS	NS
	I pyow			NS
Late transition	Hack	***	***	***
	L pyow		NS	**
	I pyow			NS
Rate of early transition	Hack	***	NS	NS
	L pyow		***	***
	I pyow			*
Rate of late transition	Hack	***	*	***
	L pyow		***	***
	I pyow			*

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

considered it likely that the male responded to non-experimental stimuli such as large branches snapping. Analyses were therefore conducted on the remaining 16 leopard trials resulting in 119 calls, and on 20 eagle trials resulting in 349 calls.

The latency to call was shorter after eagle stimuli than after leopard stimuli (median latency to respond to eagle versus leopard: 18.6 versus 53.1 s; Mann-Whitney U test: $Z = -3.15$, $N_1 = 20$, $N_2 = 16$, $P = 0.001$). Males produced a longer series of calls in response to eagle stimuli than to leopard stimuli both in terms of the number of calls produced (median number of calls in response to eagle versus leopard: 13.5 versus 4.5; $Z = -3.06$, $N_1 = 20$, $N_2 = 16$, $P = 0.002$) and in terms of the duration of the call series (median duration of call series in response to eagle versus leopard: 110.85 versus 20.64 s; $Z = -2.58$,

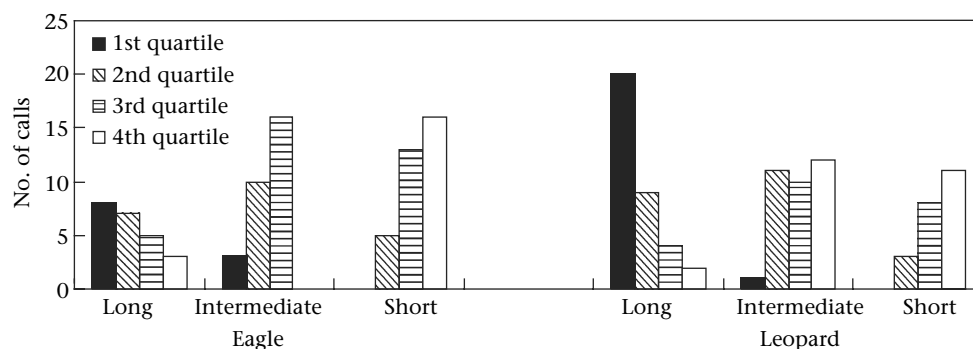


Figure 4. The distribution of long, intermediate and short pyow variants by quartile over 36 alarm-calling series given in response to playbacks of eagle and leopard stimuli and to natural stimuli.

$N_1 = 20$, $N_2 = 16$, $P = 0.009$). The call rate, however, did not differ between contexts (median call rate in response to eagle versus leopard: 0.17 versus 0.24 calls/s; $Z = -1.08$, $N_1 = 20$, $N_2 = 16$, $P = 0.29$).

Responses to eagle shrieks

Males produced 2–40 calls in response to eagle stimuli and hacks were the first calls given in response to eagle stimuli in 90% of cases (18/20). The proportion of hacks occurring within the first five calls (median 1) remained very high compared with pyows (0; Wilcoxon signed-ranks test: $Z = -3.18$, $N = 20$, $P = 0.001$). However, when the call series as a whole was considered, pyows occurred more often, especially from call five onwards (Fig. 5a) although hacks continued to predominate (median proportion of hacks = 0.93; median proportion of pyows = 0.07; Wilcoxon signed-ranks test: $Z = -2.35$, $N = 20$, $P = 0.016$).

Responses to leopard growls

In response to leopard stimuli, males produced 2–20 calls. Pyows were the first calls given in response to leopard stimuli in 93.8% of cases (15/16). Again over the whole call series, the call that was produced first predominated (median proportion of hacks = 0.21; median proportion of pyows = 0.79; Wilcoxon signed-ranks test: $Z = -2.18$, $N = 16$, $P = 0.027$). However, analysis of the first five calls in a series showed that hacks were just as likely to occur as pyows (median proportion of hacks = 0.45; median proportion of pyows = 0.55; $Z = -1.55$, $N = 16$, $P = 0.131$). Since the first call was almost always a pyow, this result is due to a high proportion of hacks occurring at positions 2–5 (Fig. 5b).

Analysis of Alarm-calling Sequences

Despite the strong biases in favour of one call type over the other in response to the two categories of predator stimuli, the frequency with which both call types occurred within a single call series was surprising. Close examination of individual cases revealed a number of structural regularities. The two call types formed part of three basic sequences, hack sequences, pyow sequences and pyow–hack sequences, which could be combined to form more complex structures: transitional series consisted of a hack sequence followed by a pyow sequence while pure hack, pure pyow or transitional series could be interrupted by a pyow–hack sequence at different locations. Figure 6 provides a graphic representation of the structural organization of the first 12 calls given to all eagle and leopard playbacks. For comparison we also provide information on natural call series recorded in unknown contexts.

In the playback trials the occurrence of each series type was generally restricted to those involving either eagle or leopard stimuli suggesting that the type of series produced was closely related to context. In 60% (12/20) of eagle trials, the males responded with a hack sequence, which in two cases was interrupted by a pyow–hack unit. Leopard trials never elicited pure hack sequences. In 30% (6/20) of eagle trials, males responded with a transitional sequence, which was once interrupted by a pyow–hack unit. In 52.9% (9/17) of leopard trials, males responded with pure pyow sequences, which were preceded by a pyow–hack unit in four cases. In 10% (2/20) of eagle trials, males also produced pure pyow sequences. In 35.3% (6/17) of leopard trials, males only produced pyow–hack units (5/17) and in one case the male produced a transitional sequence, although this was much shorter than those produced in eagle trials.

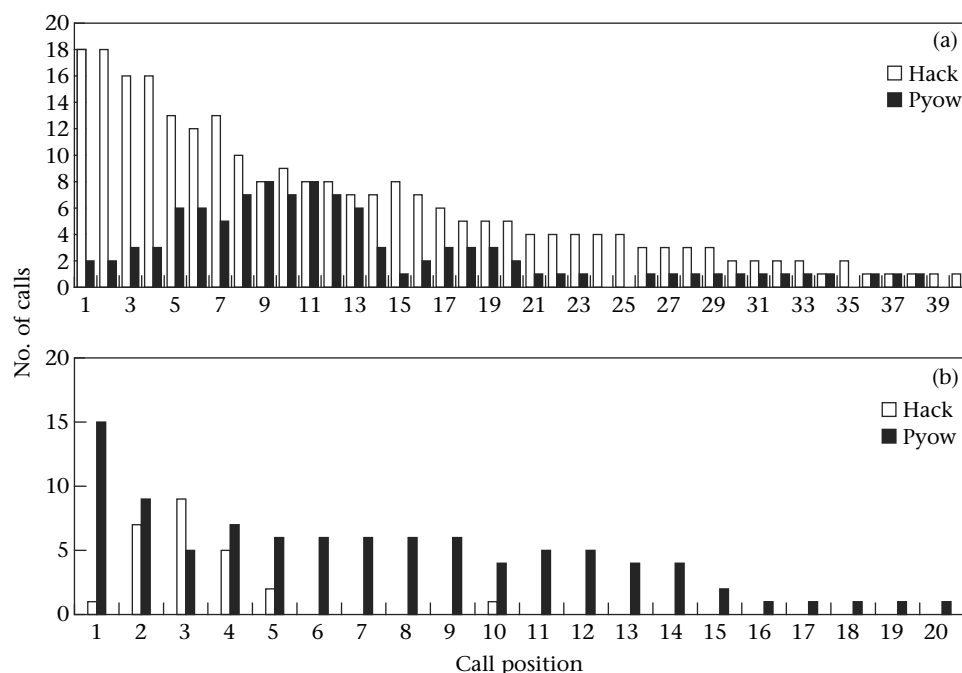


Figure 5. The distribution of hacks and pyows by call position within (a) eagle trials and (b) leopard trials.

Call position		1	2	3	4	5	6	7	8	9	10	11	12
Eagle trials													
Pure hack	N = 10	hack	hack	hack	hack	hack	hack	hack	hack	hack	hack	hack	hack
Transitional	N = 5	hack	hack	hack	hack	hack		pyow	pyow	pyow	pyow	pyow	pyow
Pure pyow	N = 2	pyow	pyow	pyow	pyow	pyow	pyow	pyow	pyow	pyow	pyow	pyow	pyow
Pure Hack –PHS _{ins}	N = 2	hack	hack	hack	hack	hack		pyow	hack	hack		hack	hack
Transitional – PHS _{ins}	N = 1	hack	hack	hack	hack	hack		pyow	hack	hack		pyow	pyow
Leopard trials													
Pure pyow	N = 5	pyow	pyow	pyow	pyow	pyow	pyow	pyow	pyow	pyow	pyow	pyow	pyow
PHS	N = 5	pyow	pyow	hack	hack	hack							
Pure pyow – PHS _{start}	N = 4	pyow	pyow	hack	hack	hack	pyow	pyow	pyow	pyow	pyow	pyow	pyow
PHS-PHS	N = 1	pyow	hack	hack		pyow	hack						
Transitional	N = 1	hack	hack	pyow									
Unknown contexts													
Pure pyow	N = 42	pyow	pyow	pyow	pyow	pyow	pyow	pyow	pyow	pyow	pyow	pyow	pyow
PHS-PHS	N = 5	pyow	pyow	hack	hack		pyow	hack	hack				
PHS	N = 4	pyow	pyow	hack									
Transitional	N = 2	hack	hack	hack	hack	hack	hack	hack		pyow	pyow	pyow	pyow
Pure pyow - PHS-PHS _{start}	N = 2	pyow	pyow	pyow	hack		pyow	pyow	pyow	hack	hack		pyow
	N = 2	pyow	pyow	hack	hack		hack		pyow	pyow	pyow	pyow	
	N = 1	pyow	pyow	pyow		pyow		hack	hack		hack		
	N = 1	pyow	pyow		pyow	pyow	pyow	hack	hack	hack	hack		pyow
	N = 1	pyow	pyow	pyow	pyow	hack	hack		hack		pyow	pyow	

Figure 6. Patterns of call production recorded in eagle and leopard trials and in unknown contexts. PHS: pyow–hack sequence; PHS_{ins}: pyow–hack sequence inserted; PHS_{start}: pyow–hack sequence at the start of the series. Series produced in unknown contexts are labelled only where they closely resemble calling patterns recorded during experimental trials. Blank spaces represent pauses i.e. intercall intervals of more than the mean + 2SD from the mean for all preceding calls. Where $N > 1$, patterns depicted are generalized. For example, in real transitional call series given in response to eagle stimuli the number of hacks at the beginning of the series ranged from three to eight (median = 5). All calls produced after position 12 are the same as that indicated at position 12.

The insertion of pyow–hack units also appeared to follow certain rules. Pyow–hack units, made up of one to three pyows followed by one to four hacks, were typically inserted after four or five hacks within an otherwise pure hack series. On one occasion a pyow–hack unit was inserted at the transition point in a transition sequence. In the hack sequence, the pyow–hack unit was inserted at the point where a transition normally occurs. In all cases,

pauses usually occurred both before and after pyow–hack units except where they introduced a pure pyow sequence.

Context of Sequence Production

A univariate analysis of variance revealed that differences in luminosity and vegetation density and the

distance between the loud speaker and caller did not explain the calling patterns. Only predator category had a significant effect on the calling sequence produced (Table 3).

DISCUSSION

Male putty-nosed monkeys produced loud calls in response to playbacks of predators and, as in other forest guenons (Zuberbühler et al. 1997; Zuberbühler 2000a, 2001; Eckhardt & Zuberbühler 2004), these responses consisted of a series of calls. Males responded more often to eagle stimuli than to leopard stimuli and also more strongly insofar that they gave more calls and responded more quickly. This finding mirrors previous work on putty-nosed monkeys, which also found that stronger vocal responses were given to acoustic models of aerial predators than terrestrial ones (Eckhardt & Zuberbühler 2004). For arboreal monkeys, raptors probably represent a greater threat than leopards since they can launch surprise attacks whereas ground predators usually rely on stealth and generally abandon a hunting attempt once they have been detected (Curio 1976; Robinson 1980; Zuberbühler et al. 1999b).

The Pyow–Hack Sequence

Our experiment shows that male putty-nosed monkeys assemble individual calls into larger units, which can be part of longer sequences. Previous studies have noted that putty-nosed males often combine hacks and pyows within the same series of calls in both predatory and non-predatory contexts (Struhsaker 1970; Gautier & Gautier-Hion 1977, 1983). The majority of call series recorded in unknown contexts were of the same general form as the responses to our experimental stimuli and also included conspicuous pauses, which broke strings of calls into discrete blocks. The pyow–hack sequence, which regularly occurred as a discrete unit, either alone or inserted at the beginning of a longer series of loud calls, was particularly conspicuous. These sequences typically consisted of one to three pyows followed by one to four hacks and were easily distinguishable by the stereotypical ordering of the pyows and hacks and by the temporal patterning of the calls within a series. This sequence has been shown to instigate group movement in a variety of contexts including predation (Arnold & Zuberbühler 2006).

Table 3. Univariate analysis of variance of the series type produced as a function of predator type, vegetation, illumination and distance

Variable	–2Log likelihood	χ^2_4	P
Intercept			
Predator type (eagle/leopard)	63.094	40.90	<0.001
Vegetation (open/closed)	28.920	6.73	0.151
Illumination (light/dark)	30.031	7.84	0.098
Distance (close/far)	28.870	6.68	0.154

Alarm Calls as Referential Signals

Putty-nosed monkey alarm calls do not function as referential calls as they have been shown to do in vervet, Diana and Campbell's monkeys (Struhsaker 1967; Seyfarth & Cheney 1980; Zuberbühler et al. 1997; Zuberbühler 2000a, 2001). If listeners attended to each individual call then they would be able to extract only mixed messages not related to a particular context. However, if listeners attended primarily to the first call, or the first few calls in a series, then they should be able to discriminate reliably between contexts. This was especially true in the case of responses to eagle playbacks since the majority of response series began with a string of hacks. Similar responses have been observed during encounters with real eagles. However, since referential signals must at least have the potential to encode specific information about the eliciting stimulus, hacks do not qualify since they occurred as part of call series given in response to leopard stimuli and also within a number of other contexts, including when baboons were fighting close by, when trees fell near to the monkeys, when branches broke as they landed on them, in response to a rape alarm and when a duck flew close by. At most, their association with the detection of eagles is probabilistic and dependent on being situated within a repetitive sequence of similar calls.

Pyows also do not qualify as referential signals by any of the established criteria. First, they occur very frequently in nonpredatory contexts (Gautier & Gautier-Hion 1977, 1983) and, second, they are given to a wide range of stimuli. While crowned eagles are regularly observed within the study area, evidence for the presence of leopards is sparse. Although leopards might have been common in the past, it is difficult to assess how much direct experience the different males have had with this predator. It is more likely that in this population of putty-nosed monkeys pyows function as general alarm calls that require additional contextual information before an external cause can be inferred.

Alarm Calls as Affective Signals

Another possibility is that male putty-nosed monkey alarm calls reflect the degree of arousal experienced by the caller at any given point in time. It may be that certain classes of stimuli reliably provoke higher levels of arousal than others, and that different degrees of arousal are associated with the production of different call types (e.g. Owren & Rendall 1997; Seyfarth & Cheney 2003). Since it is likely that crowned eagles present a greater threat to these monkeys than leopards do, hacks, which are strongly associated with the presence of eagles, might reflect higher levels of arousal than pyows. This interpretation explains the observed patterns of call production better than a referential interpretation since transitions from hacks to pyows were fairly common, whereas transitional call series showing the reverse pattern never occurred, except in the case of pyow–hack sequences. However, the association of the pyow–hack sequence with group progression is inconsistent with a purely

arousal-based mechanism of call production since it seems unlikely that the caller should always experience elevated levels of arousal in this context.

A Response Urgency System?

Despite the lack of support for a referential signalling interpretation of the putty-nosed monkey alarm-calling system, it does not fit the description of a response urgency system either. There was no evidence that varying the distance between the stimulus and the subjects had any effect on the type of responses produced. Neither were differences in local visibility reflected by differences in calling patterns. The only determinant of the male's response was predator category, although even this did not fully explain the observed responses since there was a degree of overlap between contexts. However, we cannot reject this hypothesis since we cannot be certain that our experimental manipulations were relevant to the monkeys in terms of generating sufficient variation in perceived threat. A limited number of observations of close encounters with real eagles suggest that response urgency might be conveyed in calling patterns. On five occasions, males responded by producing pure hack sequences, at least initially. On a further three occasions hacks were produced in rapid succession when large eagles circled the group near the top of the canopy. These observations suggest that high call rates might indicate high levels of threat experienced by the caller when a predator is in a position to attack.

General Conclusions

In sum, the results of this study were not in agreement with the findings of previous studies that have indicated that individual alarm calls in guenons are functionally referential. Neither can we conclude that putty-nosed monkeys use an urgency response system although there was some evidence that call rates might be influenced by perceived levels of threat. However, transitions between call types within alarm call series suggest that levels of arousal might influence call production. In this species, meaning clearly does not reside in individual calls. Further evidence is provided by the pyow–hack sequence where pyows and hacks are combined according to a structural rule that encodes information, which is not exclusively related to the context of predation.

At present it is not known whether other members of the group show differentiated responses to different call types or calling patterns. While attending to individual calls may provide ambiguous information in many cases, listeners should still be able to extract useful information from calling patterns. Series of either hacks or pyows appear to indicate different degrees of danger and have the potential to elicit differentiated responses. Habituation of two groups is presently underway which will allow this issue to be addressed. Pyow–hack sequences also have an additional role in determining receiver responses.

The patterns of alarm call production of male putty-nosed monkeys are unlike those reported for other

monkeys. They most closely resemble the responses of black-and-white ruffed lemurs in that call types have only a probabilistic association with predator categories (Macedonia 1990). Redfronted lemurs and white sifakas also respond to ground predator stimuli with calls that are associated with high arousal and that have additional social functions (Fichtel & Kappeler 2002). It is unlikely that putty-nosed monkeys do not share with vervet, Diana and Campbell's monkeys the cognitive mechanisms necessary for both production and perception of functionally referential alarm calls. It seems much more likely that environmental factors such as the presence or absence of certain predators and the utility of adopting different modes of escape (Macedonia & Evans 1993) contribute to the likelihood that differential alarm calls are manifested via a process of call individuation and learning.

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