COLLABORATIVE HUNTING IN THE YELLOW SADDLE GOATFISH

Parupeneus cyclostomus

Marc Steinegger

(Painting: Katalin Blum)

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Accepted by the dissertation committee:
Prof. Redouan Bshary, University of Neuchâtel, supervisor
Prof. Klaus Zuberbühler, University of Neuchâtel, internal examiner
Prof. Friederike Range, University of Veterinary Medicine Vienna, external examiner

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UNIVERSITÉ DE
NEUCHÂTEL

Faculté des Sciences
Secrétariat-décanat de Faculté
Rue Emile-Argand 11
2000 Neuchâtel – Suisse
Tél : + 41 (0)32 718 21 00
E-mail : secretariat.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 Marc Steinegger

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sur le rapport des membres du jury composé comme suit:

- Prof. Redouan Bshary, directeur de thèse, Université de Neuchâtel, Suisse
- Prof. Klaus Zuberbühler, Université de Neuchâtel, Suisse
- Prof. associate Friederike Range, University of Veterinary Medicine, Vienne, Autriche

Neuchâtel, le 30 octobre 2019

Le Doyen, Prof. P. Felber

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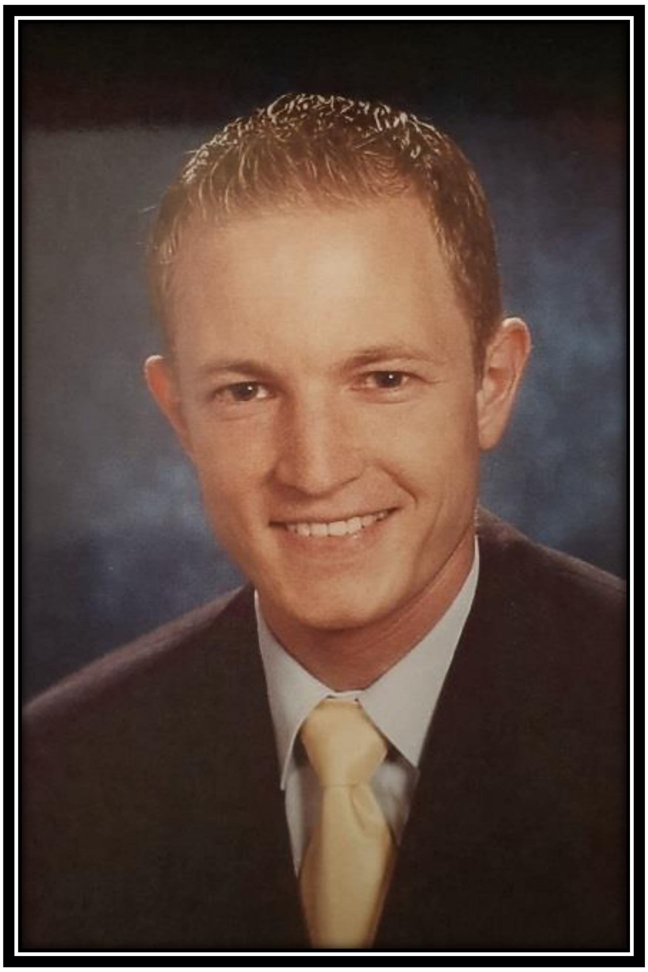

Dedicated to the memory of my beloved brother

YVES STEINEGGER

(1975 – 2008)

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GENERAL SUMMARY

Cooperation is of great interdisciplinary interest because we need to reconcile its occurrence with evolutionary theory and its emphasis on self-regarding individuals. Group hunting in various vertebrates has attracted much and continued attention from researchers because it provides the opportunity to study the evolution and stability of cooperation, the potential links between cooperation and cognitive abilities. Until now, all studies on coordinated hunting have been field observations and are hence correlative. Therefore, many conclusions are rather preliminary, like the repeatedly observed positive correlation between group size and hunting success as evidence for cooperation. In my PhD-thesis I conducted an unprecedented experimental study using yellow saddle goatfish (*Parupeneus cyclostomus*) as a study species. Yellow saddle goatfish are the first fish species described to be collaborative hunters. Individuals play different roles during a hunt (‘chasers’ and ‘blockers’), encircling prey hiding in coral crevices and trying to pry it out with means of inserting their barbels.

I designed an experimental set-up in which the yellow saddle goatfish were confronted with a) mock prey that was pulled towards a shelter with multiple entrances; b) lively mobile prey hiding in an artificial coral reef. Cameras which were installed above and below allowed me to conduct detailed behavioural analyses i) to find out which decision rules underlie collaborative hunting in the yellow saddle goatfish; ii) to test the relationship between group size and hunting success; iii) to find out which payoff matrix conforms best to the hunting scenario when yellow saddle goatfish try to pry out the prey hidden in the shelter.

The findings of my first chapter demonstrate that collaborative hunting in yellow saddle goatfish is based on simple, distance-based, self-serving decision rules. The individual that first detected the moving mock-prey always initiated a direct pursuit. Similarly, goatfish that were second to react in our experiments directly pursued the prey in almost all trials when they were in close proximity to the initiator. However, when lagging behind the initiator, the follower opted for a longer, less direct path to the prey. In the second chapter I showed that overall hunting efficiency (probability and speed of catching prey) is a function of group size. Larger groups of yellow saddle goatfish performed better and generally caught prey faster than smaller groups did. Groups of all sizes (2-4 individuals) were significantly more successful and faster than singleton hunters. Furthermore, I demonstrated that efficiency as singleton hunters did not predict hunting success when in a group. However, with my experimental set-up I could not address the question of how net calorie intake is affected by group size, as singleton success rate was already much higher than success rates observed in nature. The findings of my third chapter, where I investigated on how yellow saddle goatfish behave in order to pry out the hidden prey from the coral rock, demonstrate that actions were mainly maintained in order to obtain immediate benefits. Only the first barbel insertion decreased immediate benefits to the actor and created a public good resulting in payoff matrices similar to Snowdrift (2 players) and Volunteer's Dilemma (N-players) games. However, further insertion effort did not lower capture probability, which even increased for the individuals that touched the prey first. Hence, besides being the first to insert, barbel-insertion can be considered as self-serving. Barbel insertion effort decreased from the singleton to the group hunting level and remained constant from 2-player to N-player situations, a finding which stands in contrast to theoretical predictions. These would expect a decline in the described situations, however under the assumption that the entire game is a Snowdrift/Volunteer's Dilemma game. Interestingly, I could not find a correlation between insertion effort from singleton to group hunts, meaning that individuals seem to adjust their behaviour independently from whether they hunt alone or with others.

In conclusion, the results of my PhD-thesis show that yellow saddle goatfish predominantly hunt self-servingly by following strategies which underlie simple decision rules. Overall, I propose that seemingly complex cooperation / collaboration can be based on simple rules. The challenge for researchers studying large-brained species is hence to test whether larger brains lead to more complex decision rules or whether collaborative hunting is generally a rather simple story.

Key words
Yellow saddle goatfish; *Parupeneus cyclostomus*; collaboration; cooperation; evolutionary game theory; group hunting; decision rules; Snowdrift game; Volunteer's Dilemma.

RÉSUMÉ GÉNÉRAL

La coopération présente un grand intérêt interdisciplinaire, car nous devons la concilier avec la théorie de l’évolution et l’accent qu’elle porte sur les individus à proprement parlé. La recherche en groupe chez divers vertébrés a grandement retenu l'attention des chercheurs, car elle offre la possibilité d'étudier l'évolution ainsi que la stabilité de la coopération, les liens potentiels entre la coopération et les capacités cognitives en général. Jusqu'à présent, toutes les études sur la chasse coordonnée étaient des observations de terrain et sont donc corrélatives. Par conséquent, de nombreuses conclusions sont plutôt préliminaires, comme la corrélation positive observée à plusieurs reprises entre la taille du groupe et le succès de la chasse comme preuve de la coopération. Dans ma thèse de doctorat, j'ai mené une étude expérimentale sans précédent en utilisant comme poisson d'étude (*Parupeneus cyclostomus*). Le capucin barbet doré est la première espèce de poisson décrite comme étant un chasseur collaboratif. Les individus jouent différents rôles lors de la chasse (il y a les ‘chasseurs’ et les ‘bloqueurs’), encerclant les proies cachées dans des crevasses du récif corallien et essayant de les en sortir en insérant leurs barbeaux.

J'ai conçu une expérience dans laquelle le poisson capucin barbet doré était confronté à : a) une proie simulée qui était tirée vers un abri, plusieurs entrées étaient possibles; b) une proie vivante et mobile se cachant dans un récif de corail artificiel. Les caméras qui étaient installées au-dessus et au-dessous de l’aquarium expérimental m'ont permises d'effectuer des analyses comportementales détaillées comme i) déterminer les règles de décision qui sous-tendent la chasse collaborative chez le capucin barbet doré; ii) tester la relation entre la taille du groupe et le succès de la chasse; iii) déterminer quelle matrice de gains correspond le mieux au scénario de chasse lorsque le poisson capucin barbet doré tente de dégager la proie cachée dans l'abri.

Les résultats de mon premier chapitre démontrent que la chasse collaborative du capucin barbet doré est basée sur des règles de décision simples, basées sur la distance et sur les règles de décision s’appliquant pour soi-même. L’individu qui détectait pour la première fois la fausse proie en mouvement initiait toujours une poursuite directe. De même, les poissons qui étaient les deuxièmes à réagir dans nos expériences ont directement poursuivi la proie dans presque tous les essais

lorsqu'ils se trouvaient à proximité de l'initiateur. Cependant, lorsqu'il était à la traîne de l'initiateur, le suiveur optait pour un chemin plus long et moins direct vers la proie. Dans le deuxième chapitre, j'ai montré que l'efficacité globale de la chasse (probabilité et rapidité de capture des proies) se fait en fonction de la taille du groupe. Les grands groupes de crabes jaunes ont eu de meilleurs résultats et généralement attrapaient leurs proies plus rapidement que les petits groupes. Des groupes de toutes tailles (2 à 4 individus) étaient significativement plus performants et plus rapides que les chasseurs individuels. De plus, j'ai pu démontré que l'efficacité en tant que chasseur solitaire ne prédisait pas le succès de la chasse en groupe. Cependant, avec mon dispositif expérimental, je n’ai pu malheureusement aborder la question de comment l'apport calorique net est affecté par la taille du groupe, car le taux de réussite individuelle était déjà bien supérieur au taux de réussite observé dans la nature. Les conclusions de mon troisième chapitre, où j’ai enquêté sur le comportement du capucin barbet doré dans l’extraction de la proie cachée dans le corail, démontrent que les actions ont été principalement maintenues afin d’obtenir des avantages immédiats. Seule la première insertion de barbeau a eu pour effet de réduire les avantages immédiats pour l’acteur principal et de créer un bien public aboutissant à des matrices de gains similaires aux jeux Snowdrift (2 joueurs) et Volunteer’s Dilemma (N-joueurs). Cependant, les efforts d'insertion supplémentaires n'ont pas réduit la probabilité de capture. Cette dernière a même augmenté pour les individus qui avaient touché la proie en premier. Par conséquent, en plus d'être le premier à insérer ses barbeaux, l'insertion de barbeaux peut être considérée comme intéressée. L'effort d'insertion de barbeau a diminué du niveau individuel au niveau de la chasse en groupe est resté constant entre les situations de 2 joueurs et de N joueurs, résultat qui contraste avec les prédictions théoriques. On s’attendrait au vue de ces prédictions à un déclin dans les situations décrites, mais en supposant que le jeu entier est un jeu Snowdrift / Volunteer’s Dilemma. Il est intéressant de relever que je n’ai pas trouvé de corrélation entre l’effort d’insertion des bardeaux du chasseur solitaire et ceux de la chasse en groupe, ce qui signifie que les individus semblent ajuster leur comportement indépendamment du fait qu’ils chassent seul ou avec d’autres.

En conclusion, les résultats de ma thèse de doctorat démontrent que le capucin barbet doré chasse principalement de manière soi-même en suivant des stratégies reposant sur de simples règles de décision. Globalement, je propose la théorie selon laquelle une coopération / collaboration apparemment complexe

peut être basée sur des règles simples. Le défi pour les chercheurs qui étudient des espèces avec un cerveau dit supérieur est donc de vérifier si les grands cerveaux conduisent à des règles de décision plus complexes ou si la chasse collaborative est une histoire assez simple au final.

Mots clés

Capucin barbet doré; *Parupeneus cyclostomus*; collaboration; coopération; théorie des jeux; chasse de group; règles de décision; jeu Snowdrift; Volunteer's Dilemma.

ALLGEMEINE ZUSAMMENFASSUNG

Miteinander zu kooperieren ist von grossem interdisziplinärem Interesse, weil Kooperation mit der Evolutionstheorie und der damit verbundenen eigennützig handelnden Individuen in Zusammenhang gebracht werden möchte. Die Gruppenjagd, wie sie innerhalb verschiedener Wirbeltierarten anzutreffen ist, hat bei vielen Evolutionsforschern entsprechend grosses Interesse geweckt, da sie die Möglichkeit bietet, die Entwicklung und Stabilität der Kooperation sowie die möglichen Zusammenhänge zwischen Kooperation und kognitiven Fähigkeiten zu studieren. Bisherige Studien der kooperativen Jagd entstanden aufgrund verschiedener Feldbeobachtungen. Die dabei gemachten Schlussfolgerungen sind daher provisorisch zu interpretieren, wie zum Beispiel die oft beobachtete positive Korrelation zwischen Gruppengrösse und Jagderfolg, welche als mögliche Ursache für die Kooperation angeschaut wird. In meiner Dissertation führte ich eine umfassende experimentelle Studie mit Gelbsattel-Meerbarben (*Parupeneus cyclostomus*) durch. Die Gelbsattel-Meerbarbe ist bislang die einzig bekannte Fischart, die als kollaborativer Jäger beschrieben wurde. Gruppenmitglieder spielen während einer Jagd unterschiedliche Rollen (‘Verfolger’ oder ‘Blockierer’), indem sie die Beute in den Korallen einkreisen und versuchen, diese mittels ihrer Barteln hinauszutreiben.

Ich entwarf einen Versuchsaufbau, in dem die Gelbsattel-Meerbarben a) mit einer Scheinbeute konfrontiert wurden, die in Richtung eines Refugiums mit mehreren Eingängen gezogen wurde; b) mit lebendiger Beute konfrontiert wurden, die sich in einem künstlichen Korallenriff versteckte. Kameras wurden oberhalb sowie unterhalb der Versuchsbecken installiert und ermöglichten mir somit detaillierte Verhaltensanalysen um: i) herauszufinden welche Entscheidungsregeln der gemeinsamen Jagd der Gelbsattel-Meerbarben zugrunde liegen; ii) das Verhältnis zwischen Gruppengröße und Jagderfolg zu testen; iii) herauszufinden, welche Payoff-Matrix am besten zum Jagdszenario passt, wenn Gelbsattel-Meerbarben versuchen, die im Refugium versteckte Beute hinauszutreiben.

Die Ergebnisse des ersten Kapitels der Dissertation zeigen, dass die kollaborative Jagd bei Gelbsattel-Meerbarben auf einfachen, eigennützigen und entfernungsbasierten Entscheidungsregeln beruht. Diejenigen Individuen, die zuerst die sich bewegende Scheinbeute entdeckten, die sog. ‘Initiatoren’, leiteten

immer eine direkte Verfolgung ein. In ähnlicher Weise verfolgten Gelbsattel-Meerbarben, die in meinen Experimenten als zweite reagierten, die sog. ‘Nachfolger’, die Beute in fast allen Versuchen direkt, wenn sie sich in unmittelbarer Nähe des Initiators befanden. Wenn der Nachfolger jedoch hinter dem Initiator zurückblieb, entschied er sich für den längeren, indirekten Weg zur Beute. Im zweiten Kapitel habe ich gezeigt, dass die Gesamteffizienz der Jagd (Wahrscheinlichkeit und Geschwindigkeit des Beutefangs) von der Gruppengrösse abhängt. Grössere Gruppen von Gelbsattel-Meerbarben schnitten besser ab und fingen im Allgemeinen schneller Beute als kleinere Gruppen. Gruppen aller Grössen (2-4 Individuen) waren signifikant erfolgreicher und schneller als Einzeljäger. Darüber hinaus habe ich gezeigt, dass die Effizienz als Einzeljäger den Jagderfolg in einer Gruppe nicht voraussagt. Mit meinem Versuchsaufbau konnte ich jedoch nicht die Frage beantworten, wie sich die Nettokalorienaufnahme auf die Gruppengrösse auswirkt, da die Erfolgsrate von Einzeljägern bereits viel höher war, als die in der Natur beobachteten Erfolgsraten. Die Ergebnisse meines dritten Kapitels, in dem ich untersuchte wie sich Gelbsattel-Meerbarben verhalten, um die verborgene Beute aus dem Korallenriff herauszutreiben, belegen, dass Handlungen hauptsächlich ausgeführt wurden, um unmittelbaren Nutzen zu erzielen. Nur das erste Einführen der Barteln verringerte den unmittelbaren Nutzen für den Aktor und schuf ein öffentliches Gut (Public Good), was zur Payoff-Matrix führte, die einem Snowdrift- (für 2-Spieler) und Volunteer's-Dilemma-Spiel (für N-Spieler) ähnelt. Ein weiteres Einführen der Barteln führte jedoch nicht zu einer Verringerung der Fangwahrscheinlichkeit, sondern erhöhte diese sogar für diejenigen Individuen, welche die Beute zuerst berührten. Daher kann das Einführen von Barteln, abgesehen vom ersten Mal, als eigennützig angesehen werden. Der Aufwand, mit dem die Barteln eingeführt wurden, verringerte sich, wenn in der Gruppe gejagt wurde. Von 2-Jäger- zu N-Jäger-Situationen blieb der Aufwand hingegen konstant, ein Befund, der im Gegensatz zu theoretischen Vorhersagen steht. Diese würden nämlich in den beschriebenen Situationen einen Rückgang erwarten, jedoch unter der Annahme, dass das gesamte Spiel ein Snowdrift- / Volunteer's-Dilemma-Spiel ist. Interessanterweise konnte ich keine Korrelation zwischen dem Einführverhalten von Einzeljägern und dem Jagen in der Gruppe finden. Dies bedeutet, dass sich Einzeljäger unabhängig darüber Verhalten, ob sie alleine oder mit Artgenossen jagen.

Zusammenfassend zeigen die Ergebnisse meiner Dissertation, dass Gelbsattel-Meerbarben vorwiegend eigennützig jagen, indem sie Strategien verfolgen, die

einfachen Entscheidungsregeln zugrunde liegen. Deshalb schlage ich folgende Hypothese vor: Die scheinbar komplexe Kollaboration kann auf einfachen Regeln beruhen. Die Herausforderung für Forscher, die Arten mit grossen Gehirnen untersuchen, besteht daher darin, zu prüfen, ob grössere Gehirne zu komplexeren Entscheidungsregeln führen oder ob die gemeinsame Jagd im Allgemeinen eine eher einfache Gegebenheit ist.

Schlüsselwörter

Gelbsattel-Meerbarbe; *Parupeneus cyclostomus*; Kollaboration; Kooperation; Evolutionäre Spieltheorie; Gruppenjagd; Entscheidungsregeln; Snowdrift-Spiel; Volunteer’s-Dilemma-Spiel.

GENERAL INTRODUCTION

I.1 On the evolution of helping behaviour

Helping is a behaviour with which an individual increases the fitness of one or several other individuals. Intuitively, this raises many questions for evolutionary biologists because natural selection favours a specific behaviour only then if it increases the individual's own average lifetime fitness. Nevertheless, helping is widespread in nature and can be found on all levels of organisation, ranging from unicellular organisms to eusocial insects and complex animal and human societies (Clutton-Brock et al., 2009; Dugatkin, 1997; Maynard Smith and Szathmary, 1997).

In one form of helping, termed altruism, an individual helps others without increasing its own direct fitness (Lehmann and Keller, 2006). Hamilton (1964a,b) showed that such altruistic behaviour can persist in nature when the act of helping is directed to kin. According to Hamilton's rule (b x r > c), the inclusive fitness of an actor (the helper) is increased if the benefits to the receiver (b) multiplied by the degree of relatedness (r) between actor and receiver outweighs the costs (c) of the actor. The so-called inclusive fitness includes both the direct fitness, which is measured on its own reproductive success, as well as the indirect fitness, i.e. the success in reproduction of its kin (West et al., 2007).

In the other form of helping, termed cooperation, all participants (actor & recipient) increase their direct fitness on average (Lehmann & Keller 2006). This may turn into a problem that can be best illustrated with the well-known Prisoner's Dilemma game (PD) (Luce and Raiffa, 1957; Tucker, 1950). In the PD game, players can either cooperate or defect, leading to different payoff distributions. The matrix of the standard form of the PD game (Figure 1) shows how mutual cooperation yields three units to each player, while mutual defection yields only one. In the asymmetric situation where one player defects and the other cooperates, the former receives five units while the latter zero. Mutual cooperation is therefore better than mutual defection, but a player immediately receives even more units by defecting, regardless of the other player's behaviour. This leads to the situation in which defection is the only evolutionary stable strategy (ESS) (Maynard Smith, 1982) resulting in a social dilemma (Dawes, 1980).

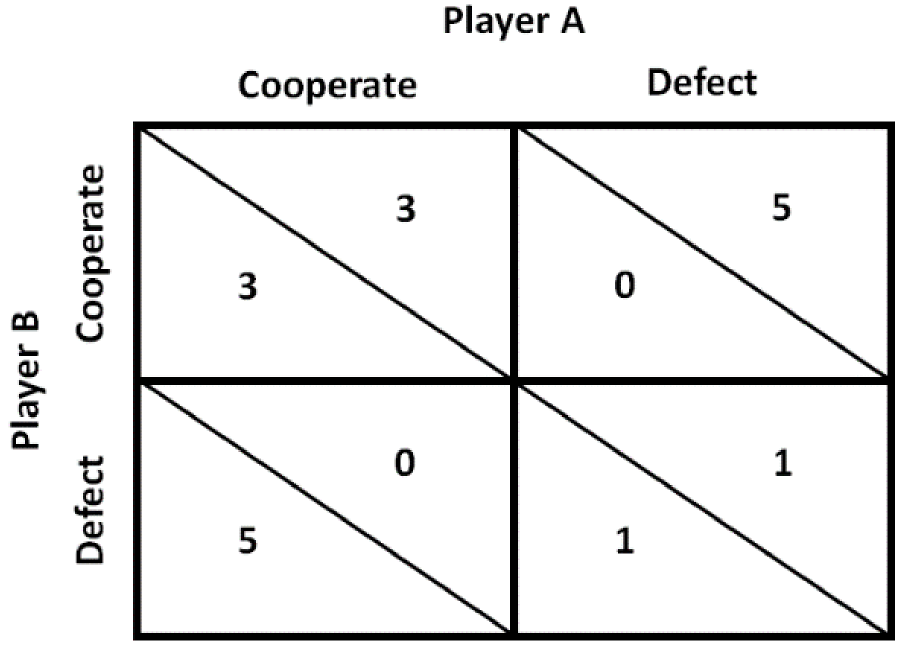

Figure 1. The Prisoner's Dilemma. The payoffs for both players are given in the matrix by numerical values. Mutual cooperation would provide the best payoff for the team (3 + 3). However, for each player the better option is to defect, regardless of whether the partner cooperates or defects. The game follows the definition of T > R > P > S, whereas T (payoff = 5) is the temptation to cheat, R (payoff = 3) the reward for mutual cooperation, P (payoff = 1) the punishment for mutual defection and S (payoff = 0) the suckers payoff for cooperation with a cheating partner (adapted from Raihani and Bshary, 2015).

The PD Game illustrates that cooperation is often an investment. Therefore, the question arises how investments may yield future benefits. Despite this conceptual issue, cooperation is frequent in nature among unrelated individuals of the same species as well as between individuals of different species. This is termed mutualism (West et al., 2007) (e.g. coordinated hunting between groupers (*Plectropomus pessuliferus)* and giant moray eels (*Gymnothorax javanicus*) (Bshary et al., 2006)). Thus, natural selection has repeatedly found ways that individuals can ensure that stable cooperation is achieved, i.e. that partners cooperate with each other (Dugatkin, 1997).

I.2 Evolutionary Game Theory

Evolutionary game theory originated in economics (Von Neumann and Morgenstern, 1944) and provides a key approach to study the evolution of cooperative behaviour focusing on different strategies and decision rules (Maynard Smith and Price, 1973). A strategy defines how an individual will behave in any given situation (Maynard Smith, 1982) and a decision rule describes the condition under which an individual chooses a specific behaviour from the available options (Bshary and Bergmüller, 2008). In the strategy Tit-for-Tat, for example, the decision rule defines that player A cooperates if player B cooperated in the previous round, and player A cheats when previously cheated by player B, respectively (Axelrod and Hamilton, 1981).

Up to now, a variety of studies embedded evolutionary game theory into their empirical research and were able to demonstrate strategies and decision rules, invoking models based on the Prisoner's Dilemma which promote cooperation in unrelated individuals. Some studies were conducted on humans (e.g. Axelrod and Hamilton, 1981; Fehr and Gächter, 2000; Wedekind and Milinski, 2000), others on non-humans (e.g. Connor, 1986; Milinski, 1987). Different control mechanisms such as punishment (Bshary and Grutter, 2005; Clutton-Brock and Parker, 1995; Fehr and Gächter, 2000; Fehr and Gächter, 2002), partner switching (Bshary and Grutter, 2005) or image-scoring (e.g. Bshary and Grutter, 2006; Wedekind and Milinski, 2000) were found to prevent partners from cheating.

I.3 Putative links between cooperation and cognitive abilities

Examples of cooperation based on strategic behaviour can exist even among species that lack a brain (e.g. mutualism between leguminous plants and Rhizobia (Kiers et al., 2003)). Regarding highly complex forms of cooperation, (e.g. collaborative hunting in which co-operators coordinate their action in space and time and perform different roles (Boesch and Boesch, 1989)), certain cognitive abilities are most likely involved. A collaborative hunting individual must learn to perform different behaviours and at the same time to notice the outcomes and actions of group members in order to be successful (Brosnan et al., 2010). Furthermore, cognition may also play a key role for strategic decisions, regarding the best behavioural option for a given situation (Brosnan et al., 2010). Therefore, the question whether cooperation requires cognitive abilities cannot simply be answered with yes or no, especially when regarding all forms of cooperation.

I.4 Forms of cooperation

First, it must be distinguished whether cooperation takes place between two players or N-players, two situations which are fundamentally different. In the latter, contributions can neither be directed nor withheld to specific individuals of the group, which results in a public good (Bshary, 2010).

I.4.1 2-Player Games

Different concepts exist to explain cooperation between two players. For a detailed overview of nine basic concepts see Bshary (2010) and Bshary and Bergmueller, (2008). In three of the concepts, i.e. by-product benefits (Bshary et al., 2016; formerly by-product mutualism (Brown, 1983)), positive direct as well as positive indirect pseudoreciprocity (Bshary and Bergmueller, 2008); two forms of positive pseudoreciprocity (Connor, 1986)), individuals outweigh their investments either by immediate payoffs or assured delayed payoffs. An example of the former are golden jackals (*Canis aureus*), which increase their hunting success up to six times compared to hunting as singletons (Lamprecht, 1978). Assured delayed payoffs can be traced in leaf cutter ants (tribe: Attini), which invest in farming fungi that as a self-serving response grows healthy colonies yielding by-product benefits to the ants (Mueller et al., 2005) or cleaner fish (*Labroides dimidiatus*), which do a better job in the presence of bystanders that self-servingly prefer cooperative cleaner fish (Bshary and Grutter, 2006)). Its existence can easily be explained because the act is self-serving. Notice that these three concepts are not restricted to 2-player games, but theoretically also work for N-player games (Bshary, 2010).

In the remaining six concepts, cooperative behaviour is linked to delayed payoffs, whereby, as mentioned earlier, various partner control mechanisms can prevent partners from cheating, which makes it very likely that certain cognitive abilities (i.e. learning, individual recognition and memory (Dugatkin, 2002)) are necessary, especially for the cases in which the cooperating partner or both co-operators are mobile.

I.4.2 N-Player Games

Cooperation in N-player situations differs from 2-player games in that it produces a public good because a contribution made by an individual will not only benefit one specific member in the group. This can lead to the following problem explained in an example with three players (A, B, C). In a first round, Player A and B cooperate by contributing to the public good, while Player C cheats by not contributing, resulting in the highest payoff for C. In the second round, Player B also cheats by not contributing, with the consequence that there will not only be a negative effect on the previous cheater C, but also on the co-operator A. Briefly said: not contributing to the public good affects all group members. The potentially resulting problem from the scenario described above can be illustrated with a N-player Prisoner's Dilemma (NPD) a specific type of Public Goods game (Archetti and Scheuring, 2011). In the NPD, similar to the above described PD, only defecting is the evolutionarily stable strategy (Maynard Smith, 1982), resulting in the so-called "tragedy of the commons" (Hardin, 1968). Many studies have been conducted on humans to explain how cooperation can be achieved in Public Goods games via partner control mechanisms (Wedekind and Milinski, 2000, Fehr and Gächter, 2000, Fehr and Gächter, 2002).

However, it has also been shown that individuals might cooperate in a self-serving way, while partners earn by-product benefits (Brown, 1983). Group living provides such an example, where individuals can, for example, benefit from the dilution-effect, meaning that many group members will decrease the probability of each single individual of being captured, or from an earlier predator detection (selfish herd (Hamilton, 1971)).

I.4.3 The Snowdrift Game and the Volunteers Dilemma Game

In contrast to the Prisoner's Dilemma, different group games have been developed with different payoff matrices, for example the Snowdrift game (SD) (Sugden, 1986), also known as Hawk-Dove (Maynard Smith and Price, 1973) or game of Chicken (Rapoport and Chammah, 1966). The payoff matrix of the SD differs from the PD in the best possible response to a partner's defection: The best response is to cooperate with $T > R > S > P$ (Hauert and Doebeli, 2004). This game also exists in the N-Player version and is called Volunteer's Dilemma (VD) (Diekmann, 1985).

Recently, scientists have argued that the payoff distribution of the Volunteer's Dilemma, which is a step function of the individual's contributions, might be more applicable to natural cooperation systems than the payoff distributions of an NPD, which is a linear function (Archetti, 2009a; Archetti and Scheuring, 2011; Archetti and Scheuring, 2012; Sherratt et al., 2009). A reasonable explanation is that just one or a few individuals can establish the public good by fulfilling a costly act (Archetti, 2009b). Examples are the formation of fruiting bodies in social amoebas (e.g. the social amoeba (*Dictyostelium discoideum*) (Bonner, 2009)), the production of yeast (Gore et al., 2009), or alarm calling in animals (e.g. meerkats (*Suricata suricatta*) (Clutton-Brock et al., 1999)).

I.5 Cooperative hunting provides a framework to study cooperation

Cooperative hunting in which two or more individuals go after the same prey is a widely distributed form of cooperative behaviour in vertebrates (Packer and Ruttan, 1988). Cooperative hunting is well-known among a range of mammals, including chimpanzees (Boesch and Boesch, 1989), carnivorans (Creel and Creel, 1995) and cetaceans (Connor and Wells, 2000; Gazda et al., 2005), as well as in some birds (Bednarz, 1988; Leonardi, 1999; Yosef and Yosef, 2009), crocodilians (Dinets, 2015) and fish (Arnegard and Carlson, 2005; Bshary et al., 2002; Herbert-Read et al., 2016) and has attracted wide interest. This is because it warrants an approach that integrates functional questions about the evolution of cooperation in mechanistic questions on the levels of coordination between participants, which is then linked to the cognitive challenges involved in joint hunting.

Collaborative hunting, where group members coordinate their actions in space and time and play different complementary actions (e.g. driving, chasing and blocking) (Boesch and Boesch, 1989), presents the highest form of cooperation. The occurrence of collaboration in species with high cognitive abilities is particularly interesting for researchers. This could result (a) either because this form of collaboration is cognitively demanding, thereby precluding many species from this form of cooperative behaviour, or (b) because collaborative hunting is a social activity that selects for high cognitive capacity, i.e. the social intelligence hypothesis (Humphrey, 1976).

Currently, published evidence for collaborative hunting is found mainly in larger-brained mammalian species (where it seems restricted to carnivorans (Bailey et al., 2013), bottlenose dolphins (Gazda et al., 2005), orcas (Smith et al., 1981) and chimpanzees (Boesch and Boesch, 1989)). Interestingly, it recently has been discovered that smaller-brained vertebrates also perform intraspecific collaborative hunting, on which, however, only a hand full of studies have been conducted up to date (a few bird studies, e.g. harris hawks (*Parabuteo unicinctus*) (Bednarz, 1988), one study on crocodilians (Dinets, 2015) and only one in a fish species, i.e. yellow saddle goatfish (*Parupeneus cyclostomus*) (Strubin et al., 2011)). In fish, published evidence for collaborative hunting is found in interspecific associations (Bshary et al., 2006), where partner species act more or less as they would on their own. Thus, individuals in interspecific associations do not show the flexibility in behaviour that characterises intraspecific collaboration. Therefore, it has been a major discovery to find this collaborative behaviour in yellow saddle goatfish, a coral reef fish that hunts in groups, where individuals act as chasers and blockers, with individuals encircling prey hiding in corals in a joint effort to pry the prey out (Strubin et al., 2011).

I.6 The PhD thesis topic

Strubin et al. (2011) discovered the first fish species to hunt in a collaborative way with their field study focusing on the hunting behaviour of yellow saddle goatfish. These findings indicate that collaborative hunting does not need to be as cognitively demanding and therefore restricted uniquely to animals with larger brains as previously believed (Boesch and Boesch, 1989; Melis et al., 2006). Another relevant factor of this discovery is that yellow saddle goatfish provide a huge advantage over apes, carnivores or cetaceans to study collaborative hunting, because they can be brought into the laboratory and subjected to experimental manipulation. As it stands, all the evidence of the collaborative nature of joint hunting is based on observations and therefore correlative. It can therefore not be excluded that the increased hunting success of groups relative to solitary individuals is due to other factors: for example, solitary hunts may occur when individuals are generally satiated or when the probability of success is low while group hunting occurs when all individuals are motivated and when capture is likely to occur.

The aim of my PhD Thesis was thus to study collaborative hunting experimentally for the first time in order to test questions regarding the adaptive nature of collaborative hunting, the underlying mechanisms (i.e. decision rules) and the strategies employed by individuals during hunts. The hunting action of yellow saddle goatfish can be divided into two phases. During the first phase, one group member becomes a chaser and accelerates towards the prey, while partners spreading out in order to block the prey's potential escape route (Strubin et al., 2011).

My aim was to identify which type of decision rules underlie the strategic behaviour of hunting yellow saddle goatfish for this phase of the hunt. The first phase most frequently ends in the prey escaping to a crevice, which is the starting point of the second phase, in which individuals of yellow saddle goatfish insert their barbels into the substrate in order to pry out the prey. For the second phase I aimed to find an answer to the question of whether hunting success is a function of group size and which strategic game (PD/NPD or SD/VD) best describes the joint hunt. The study on yellow saddle goatfish will thus provide unique data sets on key aspects of collaborative hunting.

I.7 General methodology

I.7.1 The study species

Yellow saddle goatfish *Parupeneus cyclostomus* (Lacepède, 1801) belong to the family of the Mullidae (goatfish) and are found on corals, bottoms of reef flats, seaward reefs and lagoons (Randall, 1983). They are diurnal hunters and feed primarily on small fish, but also on invertebrates such as crustaceans, cephalopods and small gastropods (Randall, 1983). In order to verify that in the Dahab area yellow saddle goatfish have a diet similar to that described in literature, I conducted a stomach content analysis on individuals (Appendix, A1). Similar to all other goatfish, they are characterized by having two well-developed barbels (Figure 2, left), which are highly maneuverable organs containing taste buds underneath their mouth (McCormick, 1993). They usually hunt in pairs (Figure 2, right) or small groups consisting of three to five individuals of similar size and are rarely observed in larger groups (Strubin et al., 2011). While single individuals often hunt for invertebrates in sandy areas, pairs and groups of yellow saddle goatfish hunt over the coral reef top, mainly on small fish hiding in shelters (Randall, 1983, Strubin et al., 2011). Hunting groups of yellow saddle goatfish are quite stable with individuals hunting together over several attempts (Strubin et al., 2011). Yellow saddle goatfish are open-water spawners. It is therefore most likely that individuals of hunting groups are not close kin, since egg and larvae stage are pelagic. This has been genetically tested on other open water spawners (Avise and Shapiro, 1986).

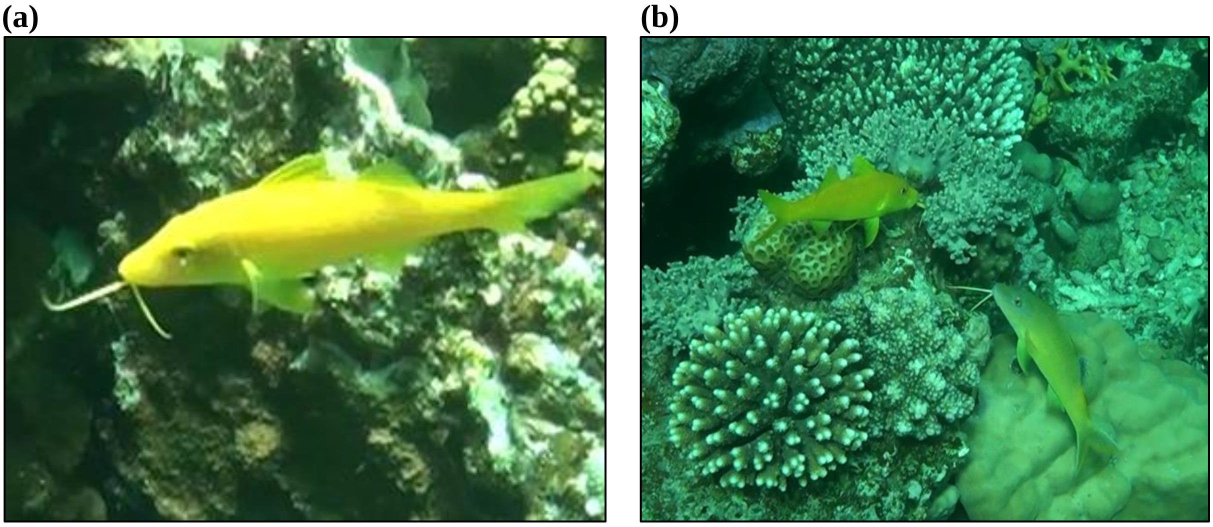

Figure 2. (a) Yellow saddle goatfish on a coral reef with extended barbels. **(b)** Two individuals encircling a prey hidden in a coral.

I.7.2 Study site, capturing and handling of fishes

All experiments for chapters one to three were conducted in the years 2010 and 2011 at the laboratory of the Dahab Marine Research Center (DMRC) on the Red Sea, located in South Sinai, Egypt. As all yellow saddle goatfish exhibit diurnal feeding activity, fish were captured during daytime (between 6 a.m. and 5 p.m.) in the Dahab Laguna or nearby dive spots (Figure 3) while scuba diving in depths between 2 and 13 meters. I tried to catch yellow saddle goatfish with an approximate total length of 15 to 30 centimeters. Smaller individuals do not frequently show coordinated hunting, while too large animals are not handy to conduct the experiments with (personal observations). This size range still leaves a broad spectrum of available fish. Furthermore, yellow saddle goatfish group by size (Strubin et al., 2011), and individual length differences should therefore not vary too much.

Figure 3. Aerial photograph of the Dahab Laguna and surroundings. Red circles next to numbers indicate where yellow saddle goatfish were captured. 1) Le Méridien, Dahab Resort; 2 & 3) Laguna beach; 4 & 5) Islands dive site (Credit: GeoEye 2010).

Fish were captured with the aid of a barrier net of 30m^2 (stretched mesh size: 20mm). After capturing, the fish were removed from the net while wearing neoprene gloves to reduce skin and mucus damage as well as to decrease the transfer of diseases (Figure 4a). The fish were transferred into a holding net (Figure 4b) and slowly brought to the surface (one meter every three minutes) to avoid rapid inflation of the swim bladder. During transportation from the sea to the laboratory, the fish were kept in opaque water tanks to reduce stress. In the laboratory, the fish were marked with the fin clipping method for individual recognition during the experiments. Fin clipping is a widely used method in marking fish and has no measurable effect on mortality or swimming ability (Ward, 2003). Then, the fish were placed in one of the two experimental tanks (Figure 5). To minimize the stress prior the experiments, the fish were measured (total length) and weighed on the day before being released to the place of capture.

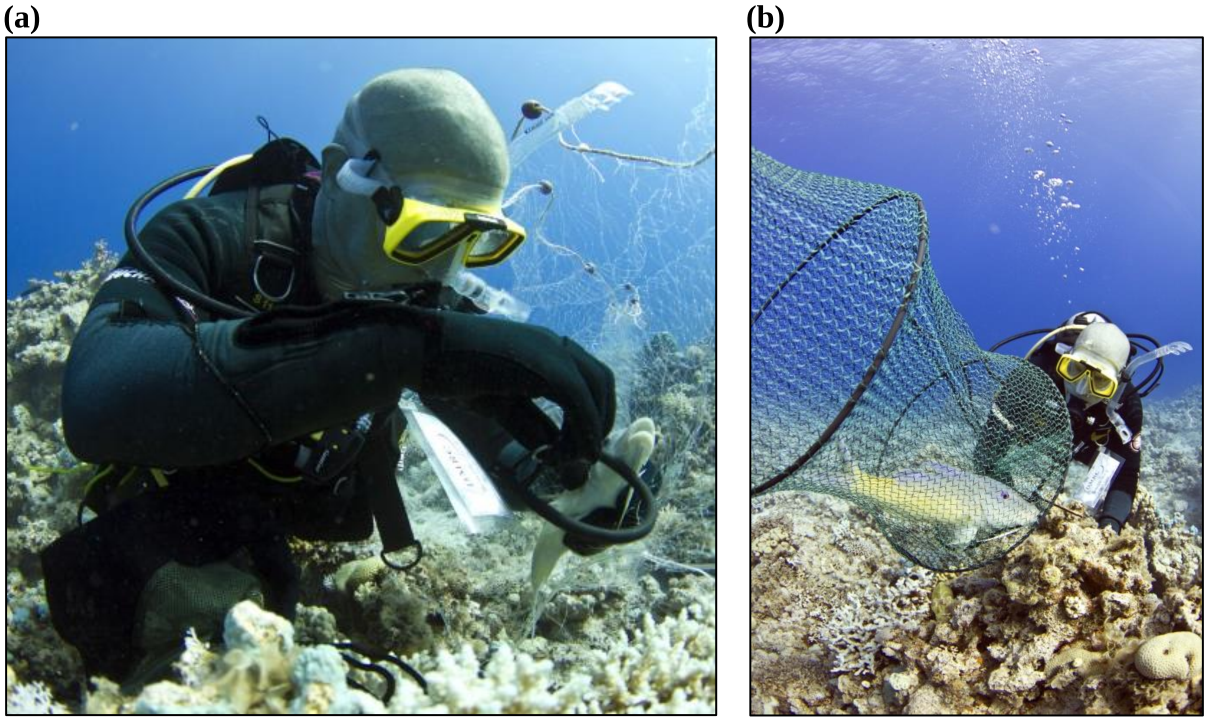

Figure 4. (a) Handling of fish during capture. To minimize damage, individuals were touched with neoprene gloves. Net lines that entangled the fish were gently cut with scissors. **(b)** Yellow saddle goatfish in a holding net (Credit: Horen Stalbe).

I.7.3 Experimental set-up

I developed an experimental set-up that allowed me to study the hunting behaviour of yellow saddle goatfish in the laboratory. In brief, I designed a small, artificial reef in a round water tank to mimic the natural habitat of yellow saddle goatfish (Figure 5a). An opaque partition wall was placed on one side in order to manipulate the group size of hunting individuals. On the other side, a transparent acryl glass was glued into the bottom. On top of the acryl glass I placed an artificial reef “food stone” with a transparent, exchangeable acryl glass tunnel system underneath. Depending on the research question, I used different tunnel systems. For chapter one I used a system with four entrances to which I pulled a mock prey via a fishing line. For chapters two and three I used tunnel systems of different sizes with different numbers of transparent/opaque partition walls for training and experimental purpose (Figure 5b). The food stone was connected to a vertical PVC-tube, which I either used to pull the mock prey via the fishing line (chapter one) to the center of the food stone or to provide food (dead or alive) for training and experimental purposes (chapter two and three).

Two cameras were installed, one above the tank and one underneath the food stone, to record the experiments. This experimental set-up allowed me to manipulate the group size and collect information on individual behaviour during joint hunting. It further helped me to pay particular attention to the yellow saddle goatfish's use of their pair of barbels. The barbels of goatfish are highly sensitive and mobile (Randall, 1983). They are used to detect hiding prey. Yellow saddle goatfish regularly insert them into crevices when they surround a coral patch with prey hiding inside (Strubin et al., 2011). The camera installed below the artificial reef (Figure 5a) allowed me to analyse under which conditions an individual inserted its barbels into the tunnel system and whether this behaviour increased either its own success rate or the success of others, in case the prey was flushed away / fled from the movement and hence approached another fish too closely.

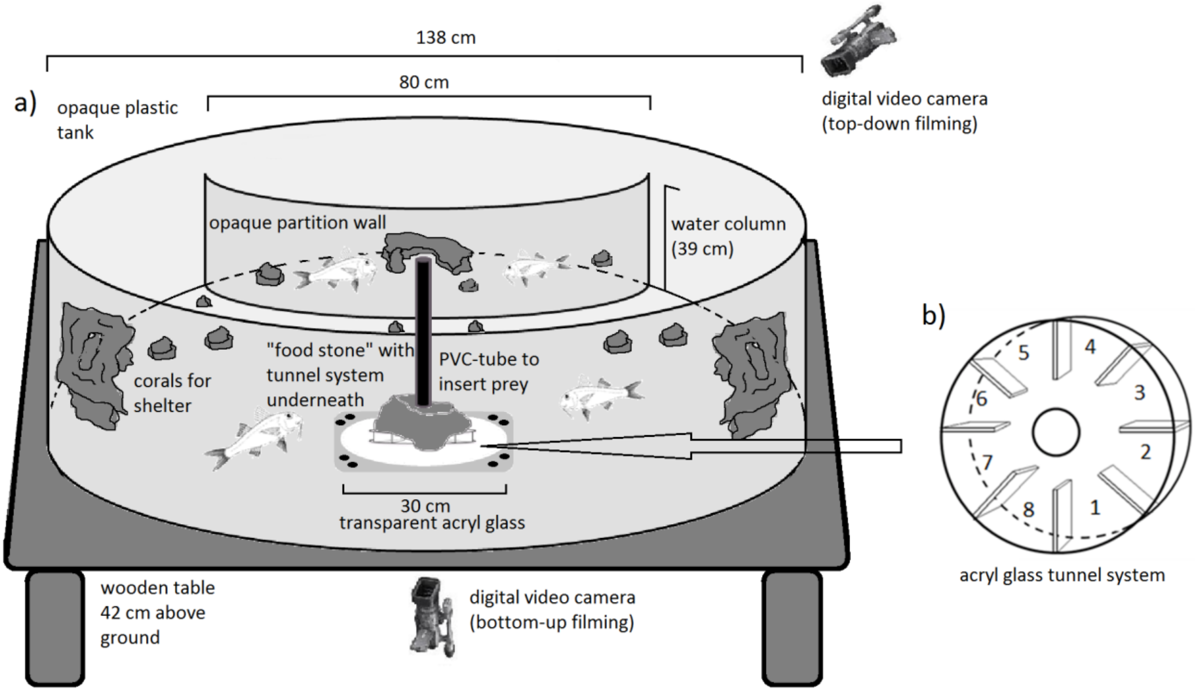

Figure 5. Illustration of one of two experimental tanks: **(a)** Round plastic tank with 138 cm diameter and a water column of 39 cm. The artificial coral reef "food stone" with a PVC-tube on top of it to insert different prey types or to pull a fishing line with a fake prey was placed over a round transparent acryl glass of 30 cm diameter. Two installed cameras (top and bottom view) to monitor the behaviour of the fish and the prey. Several large coral rocks placed on left and right side of the tank served as shelters. One centimetre of coral sand layer covered the ground and a few small coral rocks to imitate a natural habitat and to provide

additional shelter. An opaque partition wall with small holes for water exchange in the back of the tank that separated experimental- from non-experimental fish. The experimental tank was constantly supplied with fresh saltwater (about 180 litres/hour) and oxygen. **(b)** One of the used transparent acryl glass tunnel systems that was underneath the “food stone”. The one used in the figure was used for training purposes with eight similar sized compartments separated by eight similar sized transparent acryl glass partitions.

I.8 Thesis chapters

The aim of the *first chapter* was to investigate collaborative hunting in yellow saddle goatfish under experimental laboratory conditions for the first time. In the field, individuals act both in the role of chaser and blocker, with the former chasing directly after a fleeing prey while the latter deviate around obstacles like corals and coral rubble to meet the chaser behind (Strubin et al., 2011). Strubin et al. (2011) could not find any evidence for role specialisation in their field study, predicting that potential factors such as prey-proximity or prey-detection could induce the adoption of a specific role. I simulated a hunting scenario by exposing pairs of yellow saddle goatfish to a fake prey that was rapidly pulled from a shelter to one of two positions in the artificial coral reef. Having two entrances mimics the natural condition where hiding holes are limited. I asked the following questions: does the leading individual pursue the closest way towards the prey? Is there a critical distance of lagging behind where the second individual switches from a co-pursuit to deviation around the obstacle? Does such a deviation lead to the second individual reaching the second hiding entrance sometime before the leading individual? Are paired individuals equally likely to be leader or follower, or is there evidence for role specialization? Importantly, as there was no reward in any of the trials, I studied spontaneous decisions by my subjects that would not change due to variation in success.

The aim of the *second chapter* was to test whether hunting success is directly contingent on group size, which has never been attempted in the laboratory and under fully controlled conditions including live prey. Since yellow saddle goatfish are not constrained to a specific role during a hunt (Strubin et al., 2011) (I expected this hypothesis would be supported by the results from chapter one), individuals can easily be replaced, and the group size manipulated. Furthermore, yellow saddle goatfish do not share their prey among the group members and eat it whole. Therefore, I expected the active participation of all group members during the hunt and excluded free riders that mainly occur in larger groups where the killed prey is shared among the group hunting individuals (Packer and

Ruttan, 1988, Creel and Creel, 1995). For this study, I created a hunting scenario similar to the natural situation, namely that a prey had initially escaped into shelter, using an artificial coral reef system that was slightly different from the one used in the first chapter. I divided the hunting scenario into three different periods and measured (i: time to detect the prey; ii: time to touch the prey; iii: time to catch the prey) together resulting in the total duration of the hunt. I expected a decrease in time for all three periods, however not necessarily proportional to group size. Furthermore, I was interested in a potential individual variation in hunting success. More specifically, I observed whether individuals that performed well during single hunts were also more likely to catch prey when hunting in a group.

The aim of the *third chapter* was to investigate which game is played by yellow saddle goatfish. Chapter three was built on the data collected during the second chapter and required further video analyses. I paid particular attention to the yellow saddle goatfish's use of their pair of barbels. Hunting individuals regularly insert them into crevices when they surround a coral patch with prey hiding inside (Strubin et al., 2011). I investigated the questions: How does barbel-inserting-effort translate into capture probability? If the individual that puts most effort into the insertion of its barbel is the one most likely to catch the prey, then insertion may only yield by-product benefits to others but is self-serving (i.e. by-product mutualism (Brown, 1983)). If success is reduced, then it would be a Snowdrift/Volunteer's Dilemma game. If success is absent, then the result mirrors a Prisoner's Dilemma/N-Player Prisoner's Dilemma game. Depending on the outcome, I expected different adjustment strategies in groups. A decline from singleton hunters to pair hunters/larger groups would be evidence for a conflict of interest (Bshary et al., 2016). Further I observed how inserting the barbels first or touching the prey first affected the success. Finally, I checked whether total length or body condition might have an influence on the level of barbel-inserting-effort.

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CHAPTER 1 | SIMPLE DECISION RULES UNDERLIE COLLABORATIVE HUNTING IN YELLOW SADDLE GOATFISH

Authors: Marc Steinegger[1], Dominique G. Roche[1] & Redouan Bshary[1]

Affiliation: [1]Institute of Biology, University of Neuchâtel, Emile-Argand 11, 2000 Neuchâtel, Switzerland

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Abstract

Collaborative hunting, the coordination of animal behaviour in space and time to capture prey, is reported in several vertebrate species. However, previous studies are observational, hampering our ability to identify individual decision rules that result in collaboration. We experimentally investigated collaborative hunting in yellow saddle goatfish (*Parupeneus cyclostomus*) by exposing pairs to a mock prey that fled to an artificial shelter with multiple entrances. The first fish to initiate the chase (the 'initiator') was always closest to the prey and pursued it directly in its path. Conversely, the behaviour of the second goatfish (the 'follower') depended on its spatial position relative to the initiator. When the follower was less than one body length behind the initiator, it also accelerated directly towards the prey in over 95% of cases. However, if the two goatfish were separated by a distance of one body length or more, the follower chose a less direct route to reach the prey in 87% of cases. In this scenario, the follower often reached the prey's more distant refuge first, which might increase its hunting success or block the prey's escape path under natural conditions. Our findings suggest that coordinated hunting behaviour can result from simple, self-serving decisions.

Keywords: cooperation, coordination, gold-saddle goatfish, group hunting, *Parupeneus cyclostomus*, Red Sea

1.1 Introduction

Collaborative hunting, the coordination of prey capture in space and time, has been documented in a handful of vertebrate species (Boesch and Boesch, 1989; Gazda et al., 2005; Stander, 1992), and is often perceived as an advanced hunting strategy requiring large brains that allow high levels of coordination. However, recent studies have shown that interspecific collaborative hunting between small-brained species such as fishes (e.g. grouper and moray eel) and fish and invertebrates (grouper and octopus) is not only possible but can also be highly sophisticated, involving some form of planning, referential gestures and partner choice (Bshary et al., 2006; Vail et al., 2013, 2014). In collaborative hunts that involve partners of different species (e.g. moray eels and groupers (Bshary et al., 2006)), coordination might be easier to achieve because each partner performs a specialized role corresponding to its specific ecology. Conversely, intraspecific collaborative hunting is thought to require more advanced cognitive abilities because functionally similar individuals must learn to perform different tasks (Strubin et al., 2011). For example, studies have shown that large-brained mammals such as lions and dolphins are capable of specializing in roles such as chasing prey or blocking the prey's escape path to facilitate capture by the group (Gazda et al., 2005; Stander, 1992). Interestingly, cases of intraspecific collaborative hunting have also been recently documented in smaller-brained vertebrates such as birds (Bednarz, 1988), reptiles (Dinets, 2015) and fish (Strubin et al., 2011). Therefore, contrary to previous beliefs (Boesch and Boesch, 1989; Melis et al., 2006), current evidence suggests that collaborative hunting does not necessarily rely on cognitive processes that require large and complex brains. Rather, it seems possible that sophisticated hunting strategies can also emerge in relatively smaller-brained species in response to ecological needs. While it is extremely challenging to study underlying cognitive processes, it is feasible to identify the decision rules that lead to collaborative hunting and determine whether they can be simple.

We know little about the decision rules underlying intraspecific collaborative hunting because all studies to date have relied exclusively on field observations. Observational data are essential for documenting the natural occurrences of such behaviour but cannot pinpoint the specific decision rules that result in coordinated action. This limitation arises because, in the field, each hunt becomes idiosyncratic due to large variation in parameters such as habitat structure, predator and prey group size, predator motivation, or the identity, location and behaviour of prey. Such variation makes it difficult to identify the individual strategies that lead to collaborative hunts. For example, do participants display behaviours that reduce their own probability of capturing prey while increasing the probability of capture by other group members? Such helping, in which individual actions increase group benefits at a personal cost, requires an explanation centred around kin selection (Hamilton, 1964a, b), reciprocity (Trivers, 1971) based on a Prisoner's Dilemma or a Volunteer's Dilemma-type payoff matrix (Bshary et al., 2016; Raihani and Bshary, 2011), or pseudoreciprocity based on interdependence between hunting members (Connor, 1986; Roberts, 2005). In the absence of such behaviour, collaboration is said to result from simple self-serving decisions that lead to by-product benefits (Brown, 1983).

Understanding which ‘game’ partners are playing can help us identify how challenging it will be to achieve stable collaborative hunting. For example, individual investments in an iterated Prisoner's Dilemma-type game warrant more complex decision rules than self-serving decisions, which only require that one partner's behaviour is flexibly adjusted to the behavioural decisions of others. Game theoretic scenarios can be further complicated when a successful hunt leads to a carcass that is sharable, at least in principle, as is typically the case in hunts by lions and chimpanzees (Boesch and Boesch, 1989; Stander, 1992). By contrast, when a captured prey is swallowed whole, as in the case of hunting crocodiles and goatfish (Dinets, 2015; Strubin et al., 2011), the ‘game’ is simpler, facilitating the identification of decision rules employed by the participants.

Here, we examined the individual decisions of yellow saddle goatfish (*Parupeneus cyclostomus*) during group hunts in controlled laboratory experiments. Our objective was to identify decision rules that are likely to underlie collaborative hunting in the wild. In nature, *P. cyclostomus* hunts for invertebrates and prey fishes either alone or in small groups, typically consisting of two to six individuals (Figure 1). In group hunts, members regularly adopt one of two roles: either attacking and chasing prey, or blocking their escape path (Strubin et al., 2011). The attacking goatfish directly pursues a fleeing prey in its path while other group members deviate around obstacles such as coral heads, thus preventing the prey from escaping. We hypothesized that factors such as an individual's proximity and ability to detect a prey determine which function each goatfish adopts because a previous observational study on *P. cyclostomus* found no evidence of role specialization in this species (Strubin et al., 2011). We simulated a hunting scenario by exposing pairs of goatfish to a mobile (mock) prey that sought refuge under a shelter with multiple entrance points. We then tested whether goatfish displayed collaboration by adopting different spatial routes in pursuit of the prey and what specific conditions resulted in collaborative hunts. The absence of a food reward in our experiments meant that we studied spontaneous decisions by animals that were not affected by variation in prey capture success.

1.2 Material and methods

1.2.1 Study species and experimental set-up

Experiments were conducted during three field seasons at the Dahab Marine Research Center (DMRC) on the coast of the Red Sea, Egypt: in the summer of 2010, and in the spring and autumn of 2011. During each field season, we captured eight *P. cyclostomus* using a 30 m^2 barrier net (stretched mesh size 20 mm) and transported them in 20 l buckets to an air-conditioned room at the research station (27.0 ± 2.0°C, actual variation). Artificial light was provided following a L : D cycle that matched the local sunrise and sunset with 10 min of twilight at the beginning and end of the light phase. Fish were held in groups of four individuals in two separate round tanks (138 cm diameter, 39 cm water height) supplied with seawater at approximately 180 $l\ h^{-1}$ via a flow-through system with water pumped directly from the Red Sea. We grouped fish based on body size, housing the four smallest and the four largest together. The mean (±s.d.) total length (TL) and body weight of the 24 fish collected across the three field seasons were 190 ± 26.7 mm and 60 ± 38.91 g. Fish were individually recognizable based on differences in body size, coloration patterns and markings (Strubin et al., 2011).

All experiments were conducted in the fish's housing tanks. An opaque partition was placed on one side of the tank to isolate non-experimental fish from experimental ones (Figure 2). Holes in the partition allowed water exchanges with the rest of the tank and air stones provided mixing and aeration. The bottom of the tank was covered in a 1 cm layer of sand. Coral rocks were used to create two shelters at the periphery of the tank such that they did not obstruct the central area (Figure 2).

1.2.2 Feeding and training

Fish were fed small pieces of fish *ad libitum*, once a day in the late afternoon. Uneaten food was removed from the tank on the same day. Prior to the feeding session, we trained fish to pursue moving prey, beginning on day three after capture. All four fish were present in the tank during this training period. First, a food item was attached to a fishing thread and dangled in front of individuals to mimic a live prey. All fish fed in this way within 3 days from the start of training. Fish were then trained to chase a food item pulled at high velocity across the bottom of the tank. A small lead weight was attached to the end of the thread, next to the prey, so it would remain on the substrate. The start and end positions of the prey were random across trials and the prey was pulled out of the water before the goatfish could reach it. Training was completed in one tank when all four goatfish rapidly accelerated in pursuit of the prey, which is typical of this species's hunting behaviour in the wild (Strubin et al., 2011). Completing both of these training phases took between 7 and 10 days.

1.2.3 Experimental procedure

Experiments were performed on pairs of goatfish. In a given tank, one pair remained in the experimental arena and the other was isolated behind the partition described above (Figure 2). After placing the partition, we waited 30 min before starting a trial. Each pair participated in 16 trials during field season 1, and 20 trials during seasons 2 and 3. Consecutive trials were separated by 3–4 min.

To initiate a trial, the experimenter used a hook on a stick to position the mock prey (weighted plastic diamond 1.5 cm long by 1.0 cm wide) at one of two locations in the tank (labelled A and B in Figure 2*b*). Each location was marked with two small coral rocks (Figure 2*b*). We used a mock prey rather than a real food item to avoid fish striking when the experimenter positioned the prey in the tank and to avoid fish receiving a food reward. Rapid movement of the mock prey was sufficient to initiate pursuit by the goatfish (Supplementary Video). Once the prey was in a starting position, the experimenter waited between 10 and 30 s before rapidly pulling the prey across the bottom of the arena and under a shelter at the centre of the tank (Figure 2). As in the training phase, the mock prey was attached to fishing line and pulled by releasing a weight down a ramp, yielding constant acceleration across trials and fish pairs (Figure 2). The weight was released when both goatfish were approximately within one body length of a shelter and visible to the camera. The speed at which the prey travelled was such that it could not be caught by either goatfish except on rare occasions.

The shelter to which the prey retreated consisted of an acrylic disc covered in coral rock. The disc was separated into four sections (Figure 2*b*) and was sufficiently elevated from the substrate to allow the prey entering, but not the goatfish. When the prey was pulled from position A in the tank, it could enter the shelter directly (entrance a1 in Figure 2*b*) or indirectly, by circling the shelter before retreating (entrance a2 in Figure 2*b*). The same options (entrances b1 and b2) were possible when the prey was pulled from starting position B (Figure 2*b*). Different entry points were used to mimic natural conditions on the reef, where goatfish cannot predict whether and where prey will seek shelter. We counterbalanced the prey's starting position and route to the shelter for trials performed on each goatfish pair (i.e. all options were presented to each pair, in different orders).

1.2.4 Video analysis and data extraction

We recorded all trials at 25 Hz with a video camera positioned above the tank (Sony HDR-CX350VE, Sony Electronics, Tokyo, Japan). Videos were analysed frame by frame with the software Picture Motion Browser (Sony Electronics) to determine the exact position and time when each goatfish responded to the stimulus. We measured the straight distance between each fish's snout and the centre of the prey when fish made their first head movement in pursuit of the prey. Distances were measured in two dimensions because *P. cyclostomus* is a bottom dweller and the mock prey was weighted to ensure movement along the substrate. The first goatfish to respond was termed the ‘initiator’ and the second was the ‘follower’. We categorized trials into three scenarios in which the proximity of the two fish to the prey differed by: (i) one-third of a body length or less (i.e. both fish were considered equally distant from the prey; the mean body length of the pair was used), (ii) more than one-third but less than one body length (i.e. one fish was slightly closer to the prey) and (iii) more than one body length (i.e. one fish was considerably closer to the prey). In each of these scenarios, we recorded whether fish reacted simultaneously or not (i.e. in the same or different frames). Sequential frames were separated by 0.04 s. In the latter case, we noted whether the initiator and the follower directly chased the prey in its path or circled around the acrylic shelter (paths C and D, respectively, in Figure 2*b*).

To specifically evaluate collaboration between the two hunters, we identified instances when the follower chose a different route from that of the initiator, which occurred in two situations. First, the projected future position of the prey and the position of the follower at the time it initiated its response were such that circling around the shelter was in fact the shortest route to reach the prey (e.g. path D in Figure 2*b*). This case does not provide strong evidence of coordinated action by both partners because it could be a simple by-product of the follower opting for a route that minimizes the time it needs to reach the prey. Second, circling around the shelter caused the follower to take a longer route to reach the prey. This situation is indicative of 'true' collaboration because the follower bears the cost of choosing a route that lowers its chances of reaching the prey first.

1.2.5 Statistical analysis

We used a general linear mixed-effects model (LMM; 'lme' function in the R package 'nlme') to test whether goatfish exhibited signs of fatigue or habituation due to repeated stimulations (Roche et al., 2016). We included the response latency of the first fish to accelerate towards the prey as the response variable (i.e. the time it took the first fish to respond to movement by the prey); trial number was specified as a fixed (discrete) predictor and goatfish pair as a random factor to account for repeated measurements. We verified model assumptions using diagnostic plots for fixed and random effects (i.e. plot, qqPlot, qqnorm functions in R). We calculated the repeatability (R) of response latency using the 'rpt' function in the R package 'rptR' (Stoffel et al., 2017).

We used Wilcoxon signed-rank tests (hereafter Wilcoxon) to account for non-normality in the data and repeated measurements on pairs of goatfish. First, we used two tests to examine whether the same fish always assumed the initiator or follower role in a given pair and whether this depended on body size. Second, we used three tests to determine how the distance separating the follower from the initiator (i.e. the three different scenarios) influenced the follower's decision to pursue the prey via a direct or indirect route. Third, we selected only instances of scenario 3 in which a decision by the follower to circle the shelter and reach the prey would result in a longer route than direct pursuit. We tested whether the follower preferentially chose the longer route over the shorter, more direct route. Statistical analyses were done in R v. 3.3.3 (R Core Team, 2017).

1.3 Results

In nine of the 12 pairs tested, both goatfish consistently chased the mock prey upon release, yielding a total of 143 successful trials. In 62 trials (43.4%), both fish began accelerating towards the prey at the same time (i.e. within 0.04 s; table 1). In all trials where one fish responded before the other (n = 81), the initiator always pursued the prey using the most direct route. There was no evidence of fatigue or habituation to repeated stimulations (LMM, main effect of trial number: $F_{1,133}$ = 0.521, p = 0.471). Response latency was repeatable at R = 0.142 (95% CI: 0.035–0.441). With the exception of pairs 3 and 6, both fish assumed the role of initiator and follower in approximately equal proportions (Wilcoxon V = 12, n = 7, p = 0.799; table 1). Body size (weight) did not influence which fish became the initiator and which the follower (Wilcoxon V = 14.5, n = 9, p = 0.373; table 1).

The initiator always reached the mock prey's closest entrance point first (a1 or b1 in Figure 2*b*). By contrast, followers that circled the shelter tended to arrive at the prey's furthest entrance point (a2 or b2 in Figure 2*b*) before the initiator (i.e. in 18 of 24 events; Wilcoxon V = 5, n = 9, p = 0.075).

Fourteen trials corresponded to scenario 1, whereby the distance separating each fish from the prey differed by one-third of a body length or less. In 100% of these cases, both fish responded at the same time (i.e. within 0.04 s) and always pursued the prey via the shortest route. In trials corresponding to scenarios 2 and 3, and where fish responded to the stimulus at different times (n = 81), the follower's choice of route depended strongly on its position relative to the initiator. If the initiator's lead was between one-third and one body length ahead of the follower (n = 26 trials), the follower also preferentially chose the most direct route in pursuit of the prey (i.e. in 96% of cases; Wilcoxon V = 36, n = 9, p = 0.0140; Figure 3; Supplementary Video). Conversely, if the initiator was more than one body length ahead of the follower (n = 55 trials), the follower exhibited a significant preference for circling the shelter (i.e. in 89% of cases; Wilcoxon V = 0, n = 9, p = 0.0088; Figure 3; Supplementary Video). When we excluded eight of these 55 trials in which circling the shelter resulted in a shorter distance to the prey (e.g. route D in Figure 2*b*), followers still exhibited a significant preference for the longer route that involved circling the shelter (i.e. in 87% of cases; Wilcoxon V = 0, n = 9, p = 0.0090).

1.4 Discussion

Our results support the hypothesis that collaborative hunting in yellow saddle goatish is based on simple decision rules. The response of the individual that first detected the moving prey (the initiator) was always to initiate a direct pursuit. Similarly, goatfish that were second to react in our experiments (i.e. the ‘followers’) directly pursued the prey in over 95% of trials when they were in close proximity to the initiator (distance $\leq$ 1 BL). We observed a sharp drop in direct pursuits by the follower when it lagged behind the initiator by a distance greater than 1 BL. Here, the follower opted for a longer, less direct path to the prey in 87% of cases, often reaching the prey's more distant refuge first. Such a decision could increase the follower's chance of capturing the prey or blocking the prey's escape path under natural conditions. Therefore, a simple distance-based rule explains nearly all of the observed variation in the occurrence or absence of collaborative group hunting in our system.

1.4.1 Functional hypotheses for collaboration

Our experiment was not designed to quantify hunting success because we used a mock prey that could not be captured. Nevertheless, our study allows inferring the potential benefits of individual decisions. First, we note that direct pursuit of the prey by the initiator is a decision that probably maximizes its net benefits. Choosing an alternative route that is not in the prey's direct path would only be beneficial if the prey has to circle a shelter because it cannot immediately access an entry point (Figure 2*b*). However, because predators do not know the location of all hiding places in the reef and/or a prey's potential preference for a particular shelter (Shulman, 1985), direct pursuit should, on average, be the most effective (and hence preferred) option for the initiator to achieve capture.

From the follower's perspective, direct pursuit of the prey might also be the best strategic option when it is at a short distance from the initiator and has limited time for decision-making. The follower's decision to follow the initiator when both fish are in close proximity suggests that its probability of capturing the prey under these circumstances is non-negligible in nature. Alternatively, once the follower has initiated pursuit, it might lack the ability to effectively adjust its direction during the chase even if an alternative path becomes more advantageous (e.g. if the distance between the two predators widens during the chase). Our data show that, when both fish followed the prey in its path, the initiator always arrived first at the closest shelter entrance under which the prey could seek refuge. Hence, at least under these experimental conditions, followers were unable to catch up to the initiator but still never strategically adjusted their trajectory during the chase.

When the distance between hunters widens, the further the follower lags behind the initiator, the less likely it becomes that a direct pursuit will yield hunting success as the prey would be swallowed by the initiator or escape into a refuge. Conversely, given the uncertainties about the distribution of locally available refuges and unknown prey preferences for shelters, opting for a non-direct route to the prey has the potential to increase the follower's hunting success relative to a near-zero baseline. In our experiment, variable prey, behaviour and the presence of multiple possible entry points under the artificial shelter were intended to mimic the uncertainties that predators face in nature. Opting for a path that differed from that of the prey resulted in an advantageous position for the follower (i.e. closer to the prey's point of entrance to the shelter) in instances when the prey was pulled to the furthest (i.e. second) entrance around the shelter (a2 or b2 in Figure 2*b*). Therefore, it is conceivable that, under natural conditions, deviating from the prey's escape path occasionally increases the follower's chance of intercepting and capturing the prey. In other words, a self-serving decision by the follower would explain the occurrence of collaborative hunting.

Accurately determining the breakpoint in the functional form describing when the follower's choice of strategic option changes (i.e. opting for an indirect versus a direct path to the prey) would have required data with higher temporal resolution than we were able to collect. Owing to the rapidity of the goatfish's displacements, the mean distance covered by an individual once in movement was approximately 6 cm between frames in our videos (i.e. in 0.04 s). As a result, the time resolution of our video recordings only allowed us to categorize trials into three different scenarios (see Material and methods) rather than perform a more detailed analysis using continuous predictors. Nevertheless, despite this caveat, our results convincingly demonstrate that (i) the breakpoint of this functional form is situated near a distance of 1 BL between the hunters (see Figure 3 showing that followers opt for a direct path to the prey in 96% of cases when this distance is less than or equal to 1 BL and an indirect path in 87% of cases when the distance is greater than 1 BL), and (ii) the relative orientation of the hunters appears unimportant because the differences in strategic choices observed are overwhelmingly explained by distance alone, irrespective of the existing variation in the fish's relative angular position. We also note that the shape of this functional form will likely change in natural or other experimental settings that differ in the number and distance to refuges.

1.4.2 Is collaborative hunting indicative of cooperation by yellow saddle goatfish?

Demonstrating that collaborative hunting by yellow saddle goatfish constitutes cooperation requires showing that a pair's hunting success is more than double that of a single individual. We could not examine each partner's capture success in our study; however, by pursuing the prey via an indirect path, the follower reduces the prey's escape options, effectively fulfilling the role of a ‘blocker’ (Boesch and Boesch, 1989). Such collaboration is believed to increase hunting success at the group level in species such as lions and dolphins, where coordinated hunting is perceived as cooperative (Gazda et al., 2005; Stander, 1992). However, unlike these species that share a captured prey (or school of prey), only one yellow saddle goatfish can be successful during a hunt. Which hunter, if any, captures the prey will depend on the prey's behaviour when it is cornered. For example, the initiator might chase the prey towards a follower that opted for an indirect path, or the follower might surprise the prey and alter its movement (i.e. slow down or halt) or path (i.e. change direction), facilitating capture by the initiator. In addition to collaborating during the chase, goatfish must also coordinate their movements when trying to extract a cornered prey from underneath a shelter using their barbels (Strubin et al., 2011) (Figure 1). Thus, in yellow saddle goatfish, the relative success of groups versus singletons depends on the potential benefits of group hunting on both phases of a hunt. Future studies should explicitly focus on quantifying the increase in hunting success resulting from group collaboration versus solitary hunts.

Short of demonstrating cooperation, our study suggests that collaborative chases by yellow saddle goatfish are a by-product of individual decisions in an overall competitive situation where a captured prey is not shared by hunters. Here, each goatfish tries to detect a suitable prey first because the first fish to respond has the highest probability of capturing the prey. The follower then makes the most out of a bad situation, either by attempting to catch-up to the initiator and pursuing the prey in its path if it is separated from the initiator by a small distance (less than or equal to 1 BL), or by opting for an alternate route if the initiator's lead is larger (greater than 1 BL). Reciprocation is not necessary to explain the stability of this collaboration because individuals invariably behave in a self-serving way. Similarly, reciprocation is probably unnecessary to explain collaboration in other systems where field studies have described group hunting of non-shared prey (Dinets, 2015; Gazda et al., 2005). For example, simple by-product benefits probably explain why sailfish hunt in groups, allowing them to herd schools of sardines and strike at prey in turn (Herbert-Read et al., 2016), and why spotted sea trout coordinate their attacks on prey schools, inhibiting collective antipredator responses (Handegard et al., 2012).

1.4.3 Future directions

Further insights into the decision rules underlying collaborative hunting would be gained by studying other systems which are amenable to experimentation and in which prey are shared. For example, sharing the prey may offer an immediate cooperative solution to individuals that display costly behaviour (e.g. adopting a role that reduces individual success in favour of increased group success) if it can be shown that such investments are rewarded at the end of the hunt. There is evidence for this phenomenon among chimpanzees in the Taï National Park, Ivory Coast (Boesch, 1994), offering opportunities to study the role of inequity aversion (Brosnan and de Waal, 2003; Price and Brosnan, 2012) as a mechanism to regulate payoffs in return for investments.

We found little evidence for role specialization among goatfish during collaborative hunts, and no obvious indication of factors underlying the few cases in which fish tended to consistently adopt the same role (two of nine pairs). Role specialization may not be expected in a scenario where the first individual to detect a prey must respond immediately to maximize its chances of capture. By contrast, role specialization may emerge in situations where a specific behaviour can improve over time through experience; for example, in dolphins, where members of a pod tend to specialize as ‘herders’ or ‘blockers’ of fish schools (Gazda et al., 2005), or in lions, where several individuals chase prey towards a hiding pride member that takes the prey by surprise (Stander, 1992). These questions are ripe for future investigation.

1.4.4 Conclusion

Our experimental study provides strong support for the hypothesis that simple, self-serving decision rules can result in instances of coordinated hunting by partners. Therefore, the possibility that similar forms of collaboration in other species are based on sophisticated decisions that warrant reciprocity and hence advanced cognitive processes (e.g. individual recognition, memorization of past interactions (book keeping), negative inequity aversion and a degree of self-control that allows playing immediate payoff-reducing roles) should be demonstrated rather than assumed by default.

1.5 Ethics

This study was approved by the Dahab Marine Research Center and the Suez Canal University. Fish were released at their site of capture after the experiments.

1.6 Data accessibility

The data and script for this study are archived in the repository figshare following best practices (Roche et al., 2015) https://doi.org/10.6084/m9.figshare.4877783.

1.7 Authors' contributions

M.S. and R.B. designed the study. M.S. and Hanaa Sarhan collected the data. D.G.R. and M.S. analysed the data. M.S., D.G.R. and R.B. wrote the paper.

1.8 Competing interests

We declare no competing financial interests.

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1.11 Footnotes

Electronic supplementary material is available online at https://dx.doi.org/10.6084/m9.figshare.c.3969153.

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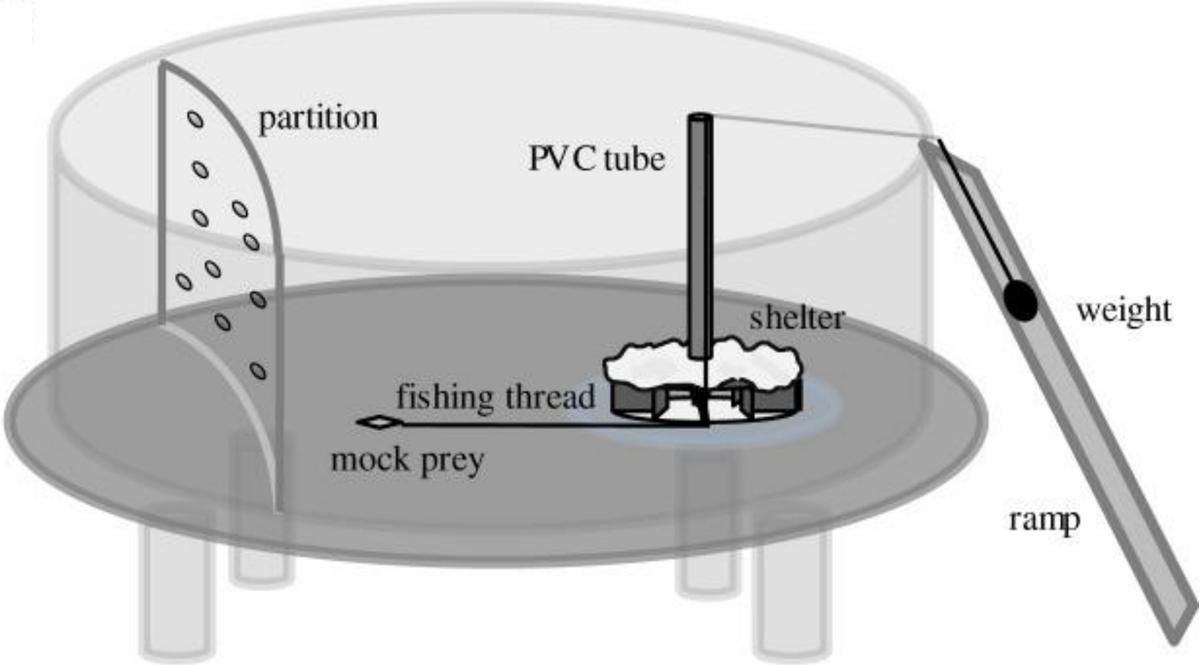
1.13 Table and Figures

Table 1. Body total length (TL, mm) and weight (g) of individuals in the nine goatfish pairs tested. Also indicated is the number of times each individual assumed the initiator role (i.e. was the first fish in the pair to respond to the stimulus) and the number of times individuals responded simultaneously (i.e. within 0.04s).

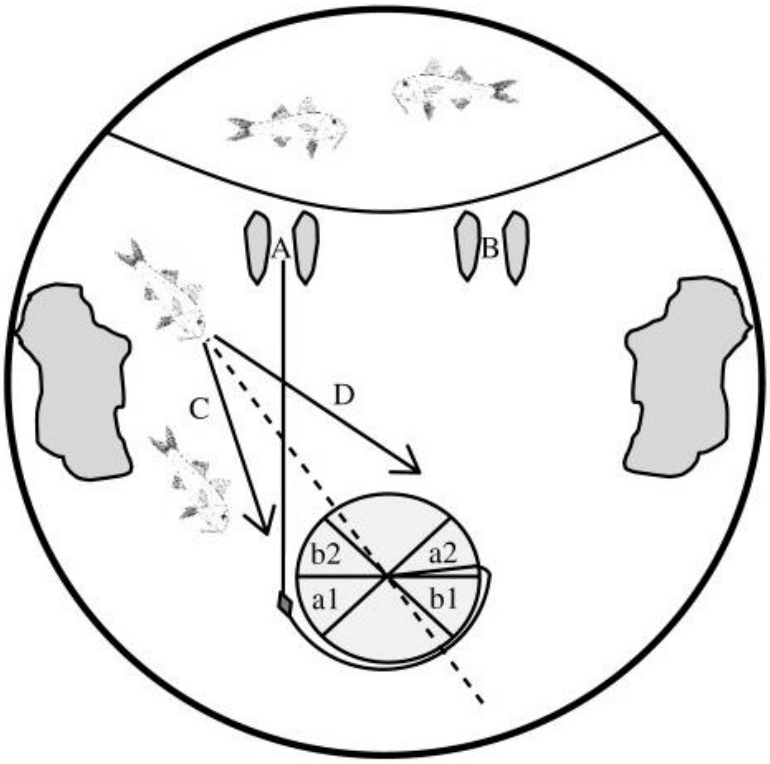
Pair	Fish	TL (mm)	Weight (g)	Initiator	Simultaneous
1	1	258	180	3	5
1	2	254	170	7	
2	1	190	65	3	2
2	2	173	50	2	
3	1	192	70	6	5
3	2	182	55	1	
4	1	175	47	7	7
4	2	170	38	4	
5	1	210	70	8	6
5	2	184	52	3	
6	1	177	56	10	9
6	2	171	34	0	
7	1	194	62	2	11
7	2	187	54	6	
8	1	238	92	4	6
8	2	219	88	7	
9	1	205	70	5	11
9	2	190	58	3	

Figure 1. Yellow saddle goatfish (*Parupeneus cyclostomus*) often hunt collaboratively for invertebrates and prey fishes on coral reefs. Group members exhibit coordinated movements during a hunt, where one individual chases the prey and others block its escape path. When a prey seeks shelter, goatfish use their barbels to try and extract it from underneath the refuge. Photograph by M.S.

(a)


partition
PVC tube
shelter
weight
fishing thread
mock prey
ramp

(b)


A
B
C
D
b2
a2
a1
b1

(c)

Figure 2. (a) Side view of the experimental arena. The mock prey was attached to fishing thread and could be pulled across the bottom of the tank to a shelter with multiple entry points. A partition separated the experimental fish from the other two fish housed in the tank. **(b)** Top view of the experimental arena. The letters A and B indicate the starting points from which the prey was pulled. The prey could enter the shelter via four entry points: a1 or a2 if the prey was in start location A; b1 or b2 if the prey was in start location B. Route C represents a situation in which the follower takes an identical route to the initiator, following the prey in its path. Route D represents a situation in which the follower opts to circle the shelter, deviating from the initiator's path; here, the follower would reach the prey before the initiator because the prey enters the refuge via entry point a2. **(c)** Top photograph of the experimental arena. The two goatfish are visible in the top right corner and the mock prey is in starting position A.

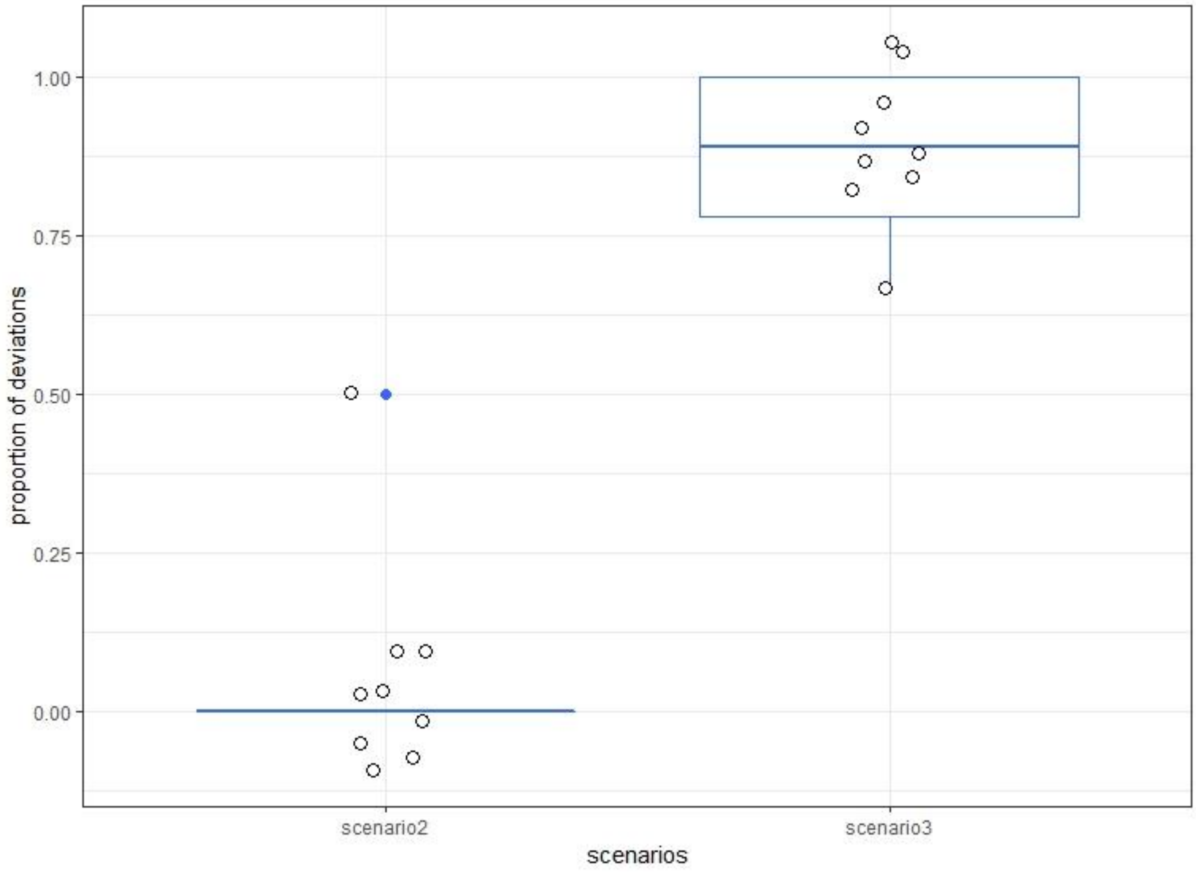


Figure 3. Box-and-whisker plots showing the proportion of times the ‘follower’ (i.e. the second goatfish to pursue the mock prey) opted to chase the prey via a longer route than the ‘initiator’ (i.e. the first goatfish to initiate pursuit) when the distance separating the two predators was either (i) between one-third and one body length (scenario 2; n_{trials} = 26) or (ii) greater than one body length (scenario 3; n_{trials} = 47). Nine goatfish pairs were tested. Whiskers extend to the highest value within 1.5 times the inter-quartile range; data points are jittered to avoid overlap.

CHAPTER 2 | LAB EXPERIMENTS REVEAL EFFECTS OF GROUP SIZE ON HUNTING PERFORMANCE IN YELLOW SADDLE GOATFISH (PARUPENEUS CYCLOSTOMUS)

Authors: Marc Steinegger[1], Hanaa Sarhan[1] & Redouan Bshary[1]

Affiliation: [1]Institute of Biology, University of Neuchâtel, Emile-Argand 11, 2000 Neuchâtel, Switzerland

Status: *Under review*

Abstract

Joint hunting where two or more individuals chase the same prey occurs in various vertebrate clades. Its evolution has typically been attributed to the resulting increased prey capture rate. Indeed, many studies documented positive correlations between the number of individuals and probability of success, concluding that joint hunting is cooperative. While the evidence leaves little doubt about this interpretation, all existing data are based on field observations and hence cannot control for factors that may also influence hunting efficiency, such as variation in habitat structure, hunting motivation, or prey state. Therefore, we conducted controlled laboratory experiments to test whether hunting performance is affected by group size in the collaboratively hunting yellow saddle goatfish *Parupeneus cyclostomus*. We presented invertebrate prey in an artificial coral reef and measured hunting performance as a function of manipulated group size, ranging from 1-4 individuals. We found that single-hunting individuals failed significantly more often to catch the prey within the trial time limit than groups did. Furthermore, we found that time until capture depended on group size, with singletons being slowest and groups of four being fastest. With few exceptions, group members were approximately equally likely to catch a prey. Hunting efficiency as a singleton did not predict an individual's prey capture probability when in a group, suggesting that group hunting involves some producer-scrounger dynamics. In conclusion, while the experiment cannot address the question of how group size affects individual net calorie intake, the results show that groups are more efficient at hunting than singletons are.

Keywords: *Parupeneus cyclostomus*, yellow saddle goatfish, collaborative hunting, cooperation, group hunting

2.1 Introduction

Group hunting, in which several hunters simultaneously go after the same prey, has been described in detail in various mammal species such as Chimpanzees (Boesch, 1994; Boesch and Boesch, 1989), social living carnivores (Creel and Creel, 2002; Schaller, 2009) cetaceans (Baird and Dill, 1996; Gazda et al., 2005; Smith et al., 1981) and also birds (Bednarz, 1988; Yosef and Yosef, 2010) and fishes (Arnegard and Carlson, 2005; Strubin et al., 2011). A broadly accepted explanation for the evolution of hunting in groups is the increased capability to capture prey (Clark and Mangel, 1986; Kruuk, 1975; Packer and Ruttan, 1988). Indeed, many field studies describe positive correlations between group size and hunting success (Baird and Dill, 1996; Boesch, 1994; Creel and Creel, 1995; Holekamp et al., 1997; Leonardi, 1999; Stander, 1992b). As to the potential underlying mechanisms, hunting in groups can facilitate the hunt on different levels, such as allocating prey, chasing, catching and finally killing the prey. In terrestrial predators, where the prey is often large relative to the predator, a certain group size can be crucial to chase and kill the prey (Creel and Creel, 1995; Macdonald, 1983). This is because the physical strength of a single attacker might not suffice to overcome the prey defenses, and the attacker could even risk getting seriously injured. Such a scenario has been proposed for cooperatively hunting African wild dogs killing wildebeests and warthogs (Creel and Creel, 1995). Another aspect of African wild dogs’ and wolves’ hunting techniques is their ability to pursue large prey over long distances, with participating individuals alternating in the role of pursuer (Creel and Creel, 1995; Mech, 1970). In contrast, many pelagic aquatic predators hunt small prey that is swallowed whole by a successful hunter, where the benefit of an increased group size is supposedly due to finding and herding gregarious prey to prevent escape (Anderson, 1991; Gotmark et al., 1986; Nøttestad et al., 2002; Schmitt and Strand, 1982; Similä and Ugarte, 1993). In some cases, hunting in groups does not lead to a simple linear increase in efficiency because of an increase in the number of hunting individuals, but an exponential increase in overall efficiency because individuals play different roles, like chaser and blocker (Boesch and Boesch, 1989; Bshary et al., 2006; Gazda et al., 2005; Stander, 1992a).

A second related topic is the question of whether an increase in hunting efficiency translates into an increased food intake rate *per capita*. Two individuals would need to more than double hunting efficiency compared to solitary hunting to make joint hunting mutually beneficial. More generally formulated, a group of n individuals needs to be more than n times more efficient than singletons so that joined hunting yields on average an increase in net benefits for participants. Therefore, it appears that any increase in hunting efficiency is more likely to be maximal in small groups and then to decline again as group size increases further. Indeed, such a relationship has been reported in social-living carnivores (where the *per capita* intake peaks somewhere from two to five hunting animals (Kruuk, 1972; MacNulty et al., 2012; Schaller, 2009; Stander, 1992b)) and in fish-hunting birds (Gotmark et al., 1986; Macdonald, 1983). Efficient larger groups have rarely been described (see Etosha lions (Stander, 1992b) and sailfish (Herbert-Read et al., 2016a) as apparent exceptions).

The analyses on optimal hunting group size rely on the assumption that the positive correlations between group size and hunting success capture a causal relationship between the two variables. However, to our knowledge there is not a single study that has demonstrated such a causal relationship as all the evidence is based on field observations. Correlations cannot exclude alternative explanations such as for instance: i) the larger the group the more likely it contains top individual hunters, which would have been fast also if hunting alone (Gilby et al., 2008; Gilby et al., 2015); ii) the more promising the situation (i.e. the more likely it seems that a hunt will be successful), the more individuals join in; iii) the hungrier the members of a group, the more likely a hunting group will grow in size, meaning the increased success is driven by increased motivation rather than by increased efficiency. Thus, there is a need for studies that selectively manipulate group size while keeping other factors constant.

We therefore conducted an experimental lab-based study on the relationship between group size and hunting efficiency in yellow saddle goatfish (*Parupeneus cyclostomus*). In their natural environment, adult yellow saddle goatfish form relatively stable hunting groups composed of similar-sized individuals (Strubin et al., 2011). They mainly hunt small fish on the coral reef (Randall, 1983). Yellow saddle goatfish are open-water spawners with pelagic egg and larval stages, making it highly unlikely that individuals of hunting groups are close kin, a supposition also in line with genetic studies on other open water spawners (Avise and Shapiro, 1986). Group hunts often consist of two phases that are both characterized by high levels of coordination between participants. During the first phase, one individual suddenly accelerates, chasing after a prey, which also triggers acceleration by the others (Strubin et al., 2011). Importantly, the other group member(s) do not simply follow the leader but deviate around reef structures such that they may potentially block the prey's escape path (Steinegger et al., 2018; Strubin et al., 2011). Such resulting collaboration between group members is apparently based on self-serving decision rules, given that whoever catches the prey swallows it immediately and whole (Strubin et al., 2011). Most often, however, prey escapes into a crevice, which triggers the second phase of a joint hunt: the goatfish aggregate around the reef structure in which the prey is hiding, spacing out such that a prey who decides to flee to another crevice cannot avoid passing near one of the hunters (Steinegger et al., 2018; Strubin et al., 2011). Then, yellow saddle goatfish insert their highly motile and chemosensory barbels into the crevices of the reef structure to either detect and catch the prey with a suction opening of their mouth, or to startle prey into leaving the protection of the hide and catch it outside (Strubin et al., 2011).

In our study, we experimentally created the second phase of a hunt, providing an invertebrate prey inside a standardized artificial reef structure. In each tank we had four individuals, which allowed us to vary the experimental group size from one to four. If group hunting is indeed more efficient, we expected that singletons would have a higher probability of failure and take longer to catch a prey compared to groups. For groups of different sizes, we did not have specific predictions as more than two hunters could in principle cause both more hunting activity and/or more interference. In addition to the total time until capture, we also measured the duration of three additive time periods: time from the start of a trial until the first individual inserted its barbels in the structure, time from first insertion until the first barbel touched the prey, and time from first touch until capture/consumption of prey. Note that in groups each time period may be terminated by a different individual. Touching the prey with barbels is often a necessary step for capture as the prey’s escape response typically leads to it ending up closer to the edge of the hiding place and hence more accessible for capture. Yellow saddle goatfish swing out their jaws to form a long tube which creates suction to catch prey, but barbels seem to reach out further than the distance over which the suction operates (author’s personal observation). In principle, group hunting could be more efficient in any of these three time periods but because of different factors: faster initiation of the hunt, increased probability of startling the prey, and increased probability of capturing a startled prey.

Since individuals are not constrained to a specific role during a hunt, they can easily be replaced or added to manipulate the group size (Steinegger et al., 2018). Furthermore, yellow saddle goatfish do not share their prey among the group members but the successful hunter eats it immediately and whole. We could hence expect the participation of all group members during the hunt, as the option of not hunting but joining at a carcass does not exist (Packer and Ruttan, 1988) (e.g. African wild dogs (Creel and Creel, 1995)). This enabled us to measure hunting success as a function of group size. Nevertheless, we were also interested in potential individual variation in hunting success. More specifically, we examined whether individual success rates when hunting alone are similar to their success rates in a group, and whether individuals that performed well during single hunts were also more likely to catch prey when hunting in a group. A correlation between the two would be expected if individual hunting skills are a trait that is independent of group size. Alternatively, group hunting may require some adjustments in individual hunting techniques to outcompete other group members. In particular the possibility that disturbing a prey with a barbel may startle it to move towards another group member may lead to some producer-scrounger dynamics (Barnard and Sibly, 1981). Applied to the study, producer-scrounger dynamics describe the relation and balance between individuals that hunt fish (asserting dominance and advantage) and those hunters that are then attracted by the former and join in (profiting from the food). In that case we would either expect no correlation or even negative correlations between hunting success as singleton and in a group.

2.2 Methods

Experiments were conducted between February 14th 2011 and October 5th 2011, at the laboratory of the Dahab Marine Research Center (DMRC) Egypt, Red Sea. All experiments were approved and conducted in accordance with the rules and regulations of the Dahab Marine Research Center for animal research under supervision of the Suez Canal University.

20 yellow saddle goatfish *Parupeneus cyclostomus*, ranging between 16.2 and 23.8 cm in total length and 30 to 92 g in weight, were captured while scuba diving during day time (between 6 a.m. and 5 p.m.) in the waters around the DMRC or at nearby dive sites in depths between two and 13 meters.

The fish were captured using a 30 m^2 barrier net (stretched mesh size 20 mm) and removed from the net wearing neoprene gloves to reduce skin and mucus damage as well as to avoid contagion with diseases. Fish were transferred to a holding net and then slowly transported to the surface (approx. one meter every three minutes) to avoid rapid inflation of the swim bladder. During transportation from the sea to the laboratory, the fish were kept in opaque, round water tanks (35cm in diameter, 50cm in height). In the lab, the fish were initially marked by cutting small parts in the shape of a “V” from their ventral or pectoral fin membrane, following a technique by Noakes and Leatherland (1977) in which small holes were punched into the fin membrane. Marked fish were then assigned into groups of four individuals and put to one of the two experimental tanks, Figure 1a. Fish were all measured (total length to nearest 1.0 mm) and weighed (nearest 1.0 g) on the day after the experiments before they were released to the site of capture.

2.2.1 Laboratory and experimental set-up

A 4x4m air-conditioned room with opaque glass windows of the DMRC served as the laboratory. The light regime was set to an L:D cycle that matched the local sunrise and sunset with 10 min twilight at the beginning and end of the light phase. The water temperature was kept at 27 ± 2 °C.

Two round plastic tanks with a diameter of 138 cm, with a water column of 39 cm, were placed in the laboratory and served as experimental tanks (Figure 1a). An opaque and ecliptic partition wall with small holes for water exchange was placed on one side of the tank. It served to separate experimental from non-experimental fish. On the other side of the tank, a round acrylic window (30 cm in diameter) was glued into the bottom to allow filming from below. An artificial reef was then placed over the window, Figure 1b. The artificial reef was constructed from two similar sized (16 cm in diameter) round acrylic glass discs. The upper disc had a round opening (3cm in diameter) in the center to which a 45cm long PVC tube was glued. Inside this tube was another short opaque tube which could then be pulled up with a fishing line to expose the crab that was previously added via the top end of the larger tube. Between the two parallel laying discs, 12 thin acrylic glass plates (3 cm in length, 2 cm in height) were glued so that they were all in a similar distance to each other, facing the center of the reef and touching the outer edge of the acrylic glasses. The amount and the height of these partition walls were chosen in a way to allow our experimental species to stick their barbels and part of the head into one of the 12 slots to almost reach the center with the tip of the barbels. Additionally, the plates and the upper disc were covered with black tape to lower the visual detectability of the prey. To keep the artificial reef on the ground, a round coral rock, similar in size to the disc, was placed on top of it. One centimeter of coral sand layer covered the ground and a few small coral rocks were placed on the sides of the tank to provide additional shelter. The experimental tanks were constantly supplied with fresh salt water from the Red Sea (approx. 180 l/h) and oxygen was additionally provided.

2.2.2 Feeding and training of fish

Fish were fed once per day *ad lib* by small pieces of fresh or frozen fish. Leftover items were removed from the tank with a net. Fish were trained from the third day of captivity. We split the training into three different levels:

Level 1 (duration: 7-10 days): Pieces of fresh fish were fixed on a fishing line and presented initially directly in front of the yellow saddle goatfish's mouth and later next to the artificial reef.

Level 2 (duration: 5-7 days): During this level, all four individuals were trained as a group. Pieces of fresh fish were added through a PVC tube to the center of an easy-access artificial reef, designed for training purposes. This artificial reef was 8 cm in diameter and 6 cm in height. It contained only eight partition walls and the slots to the center were larger. Furthermore, the training reef was fully transparent to help the fish to detect their prey easier. When the yellow saddle goatfish managed to catch the food items, the latter were replaced with live crabs. Previous stomach content analyses had shown that adult yellow saddle goatfish eat both crustaceans and fish. We therefore opted for crustaceans as prey in our experiments to avoid having vertebrates as prey for ethical considerations.

Level 3 (duration: 2 days): The easy-access artificial reef was replaced with a more challenging artificial reef, which was 16 cm in diameter, 8 cm in height and contained 12 partition walls with narrower slots to the center. The only difference between this training reef and the experimental reef was that it was fully transparent. For this level, fish were trained the first day uniquely in groups of four individuals. On the second day of training, fish were trained as singletons (6 subsequent trials per individual), as a pair (8 subsequent trials) and one more time in a group of four individuals (12 subsequent trials).

2.2.3 Experimental schedule

The experiment was conducted following a pre-determined schedule:

Each of the five hunting groups, consisting of four individuals, were tested in all possible combinations, during four subsequent days (Table 1). Single hunting individuals, groups of three and four fishes were tested during all four testing days, while pairs were tested only during three days. With this schedule we avoided testing certain pairings more often than other ones.

Each *day* was divided into four *testing times* (Table 1b). Two were in the morning (7:00 and 10:00) and two in the afternoon (13:00 and 16:00). To counterbalance a possible effect of *day* and *testing time* on the outcome, the possible fish configurations were organized within Latin Squares (Bradley, 1958). During each *testing time*, combinations of the same *group size* were tested in a set of trials. Single hunting individuals were tested with 6 subsequent trials per set; groups of two hunting individuals with 8 subsequent trials per set and groups of three and four hunting individuals with 12 subsequent trials per set.

2.2.4 Experimental procedure

Prior to each set, non-participating fishes were separated behind an opaque partition wall, Figure 1a. After ten minutes of acclimation time, the set started. A live crab was added by the experimenter via the PVC tube. Each trial per set began when no fish were seen in the round acrylic window. An external monitor that was linked to the bottom-camera provided the experimenter with this information.

Trials were considered as successful if the crab was caught within 180 seconds. If the fish did not manage to catch the prey within 180 seconds the trial was considered as not successful and the crab was caught and removed by the experimenter. Trials were aborted and repeated if the experimenter accidently interrupted the hunt e.g. touching the tank or if the prey got stuck in the tube or swam back into it during the hunt. If the prey swam outside of the artificial reef prior to fish arrival it was considered non-valid. Trials were also considered non-valid when not all fish participated in the hunt, i.e. if one or several fish did not appear over the acrylic bottom window in the time between the lifted-up tube and the capture of the crab, or if none of the tested fish introduced their barbels into the experimental reef within 180 seconds. Non-valid results were excluded from all data analyses. In the course of the experimental procedure, the fish behind the partition wall were fed the same proportional amount of live crab as the experimental fish, to keep them at a similar hunger level. After each experiment, the opaque partition wall was removed from the tank.

2.2.5 Video analysis

All trials were recorded with a bottom-view camera (SONY HDR-CX350VE, Sony Electronics, Tokyo, Japan) which displays 25 frames per second and later analyzed with the program Adobe Premiere. For each successful trial we measured the total time (*tt*) of the hunt (measured from the lifted-up tube until the capture of the prey) as well as three specific time intervals from the total time. *i*: Time from exposing the crab until the first insertion of the barbels. *ii*: Time from the end of the first interval until the first touching of the prey. *iii*: Time measured from the end of the second interval until prey capture. For each successful group hunt, we additionally noted the identity of the individual that caught the prey. Example videos have been uploaded in the supplements (Supplementary Video with a single hunting individual; Supplementary Video with a group of 4 hunting individuals).

2.2.6 Statistical analysis

Statistics were mainly performed with R v. 3.2.1. GLMM was performed with the R package ‘lme4’ (Bates et al., 2014). LMMs were performed with the R package ‘nlme’ (Pinheiro et al., 2015). Tukey contrasts were obtained with the R package ‘multcomp’ (Hothorn et al., 2008). Figures 2-5 were created with Microsoft Excel 2016.

In a first step we tested whether group size affects the ability to catch the prey within three minutes. We were using a generalized linear mixed-effect model (GLMM) with binary response (tube up intro within 3 minutes: yes / no) in which we used *group size* as fixed effect, and as nested random effects *group, day*, *testing time* and *trial number*. Pairwise comparisons between group sizes were conducted using a post-hoc Tukey test.

In a second step we pooled the data by collapsing all trials per set in which the prey was caught within three minutes. Then we used as the response the averages of the total time (*tt*) as well as three specific time intervals from the total time (*i – iii*) as the dependent variable. We were using a linear mixed-effect model (LME) with the main effects of *day, testing time* and *group size* and as random effects, *group* nested within *day*. In order to stabilize variances with respect to the means we log-transformed the outcome-variable (log(*tt*-0.3); log(*i*+0.05); log(*ii*+0.1); log(*iii*+0.25)). Moreover, to account for heteroscedasticity we used standard variance functions in “nlme”, which allow for different variances for each level of *group size* (Pinheiro and Bates, 2006). The pair wise differences between *group size* levels were assessed by post-hoc Tukey test.

In additional analyses we ranked the four individuals within each hunting group according to the average of the total time (*tt*) of the individual’s singleton trials as well as the average for each of the three time intervals (*i – iii*) and took from each hunting group only the fastest singleton hunter and compared it with group size two, three, and four. We conducted a similar linear mixed-effect model (LME) as described above for which we log-transformed the outcome-variable ((log(*tt*-1.7); log(*i*-0.25); log(*ii*-0.15); log(*iii*+0.3)) with the difference that we performed the analyses for each of the five groups separately.

Further we assessed the hunting efficiency of each individual on the single and group hunting level and checked for a possible correlation. For the single hunting level, we took the ranks as previously calculated. Then we were using a generalized linear mixed-effect model (GLMM) with binary response (1 if the faster as single is also the one who catches the prey in group, 0 otherwise) in which we used *group size* as a fixed effect, and as random effects *group* and *testing time* nested within *group*. Using the estimate of this model, we compared the proportion of cases in which the quicker singleton is also the individual that catches the prey first, with values of 50% (in pairs), 33% (in groups with three) and 25% (in groups with four) representing random occurrence. Pairwise comparisons between group sizes were conducted using a post-hoc Tukey test.

To assess whether some individuals were more/less successful than other ones in catching the prey, we performed a Chi-square test for each group by comparing individual success with expected prey capture rates for all three group sizes combined. More precisely, we summed for each individual its total number of successes (observed values) and calculated predicted values by summing up the number of trials in pairs divided by 2, the number of trials in triplets divided by 3, and the number of trials in quadruplets divided by 4. In order to conduct the Chi-square tests the expected prey capture rates were rounded to the nearest whole number.

2.3 Results

In our analyses, we controlled for day as increased familiarity with the experimental setup may affect hunting efficiency. Furthermore, time of day may affect performance due to changes in hunger levels and hence motivation. Indeed, we found significant effects for ´day´. As these effects are not the focus of our study, we report the results in Supplementary Tables S1 and S2. The main results reported below are also controlled for day and time of day.

2.3.1 General effect of group size on hunting success

From all valid trials (962) the fish successfully captured the prey within 180 seconds in 886 trials. Single fish failed in more than 16% of the hunts (70 trials) while pairs in about 2% (4 trials) and groups of three or four individuals in less than 1% of the cases (1 trial), Table 2. A closer analysis revealed that group size significantly affected the probability to fail to catch the prey within the maximal 3 min duration of a trial (GLMM; Wald chisquare-test: χ^2 ($df = 3$, $n = 20$) = 36.53, $P < 0.001$). Pairwise comparisons between group sizes assessed with post-hoc Tukey test revealed that single hunting individuals failed to catch the prey significantly more often than pairs ($z = -4.100$, $P < 0.001$) and groups of three ($z = -3.446$, $P = 0.003$) and four ($z = -3.387$, $P = 0.003$). No difference was found between pairs and groups of three ($z = -1.107$, $P = 0.663$) or four individuals (z = -1.055, P = 0.696), neither between groups of three and four individuals (z = 0.041, P = 1), Figure 2.

2.3.2 Effect of "group size" on the duration of successful hunts

Group size had a significant effect on the total time (*tt*) of the hunts (Anova Type I: F = 46.369, P < 0.001) and on all three time intervals (Anova Type I: Inverval *i*: F = 16.683, P < 0.001; Inverval *ii*: F = 21.988, P < 0.001; Inverval *iii*: F = 36.120, P < 0.001). With regard to the total time (*tt*), pairwise comparisons between group sizes assessed with post-hoc Tukey test revealed that single hunting individuals took significantly longer than pairs (z = -6.271, P < 0.001), groups of three (z = -7.904, P < 0.001) and groups of four (z = -9.710, P < 0.001). Pairs took significantly longer than groups of four (z = -3.727, P = 0.001). No significant differences were found between groups consisting of two and three individuals (z = -2.050, P = 0.166) nor between groups of three and four individuals (z = -1.586, P = 0.380), Figure 3.

The additional analysis of the total time (*tt*) revealed that the fastest singleton hunters of each group, with one exception (Supplementary Table S3), took longer to catch the prey than groups consisting of two up to four individuals (Figure 3).

With regard to the three different time intervals (*i* – *iii*), pairwise comparisons between group sizes assessed with post-hoc Tukey test revealed that single hunting individuals took significantly longer than pairs (Interval *i*: z = -4.638, P < 0.001; Interval *ii*: z = -4.005, P < 0.001; Interval *iii*: z = -6.872, P < 0.001), groups of three (Interval *i*: z = -4.073, P < 0.001; Interval *ii*: z = -5.952, P < 0.001; Interval *iii*: z = -6.538, P < 0.001) and groups of four (Interval *i*: z = -6.818, P < 0.001; Interval *ii*: z = -7.658, P < 0.001; Interval *iii*: z = -8.622, P < 0.001). Pairs took longer than groups of four for interval *ii* (z = -3.154, P = 0.009) and *iii* (z = -3.716, P = 0.001) and groups of three were slower than groups of four for interval *i* (z = -2.580, P = 0.048). Between groups consisting of two and three individuals, no significant differences in any of the three intervals were found, Figure 4. Additional analyses of the three time intervals (*i* – *iii*) revealed that on the third time interval, the fastest singleton hunters of each group took longer to catch the prey than groups consisting of two up to four individuals (Figure 4). Results in Supplementary Table S3.

2.3.3 Individual hunting success when solitary vs. group hunting

The most successful individuals (hunting as singletons) were not more successful than expected by chance when hunting in groups of any size (group size two with an expected 50% chance: $z = 2.082$, $P = 0.107$; group size three with an expected 33% chance: $z = 2.189$, $P = 0.082$; group size four with an expected chance of 25%: $z = 1.251$, $P = 0.503$).

2.3.4 Inter-individual variation in hunting success

All 20 analysed individuals from the five different groups managed to catch prey when hunting in pairs and most individuals did so when hunting in groups of three or four (Figure 5). Chi-square tests revealed that in group four and in group five, individuals differed with respect to hunting success when all group conditions were combined (Group 4: χ^2 ($df = 3$, $n = 105$) = 9.28, $P = 0.026$; Group 5: χ^2 ($df = 3$, $n = 132$) = 17.00, $P < 0.001$) while in the other three groups we could not find a difference (Group 1: χ^2 ($df = 3$, $n = 106$) = 4.56, $P = 0.207$; Group 2: χ^2 ($df = 3$, $n = 136$) = 0.21, $P = 0.976$; Group 3: χ^2 ($df = 3$, n = 47) = 2.87, $P = 0.412$). In group four, individual (D) performed well below chance, being only successful in 9 trials relative to an expected success of 25. In group five, individuals (A) & (B) performed poorly (A: 15 / 33; B 18 / 33 (trials with success / expected success)) while individuals (C) & (D) performed above chance levels (C: 47 / 34; D 52 / 34 (trials with success / expected success)), Table 3.

2.4 Discussion

The primary purpose of this study was to experimentally examine whether likelihood and speed of prey capture is a function of hunting group size. Indeed, the results show a link between group size and these measures of overall hunting success. Groups of all sizes performed better than singletons, and groups of four individuals caught prey faster than groups of two individuals. Thus, our experiment fits various previous correlational evidence showing that prey capture is positively correlated with hunting group size (Packer et al., 1990; Stander, 1992b). A second question was whether individuals' lone hunting success predicts their success when hunting in a group. We found no evidence for this hypothesis. Below, we will discuss these two major findings in more detail.

2.4.1 Hunting success probability and speed of success as a function of group size

From the video footage, two main factors emerged to explain why singletons sometimes failed to capture a prey while groups of any size virtually never failed. First, two or more individuals hunting simultaneously made it highly unlikely that a prey leaving the shelter would go unnoticed. Second, the presence of two or more individuals made it more likely that prey was caught before it could move back to the centre where it would have been largely out of reach. These results are analogous to the ‘many eyes and ears’ benefits that enable groups of prey to increase the likelihood of spotting a predator and to flee in time (Kenward, 1978). The same logic applies to the increased speed of capture as a function of group size at all stages of the hunt: groups achieved faster initiation, faster startling of prey, and faster capture of prey in accessible position. At least for our experiments with a maximum of four individuals, there was no evidence that larger groups cause so much interference between individuals thereby decreasing the speed of capture. Furthermore, our results indicate that it is predominantly the last stage of the hunt, i.e. the prey capture, where even otherwise fast singleton hunters experience reduced efficiency compared to groups of any size (Figure 4).

It is important to point out that our results should be qualified as we used a specific experimental setup, which was likely influential in producing the result that groups of four were about double as fast in capturing prey than groups of two and four times as fast as singletons. The task was much easier to solve than hunting under natural conditions, where most attempts to pry prey out of its shelter fail (Strubin et al., 2011; authors unpublished observations). Our shelter was smaller and more accessible than natural hiding places, and the invertebrates used in our experiments were very likely easier to catch than a prey fish: they responded with a saltatory move to being disturbed and then remained briefly where the move took them, readily accessible to a hunter. Habitat structure has been suggested to influence the group size of hunters, for example in the chimpanzees of the Taï forest in Ivory Coast (Boesch and

Boesch, 1989). However, such results, including the results of the current study, do not allow us to draw conclusions about optimal hunting group size. To assess this, the benefits of increased hunting efficiency in groups would need to be corrected for increased competition under natural conditions. Nevertheless, the fact that singletons both repeatedly failed to catch prey, and when they did they took much longer than groups in our experimental design, suggests that singletons would indeed be highly inefficient in a natural habitat, making hunting in groups of two or more individuals a win-win situation (unless group size exceeds a critical threshold, which we have yet to determine).

In order to assess the impact of group size on hunting success and efficiency more accurately, we suggest that future studies employ an experimental setup in which a single hunter would almost always fail to catch the prey within a certain time window, for example by adding more structures to provide more hiding opportunities in a shelter. Pushing the probability of a singleton’s hunting success clearly below 25% would allow for the possibility that groups of up to four individuals can obtain a higher prey capture rate per participant than singletons.

2.4.2 What kind of cooperation game may describe cooperative hunting in yellow saddle goatfish?

Focusing on the hunting success of individuals, we found no relation between the fastest singleton hunters’ success rates (based on speed of capture) and their success when hunting in groups (based on number of successful captures). Furthermore, we found that with few exceptions, individuals were rather similar with respect to capture probabilities when hunting in groups. The combination of these two results has several implications. First, it appears that the higher capture efficiency of groups was not simply a function of the presence of the best solitary hunters compensating for the inefficiency of the other group members. Instead, being in a group increases hunting efficiency independently of individual skills when hunting alone, i.e. through the coordinated effort. Second, the results suggest that joint hunting is typically mutually beneficial if the task gets sufficiently difficult, leading to an overall cooperative outcome. Finally, the results suggest that some additional or different skills play a role in individual success when hunting in a group compared to hunting alone.

Individual capture rates are the key factor defining success as yellow saddle goatfish swallow a captured prey immediately and whole. In contrast to most mammalian predators, there is hence no carcass to be shared, which changes the game-theoretic structure of a joint hunt (Packer and Ruttan, 1988). With a carcass, cooperation during the hunt may yield by-product benefits to all involved individuals due to increased efficiency (Brown, 1983a), leading to individuals benefitting unconditionally from joining as long as the cost of joining is more than compensated by the increase in capture probability (Lamprecht, 1978). Conflict may only arise over the sharing of the carcass among hunters, a problem that does not exist when successful hunters immediately swallow the entire prey (Bshary et al., 2006).

In our specific case, prey may be startled by one individual with its barbels but then consumed by another individual that was waiting in the direction of prey flight. While the extent to which this happens needs to be quantified, we hypothesise that the cooperative hunting in yellow saddle goatfish is well described by a Snowdrift game (when two players are involved) (Sugden, 1986) or a Volunteer's Dilemma game (when n players are involved) (Diekmann, 1985). In these games, cooperative and defective behaviour are both under negative frequency dependent selection, as the best responses are to cooperate with a cheater and to cheat with a co-operator. Applied to our reef, it may be best to insert the barbels if no one else does it and best to wait if others already inserted their barbels. This possibility clearly needs further investigation, with a particular emphasis on individual decision rules. According to theoretical predictions, it is possible that all individuals insert barbels with a certain frequency (Archetti, 2009), but alternatively yellow saddle goatfish individuals might split into producers and scroungers (Barnard and Sibly, 1981) which has been documented in various bird species in the context of finding profitable patches (Giraldeau et al., 1994; Giraldeau et al., 1990). In conclusion, group hunting in yellow saddle goatfish leads to an increased overall hunting efficiency due to an effect of the number of participants, and likely to different skills they employ to engage in such cooperative hunts, rather than the summation of individual hunters' abilities. Yellow saddle goatfish hence provide a rare opportunity to study individual strategies in N-player cooperation games in a non-human animal, using an experimental approach in an ecologically relevant context.

2.5 Data accessibility

The data and script for this study will be archived and available to editors and reviewers prior publication.

2.6 Author contributions

MS and RB designed the study. MS and HS collected the data. MS and HS analysed the data. MS and RB wrote the paper.

2.7 Competing financial interests

We declare no competing financial interests.

2.8 Acknowledgements

We thank Radu Alexandru Slobodeanu for statistical support and Jennifer McClung for reviewing our manuscript. We also thank Claire Meugnier and Moustafa Elfar for their help during the experiments and data collection as well as Salem Hassan and Tom Ruthenberg for their help in catching fish and the technical support. Further, we thank the local staff Ibrahim and Talat for technical support and to keep our lab clean and tidy. Finally, we thank Magdy El-Alwany, scientific advisor of the Marine Environmental Center from Suez Canal University. The project was funded by the Swiss Science Foundation (individual grant to RB).

We dedicate this paper in loving memory to Andy Tischer, the founder of the Dahab Marine Research Center, who was tragically lost during the course of this work.

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2.10 Tables and Figures

Table 1. Possible testing combinations for one up to four individuals. **(a)** Given are all possible testing combinations for single hunting fishes and hunting groups containing two, three and four fishes. Letters A-D represents individuals. **(b)** All possible testing combinations from Table 1a were counterbalanced for *day* and *testing time* in a Latin Square. The comma splits the different sets within the same day and testing time.

(a)

Single hunting fishes				Groups of										
				Two						Three				Four
A	B	C	D	AB	CD	AC	BD	AD	BC	ABC	BCD	ACD	ABD	ABCD

(b)

Testing time Day	07:00	10:00	13:00	16:00
1	A,B,C,D	AB,CD	ABC	ABCD
2	ABCD	B,C,D,A	AC,BD	BCD
3	ACD	ABCD	C,D,A,B	AD,BC
4	----------	ABD	ABCD	D,A,B,C

Table 2. All valid trials obtained from the four different group sizes. Valid experimental trials were split in cases in which prey was caught within 180 s after the onset of a trial ‘Yes’ and cases in which prey was not caught ‘No’.

Group size	**Valid experimental trials**	**Prey caught within 180 seconds**	
		Yes	No
1	428	358	70 (16.36%)
2	198	194	4 (2.02 %)
3	173	172	1 (0.58 %)
4	163	162	1 (0.61 %)
Total	962	886	76 (7.90 %)

Table 3. Successful trials in relation to the expected success. Total number of trials (sum from all trials of group size 2, 3 and 4) in which an individual succeeded in relation to the expected success (sum from all trials of group size 2, 3 and 4 in which an individual participated divided by the number of hunters of each group size). Expected success was rounded to the nearest whole number.

	Individual A		**Individual B**		**Individual C**		**Individual D**	
	Total of:		Total of:		Total of:		Total of:	
Group	successful trials	expected success	successful trials	expected success	successful trials	expected success	successful trials	expected success
One	19	26	18	25	30	27	39	27
Two	35	34	31	34	36	34	34	34
Three	14	13	18	13	13	14	2	6
Four	32	27	37	28	27	25	9	25
Five	15	33	18	33	47	34	52	34

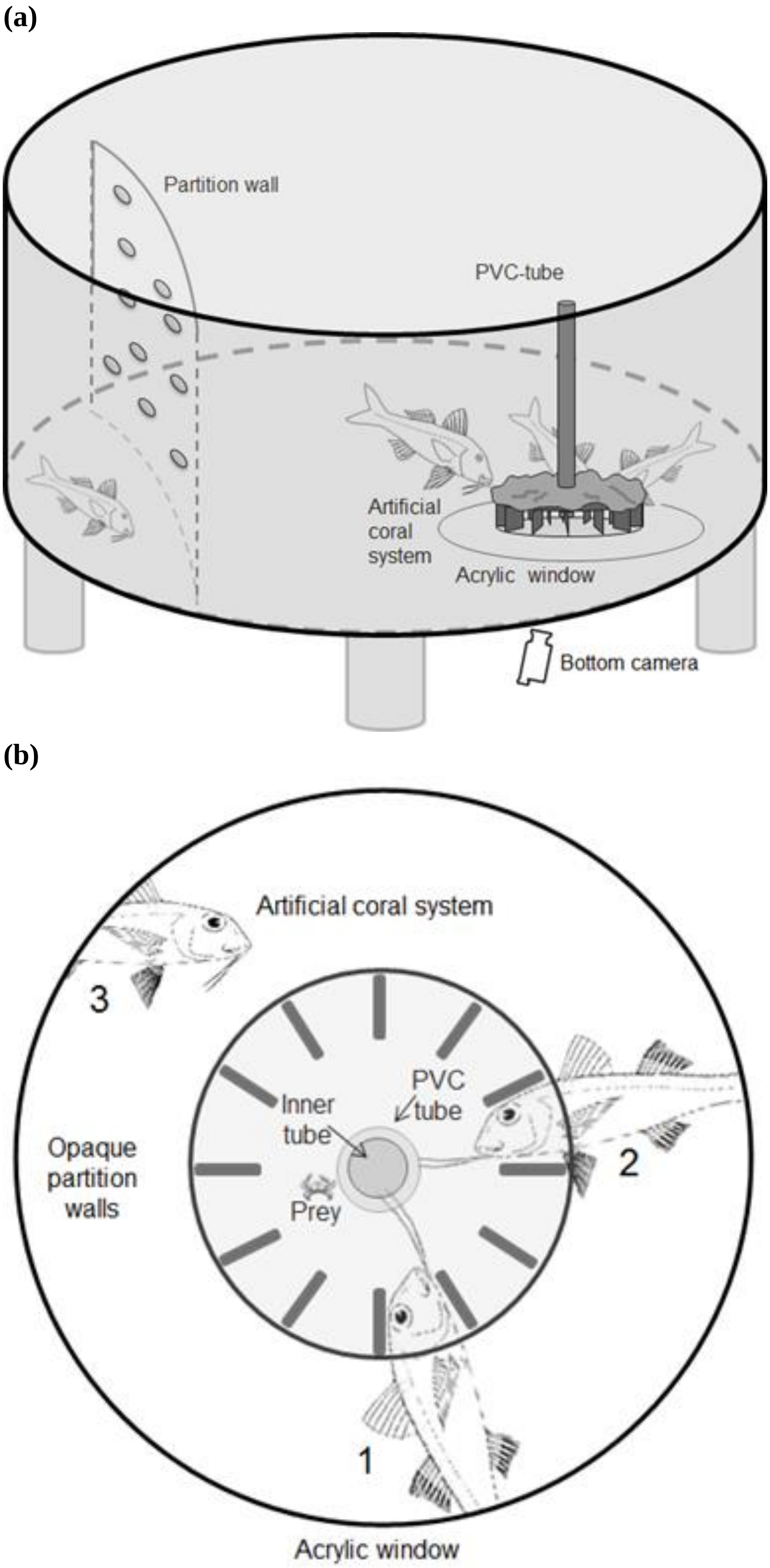

Figure 1. (a) Experimental tank with a diameter of 138 cm and a water column of 39 cm (side view). On the left side, an opaque and ecliptic partition wall with small holes for water

exchange to separate experimental- from non-experimental fish. On the right side, a round acrylic window (30 cm in diameter) glued into the bottom for observational purposes. An artificial, removable experimental system, containing a transparent acrylic bottom, placed above the acrylic window. Through an opaque PVC tube, a prey can be introduced to the coral reef. An HD camera (Sony) placed below the tank. In this scenario, three yellow saddle goatfish are hunting for the prey while the fourth individual is separated.

(b) Bottom-up view through the acrylic window. Visible are the three hunting yellow saddle goatfish, the artificial coral reef with the transparent bottom, the 12 opaque partition walls and the PVC tube with the inner tube to release the crab into the system. In this scenario two yellow saddle goatfish (no. 1 and 2) are chasing the crab by squeezing themselves between the partition walls and introducing their barbels. No. 3 is not introducing the barbels into the system, but because of its proximity to the system still considered as participating in the hunt.

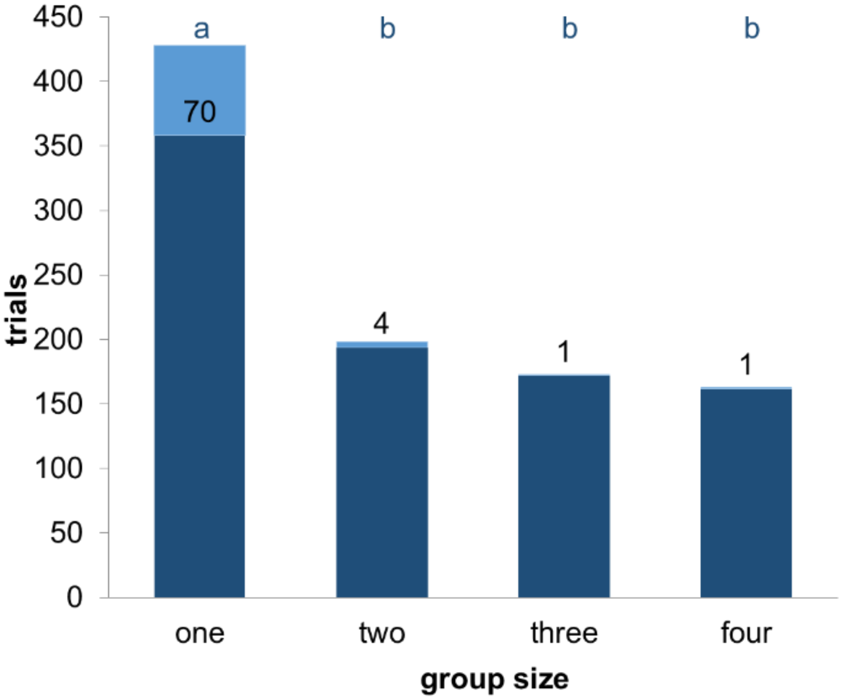

Figure 2. All the valid experimental trials of single hunting fish and groups consisting of two, three and four individuals. Darker parts of the bar represent all the trials in which the prey was caught within 180s after the onset of a trial and lighter parts (additionally shown as numbers in / above the bars) represent the trials in which the prey was not caught. Letters (a, b) indicate significant differences between different group sizes.

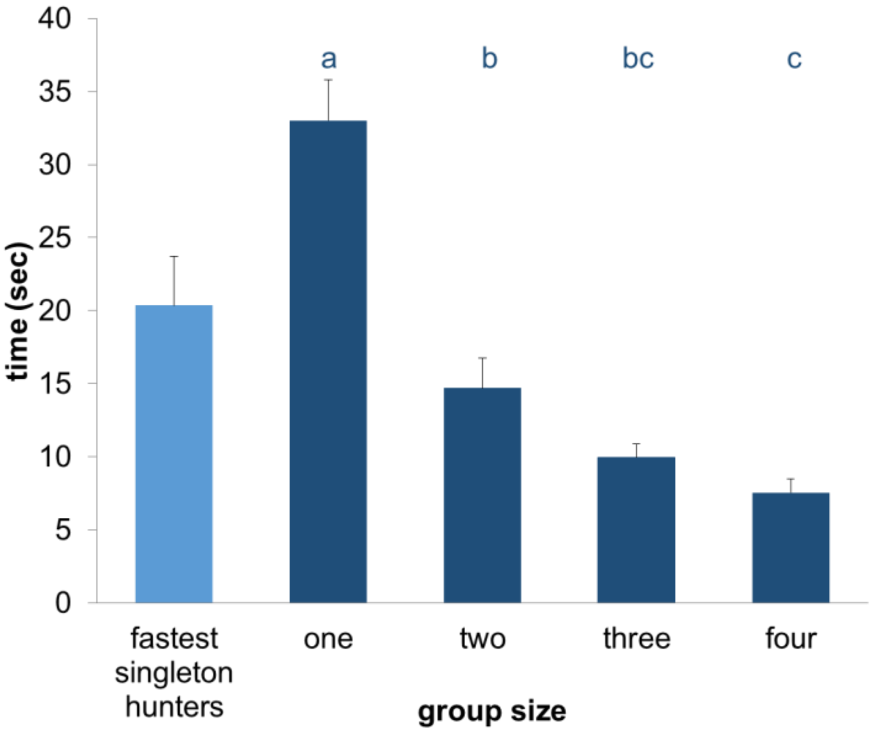

Figure 3. Dark bars represent the mean of the total time the different sized groups needed to catch the prey. The light bar represents the mean of the total time of the fastest singleton hunters of each group (*n*=5) needed to catch the prey. Whiskers indicate the standard errors and letters (a – c) the significant differences between different group sizes.

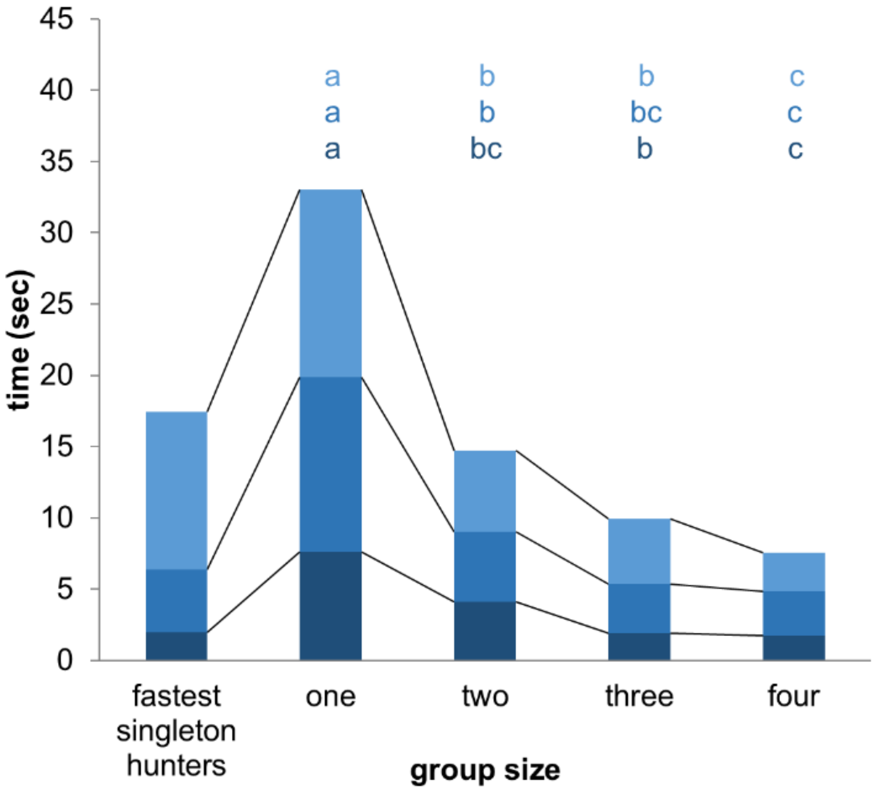

Figure 4. The second to fifth bar represent the mean amount of time the different group sizes (groups one to four) needed to catch the prey. Each bar contains the three different time intervals measured. Dark: First interval (from the moment the tube was lifted up until either of the fish inserted barbels for the first time into the system); Intermediate: Second interval (from the first insertion of the barbels until the prey was touched for the first time); Light: Third interval (from the first touch of the prey until prey capture). Letters (a – c) indicate significant differences between different group sizes. The first bar corresponds to the mean amount of time the fastest singleton hunters per time interval needed to catch the prey.

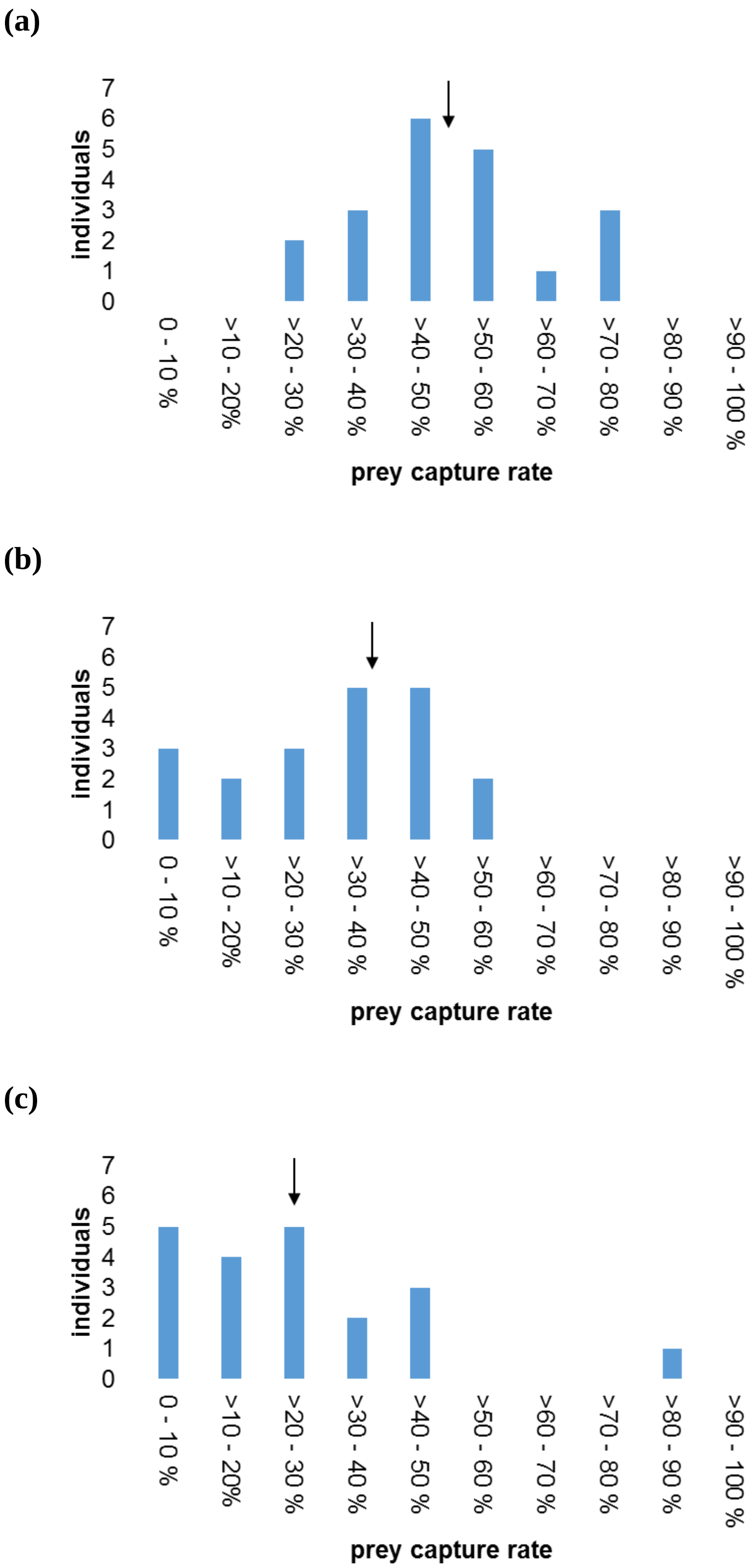

Figure 5. Inter individual hunting success within the different group sizes (**a**: two, **b**: three, **c**: four). The arrow in each graph indicates the expected prey capture rate for each individual (**a**: 50%, **b**: 33%, **c**: 25%) (*n*=20).

2.11 Supplementary materials for chapter 2

Table S1. Effect of Day and Testing time on the performance. Anova Type I (sequential) of the LMM with *day* and *testing time* as fixed effects and *group* nested within *day* as random effect. Significant results are marked bold.

			Three time intervals					
	Total time		***i***		***ii***		***iii***	
Effects	***F* - value**	***P* - value**	***F* - value**	***P* - value**	***F* - value**	***P* - value**	***F* - value**	***P* - value**
Day	$F_{3,12}$=5.618	**0.012**	$F_{3,12}$=5.169	**0.016**	$F_{3,12}$=6.239	**0.009**	$F_{3,12}$=1.465	0.273
Testing time	$F_{3,115}$=0.943	0.423	$F_{3,112}$=2.410	0.071	$F_{3,114}$=1.111	0.348	$F_{3,113}$=1.837	0.145

Table S2. Pairwise comparisons between different days. Pairwise comparisons between different days for the *total time* (from lifting up the tube until prey capture) and for each of the *three time intervals* (i: tubeup to barbelintro; ii: barbelintro to barbeltouch; iii: barbeltouch to prey capture). Results obtained with Tukey test. Significant results are marked bold.

			Three time intervals					
	Total time		**i**		**ii**		**iii**	
Day	***z* - value**	***P* - value**	***z* - value**	***P* - value**	***z* - value**	***P* - value**	***z* - value**	***P* - value**
1 with 2	-2.729	**0.032**	-3.402	**0.004**	-3.002	**0.014**	-0.744	0.879
1 with 3	-3.585	**0.002**	-3.301	**0.005**	-3.394	**0.004**	-1.797	0.275
1 with 4	-3.513	**0.002**	-3.709	**0.001**	-3.94	< **0.001**	-0.714	0.892
2 with 3	-0.752	0.876	0.24	0.9951	-0.26	0.994	-1	0.749
2 with 4	-0.817	0.847	-0.395	0.9791	-0.942	0.782	0.012	1
3 with 4	-0.103	1	-0.638	0.9196	-0.717	0.890	1.006	0.746

Table S3. Fastest singleton hunters in comparison to hunting groups. Given for each group (for the total time (tt), and the three time intervals (i-iii)) whether the fastest singleton hunter (group size *1*) took longer (neg. estimate for the difference), respectively was faster (pos. estimate for the differences) than groups consisting of two, three or four hunters. Significant p-values in bold; neg. estimates for the difference highlighted grey.

		total time (tt)				**time interval (i)**				**time interval (ii)**				**time interval (iii)**			
group	**group size**	***estimates***	***df***	**t - value**	***p* - value**	***estimates***	***df***	**t - value**	***p* - value**	***estimates***	***df***	**t - value**	***p* - value**	***estimates***	***df***	**t - value**	***p* - value**
1	*1*	*2.8512*				*1.4442*				*0.8205*				*1.4737*			
	2-*1*	-0.5032	7	-1.0388	0.3334	-0.5546	6	-1.7104	0.138	0.0607	7	0.066	0.9492	0.4208	7	0.5874	0.5754
	3-*1*	-0.5536	7	-1.1429	0.2906	-0.5338	6	-1.6462	0.1508	0.4645	7	0.5049	0.6291	-0.0324	7	-0.0452	0.9652
	4-*1*	-0.9942	7	-2.2169	0.0622	-1.0026	6	-3.3868	**0.0147**	0.3191	7	0.3747	0.719	-0.285	7	-0.4297	0.6803
2	*1*	*2.8302*				*0.6077*				*0.8561*				*2.9559*			
	2-*1*	-0.4151	7	-2.1269	0.071	0.18711	7	0.563	0.591	0.657	7	2.1806	0.0656	-1.3288	7	-3.8055	**0.0067**
	3-*1*	-0.9722	7	-4.9811	**0.0016**	0.147	7	0.4424	0.6716	-0.6203	7	-2.0591	0.0785	-1.2663	7	-3.6266	**0.0084**
	4-*1*	-1.6499	7	-9.2888	< **0.0001**	-0.3768	7	-1.2474	0.2524	-0.4437	7	-1.6081	0.1518	-2.2529	7	-7.0638	**0.0002**
3	*1*	*3.2425*				*-0.5026*				*0.9794*				*1.0522*			
	2-*1*	-0.5524	7	-1.0971	0.3089	0.5005	7	0.5238	0.6166	0.3141	6	0.7018	0.5091	0.3788	6	0.6573	0.5354
	3-*1*	-1.0745	7	-2.1339	0.0703	0.5773	7	0.6042	0.5648	-0.0809	6	-1.807	0.8626	0.4513	6	0.8257	0.4406
	4-*1*	-1.3622	7	-2.922	**0.0223**	-0.4812	7	-0.5508	0.5989	0.164	6	0.3917	0.7088	-0.0217	6	-0.0415	0.9683
4	*1*	*2.1878*				*-0.6931*				*1.1275*				*1.7503*			
	2-*1*	0.648	7	1.7573	0.1294	1.6765	6	2.7272	**0.0343**	0.7121	6	1.5315	0.1765	-0.265	7	-0.8855	0.4053
	3-*1*	-0.2211	7	-0.6028	0.5687	-0.0229	6	-0.0372	0.9715	0.2683	6	0.577	0.5849	-0.2032	7	-0.6791	0.5189
	4-*1*	-0.6338	7	-1.8432	0.1149	-0.153	6	-0.2661	0.7991	-1.1058	6	-0.2431	0.816	-0.6386	7	-2.305	0.0546
5	*1*	*2.5463*				*-0.1599*				*1.1917*				*2.0952*			
	2-*1*	-0.539	7	-0.9911	0.3546	-0.376	7	-0.6566	0.5324	-0.327	7	-0.7328	0.4875	-0.5104	7	-0.9275	0.3845
	3-*1*	-1.1337	7	-2.0845	0.0756	-0.8279	7	-1.4456	0.1915	-0.5662	7	-1.2691	0.245	-0.8514	7	-1.547	0.1657
	4-*1*	-0.9799	7	-1.9727	0.0891	-0.9422	7	-1.777	0.1188	-0.1136	7	-0.2786	0.7886	-1.0228	7	-2.0077	0.0847

CHAPTER 3 | PUBLIC GOODS WITH LOW PRODUCER-SCROUNGER DYNAMICS IN COLLABORATIVELY HUNTING YELLOW SADDLE GOATFISH

Authors: Marc Steinegger[1] & Redouan Bshary[1]

Affiliation: [1]Institute of Biology, University of Neuchâtel, Emile-Argand 11, 2000 Neuchâtel, Switzerland

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Abstract

Lab-based games with known payoff matrices have yielded important insights regarding the decision rules underlying N-player cooperation in humans. In contrast, we know little about the payoff structure and decision rules underlying group cooperation in other species. Here, we address these issues with experimental data on collaboratively hunting yellow saddle goatfish (*Parupeneus cyclostomus*). These fish coordinate by inserting their barbels into different entrances to crevices in coral reefs to startle hiding prey out of its shelter. We presented invertebrate prey in an artificial coral reef system and measured hunting performance as a function of manipulated group size, ranging from 1-4 individuals. We found that in all group situations, being the first to insert barbels into the system lowered the probability of success. In contrast, being the first to actually touch the prey with the barbels predicted success. Thus, yellow saddle goatfish face a Snowdrift game (2 players), or a Volunteer's Dilemma (>2 players) payoff matrix, respectively. Individuals adjusted by reducing barbel insertion rates from singleton to group hunts but do not distinguish between 2-player and N-player situations, while theory would predict a decline of effort with increasing group size. As individual insertion rates as singletons do not predict insertion rates in group situations, yellow saddle goatfish apparently make independent decisions about how to behave when alone and when with others. Our study highlights the importance of exploring cooperation games with intermediate levels of conflicts of interest between partners.

Keywords: cooperation, public goods, producer-scrounger, Snowdrift game, Volunteer's Dilemma, yellow saddle goatfish

3.1 Introduction

To cooperate between unrelated individuals often involves an investment, i.e. to act in a way that current payoffs are lower than possible with alternative behavioural options. Any investment needs to yield more than compensating future benefits to be under positive selection. The potentially resulting problems are typically illustrated with the iterated Prisoner's Dilemma game, where two players have the option to either cooperate or to defect (Luce and Raiffa, 1957). The payoffs are such that mutual cooperation yields higher payoffs for both players than mutual defection does, but that defection yields a higher payoff than to cooperate irrespective of the partner's action. As a consequence, studies of iterated Prisoner's Dilemma games typically focussed on the question how defection can be overcome in order to achieve stable cooperation, describing a variety of conditionally cooperative strategies as solutions (Binmore, 2005; Dugatkin, 1997). The issue of how to control defection becomes particularly challenging when more than two players interact simultaneously (henceforth called N-player games), yielding a public goods problem and leading to the 'tragedy of the commons' (Hardin, 1968). A large corpus of literature aims at explaining how humans may achieve cooperation in Public Goods games (Fehr and Gächter, 2000; Fehr and Gächter, 2002; Gintis et al., 2003; Ostrom, 1990).

Alternatively, it has been pointed out that many cooperative behaviours may be inherently self-serving, while partners benefit as a by-product (Brown, 1983). Various benefits of group-living seem to fit this scenario, like safety in numbers, confusion effects and early detection of predators (i.e. the selfish herd (Hamilton, 1971)). The concept of group augmentation includes these examples (Kokko et al., 2001). A third type of payoff distribution that has attracted comparatively less attention is that to cooperate and to defect may both be under positive selection if rare and under negative selection if frequent (negative frequency-dependent selection). Such a dynamic is captured by the Snowdrift game (SD) (Sugden, 1986) for two player interactions, where the best response to the partner defecting is to cooperate and vice versa. The N-player version of this game is called the Volunteer's Dilemma (VD) (Diekmann, 1985). Due to a lack of studies of such payoff distributions, it is largely unclear what kind of strategies individuals may use in such games. Theoretical analyses of strategies are abound for the two player version under its alternative name, the hawk-dove game (Maynard Smith and Price, 1973). In theory, all players may cooperate (play dove) with a certain probability or divide into doves (cooperators) and defectors (hawks) in proportions that reflect the relationship between the benefits of receiving help and the costs of giving help (Maynard Smith, 1982). A recent reinforcement learning model proposes that pure strategies are more likely to emerge (Dridi and Lehmann, 2014). In the Volunteer's Dilemma, analyses focused on the general principle and assumed that everybody cooperates with a certain probability (Archetti, 2009a; Archetti, 2009b; Archetti and Scheuring, 2011; Archetti and Scheuring, 2012).

It has been argued that the Volunteer's Dilemma payoff distribution may apply to more natural cases of cooperation than the N-player Prisoner's Dilemma payoff distribution (Archetti, 2009a; Archetti and Scheuring, 2011; Archetti and Scheuring, 2012. Examples are the formation of fruiting bodies in social amoebas (e.g. the social amoeba (*Dictyostelium discoideum*) (Bonner, 2009)) or the production of yeast (Gore et al., 2009)). The argument is based on the proposition that many public goods can be achieved by few individuals contributing, where additional contributors would only add diminishing returns and hence actually lower the overall group net benefit (i.e. the benefit function is supposed to be sigmoid). In contrast, the NPD assumes a linear relationship between the amount of contributions and the benefits achieved (Archetti and Scheuring, 2011). The question of the relative ecological relevance of the two types of payoff distributions can only be addressed with real biological case studies. Here, we study the game structure and individual strategies within a classic context of animal cooperation: cooperative hunting. A variety of vertebrate species belonging to different mammalian, bird and fish clades, are known to hunt in groups (Lang et al., 2017). Various studies report positive correlations between the number of participants and hunting success (Gotmark et al., 1986; Herbert-Read et al., 2016; Kruuk, 1972; MacNulty et al., 2012; Schaller, 2009; Stander, 1992). The increased hunting success probability has been demonstrated causally in yellow saddle goatfish *Parupeneus cyclostomus*, our study species (Steinegger et al. submitted).

Yellow saddle goatfish live on coral reefs where they hunt small fish and crustaceans (Randall, 1983). They coordinate their hunting actions during two phases of a hunt. The first phase is characterized by one individual accelerating towards a potential prey, which leads to partners spreading out and thereby potentially blocking a prey's escape routes in the complex three-dimensional coral reef structure (Steinegger et al., 2018; Strubin et al., 2011). Most often, the prey escapes into a crevice, which may lead to the second phase in which group members surround the reef structure and insert their barbels into any crevice of the reef structure (there are often tunnel systems), trying to startle prey into making mistakes so that it can be caught. Whoever catches a prey, swallows it immediately and whole, so there is no sharing (Strubin et al., 2011; Steinegger et al. submitted). We exposed one to four yellow goatfish to the second phase, providing invertebrate prey in an artificial reef (Figure 1a). For all group situations and each trial, we noted which individual inserted its barbels first, which one touched the prey first, and which one captured and ate the prey. Singleton trials were used as a baseline to quantify on which effort individuals insert their barbels when all costs and resulting benefits from doing so are theirs. This effort was then compared to the 2-player situation and the N-player situations. We first asked which kind of payoff matrix best describes the joint hunt. While it is clear that barbels must be inserted in order to achieve any hunting success, the payoff matrix could conform to a PD / NPD if being the first to insert the barbels yields virtually zero hunting success. Alternatively, if inserting the barbels first yields a lower success than inserting barbels later, in combination with touching the prey first being the best predictor of hunting success, the payoff matrix would conform to a SD / VD. Finally, if the individual that inserts its barbels first is the most likely to catch the prey, any benefits to other individuals would be a by-product of a self-serving action. If the payoff matrix shows that delaying barbel insertion is beneficial, we expected that individuals reduce barbel insertions when hunting in groups compared to solitary hunts, and an overall negative correlation between group size and barbel insertion effort as the game changes from a 2-player situation to N-player situations. Further we tested whether there is individual variation in barbel insertion effort and if so, whether it correlates to body condition or group size. We could expect a potential dominance of larger individuals that hinder smaller ones from inserting barbels or that individuals with a higher body condition insert on a higher effort as proposed by the handicap principle (Roberts, 1998). Finally, we tested whether individual barbel insertion correlates between the four conditions (group size 1-4). These analyses will show how consistent individuals behave in the task and in how far different individuals play different strategies.

3.2 Materials & Methods

All experiments were conducted between February and October 2011 at the Dahab Marine Research Center (DMRC) Egypt, Red Sea. Yellow saddle goatfish belong to the family of Mullidae (goatfishes) and are characterized by typically having two well-developed barbels, which are highly maneuverable organs containing taste buds underneath their mouth (McCormick, 1993). They usually hunt in pairs or small groups consisting of three to five individuals of similar size but may also be observed in larger groups (Strubin et al., 2011).

While single individuals often hunt in sandy areas for invertebrates, pairs and groups of yellow saddle goatfish hunt over the coral-reef top, mainly on small fish hiding in shelters (Randall, 1983; Strubin et al., 2011). Hunting groups of yellow saddle goatfish are quite stable with individuals hunting together over several successive attempts (Strubin et al., 2011).

20 wild-caught fish were used to form five groups consisting of four individuals. The mean (+s.d.) total length (TL), body weight and body condition (Fulton's condition factor; adapted from Froese (2006)) of the 20 fish were 188 + 18.26 mm, 56.8 + 16.05 g and 2.15 + 0.25, Supplementary Table S1. For individual recognition, each fish was marked with a small V-shaped cut in their ventral or pectoral fin membrane, following a technique by Noakes and Leatherland (1977). After the experiments, all fish were released to the site of capture. The general methods of catching, training and the experimental setup are described in detail in Steinegger et al. submitted, a paper that focuses on the effect of group size on hunting success. Here, we provide a short summary and focus on the details of the current study.

3.2.1 Laboratory and experimental set-up

The fish were kept in the 4 x 4 m air-conditioned laboratory of the DMRC, with a light regime that matched the local sunrise and sunset with 10 min twilight at the beginning and end of the light phase. The water temperature was kept at 27 ± 2 °C. A maximum of two groups was kept simultaneously, using two round plastic tanks with a diameter of 138 cm (water column of 39 cm). On one side of the tank there was a removable opaque and ecliptic partition wall to separate experimental- from non-experimental individuals and on the bottom of a window (30 cm) in diameter for filming purpose (Steinegger et al. submitted). A round artificial coral reef, with 12 similarly sized slots that provide access to the prey was placed in the middle of the window (Figure 1a). In order to increase the difficulty level of visual detection of the prey, the partition walls of the twelve slots were darkened by black tape. Via an opaque PVC tube, the experimenter put a live invertebrate prey to the center of the artificial reef that was at first invisible to the fish. By pulling-up a smaller tube that was within the PVC tube, the prey became visible and available to the hunting fish. Yellow saddle goatfish could then hunt for the prey via the 12 slots. Sizes of the slots were adapted to the size of the fish, in a way that they could partly enter the reef and almost reach to the center with their extended barbels (Figure 1a).

3.2.2 Experimental schedule

All fish had been trained prior to the beginning of the experiments to hunt crustaceans that were placed at the bottom centre of the structure (Steinegger et al., submitted). The four individuals in each tank were tested in all possible group sizes (one to four and individual-combinations) over the duration of four subsequent days following a Latin Square Model (Bradley, 1958) to counterbalance a possible effect of ‘day’ and ‘testing time’. Experimental sessions were conducted each day at 7:00, 10:00, 13:00 and 16:00. The amount of conducted trials per experimental session were adjusted to the tested group size (groups size one: 6 trials; group size two: 8 trials; group size three and four: 12 trials) resulting in a total of 1200 trials for the 5 tested groups.

3.2.3 Experimental procedure

Ten minutes before the start of an experiment, non-participating individuals were separated via the partition wall for acclimation reason. Then the experimenter started the first trial by adding a prey via the PVC tube to the center of the artificial reef. When no fish was visible from the window below, the prey was released and the trial started. A trial lasted until successful prey capture or, in case of failure, a maximum of 180 seconds (from the time the tube was pulled up). In order to keep the hunger level constant among all fish per tank, non-participating individuals were fed with the same proportion of crustacean as experimental fish. After each session, the partition wall was removed.

3.2.4 Video analysis

Trials were filmed with a camera (SONY HDR-CX350VE, Sony Electronics, Tokyo, Japan) that records 25 frames per second. Later, all trials were analysed with the program Adobe Premiere and judged valid or non-valid (Supplementary

Table S3 provides a complete overview on the criteria for valid / non-valid trials). As not all individuals participated in every trial, we corrected the number of assigned individuals per trial with the actual number of individuals participating actively in the hunt. For example, if in a specific trial with four assigned hunters (i.e. group size four) one individual did not participate, the group size was downgraded to three. Those individuals that were seen fully above the acrylic window during the trial time were considered as active participants.

We noted the identity of the individuals performing the following actions: i) being the first to insert barbels into system. ii) being the first to touch prey with barbels. iii) being the one capturing the prey (either by using barbels to touch the prey immediately before the capture or by direct capture, without using the barbels).

Furthermore, for each individual we quantified the frequency with which it inserted barbels into the system as a measure of ‘hunting effort’. More specifically, the moment the first individual inserted its barbels was set as time zero, and we analysed the video-frames after exactly one, two, three and four seconds to score which individuals were in proximity of the system (seen above the acrylic window) and which of them had at least a part of one barbel inserted into the system. If the prey was caught in less than 4 seconds after the first barbel insertion, we analyzed only the frames before the capture. If the prey was caught exactly during an assigned frame, that information was also discarded. Note that our method does not distinguish whether a high score was achieved with a single insertion over a long time or multiple insertions for shorter periods.

3.2.5 Statistical analysis

Statistical analyses were performed in R v. 3.5.1 (Team, 2018).

Depending on the statistical tests performed, not all valid trials were used: for the tests concerning the outcome of the hunt, i.e. which individual was successful, we excluded the trials (n = 77) in which the prey was not caught within the 180 sec trial-time; for the tests concerning the question which individual inserted first, or touched the prey first, respectively, the trials (n = 5) in which this was not observed were excluded (Supplementary Table S2).

We used a generalized linear mixed effect model (´glmer´ function in the R package ´lme4´ (Bates et al., 2014) with intercept only. The output variable is a binary response that scores whether or not the outcome of inserting the barbel first is the same as the outcome of capturing the prey (for the same individual); group, (nested) day and period are random effects. To test whether inserting the barbels first, or touching the prey first, respectively, affects the likelihood of catching the prey, the mean probability estimated by the model was tested against an offset value which is: 1/2, 1/3 and 1/4 for the respective group sizes two, three and four.

We used a linear mixed effect model (LMM; ´lmer´ function in the R package ´lme4´ (Bates et al., 2014)) with fish-ID as random factor accounting for pseudo-replication to estimate the relative proportion of barbel insertion effort for individuals who caught the prey in their respective group. By ‘relative proportion of barbel insertion effort’ we mean the difference between the actual proportion of a specific individual and the average proportion of all participating fish in each trial. Based on the LMM summary we assessed whether this relative proportion of hunting effort was significantly different from zero. We performed separate analyses for each group size.

We used a generalized linear model (GLM; ´glm´ function in the R package ´effects´ (Fox, 2003)) with Quasibinomial Error Distribution to test whether singletons made a significantly higher inserting effort than pairs or groups. We used day and periods as fixed factors in order to have an adjusted effect of the effective group size. Pairwise comparisons between the effective group sizes were conducted using a post-hoc Tukey test with the R package ´multcomp´ (Hothorn et al., 2008)).

To assess whether there are inter-individual differences with regard to the inserting effort, we calculated the effort for all four group sizes, separately for each trial, as described in the section “Video analysis” and then performed a Kruskal-Wallis Test.

To test whether body condition (Fulton’s condition factor) or total length had an effect on the barbel insertion effort, we used a linear mixed-effect model (LME) from the R package ´nlme´ (Pinheiro et al., 2015). The barbel insertion effort was the response variable, and the body condition, or the total length, respectively, functioning as a covariate with group size as a categorical predictor (the four group sizes were combined). Fish-ID nested within group-ID were added to the model as random factors. Post-hoc analyses were conducted with the R package ´emmeans´ (Lenth, 2018) to test the relationship of frequency of insertion and either total length or body condition within each level of the group size.

We used the same model to test whether first barbel insertion correlates with the barbel insertion effort.

To assess whether there are inter-individual differences with regard to inserting the barbels first during group trials, we performed Chi-square tests separately for each of the five groups. For each individual, we combined insertion events for group sizes two, three and four. We then compared the observed sum of each individual first inserting barbels with the expected proportion, by means of a glmer with binomial errors.

In order to assess whether the barbel insertion effort as a singleton correlates with insertion effort in groups, and whether individual insertion effort correlates between the different group size conditions, we performed linear mixed effects models (LMMs; ´lmer´ function in the R package ´lme4´) with random intercept and slopes, taking into account possible auto-correlation inside each of the five groups (group is set as random factor). P-values were then adjusted for multiple comparisons using the sequentially rejective multiple test procedure (Holm, 1979).

3.3 Results

3.3.1 Influence of barbel insertion on the individual hunting success

The individual inserting the barbels into the system first caught the prey with a significantly lower probability, independently of group size (GLMMs, 2 individuals: $z = -4.145$, $p < 0.001$, $n = 20$; 3 individuals: $z = -3.566$, $p < 0.001$, $n = 19$; 4 individuals: $z = -2.567$, $p = 0.010$, $n = 15$, Figure 2a). In contrast, the individual touching the prey first caught the prey significantly more often, irrespective of group size (GLMMs, 2 individuals: $z = 2.966$, $p = 0.003$, $n = 19$; 3 individuals: $z = 4.112$, $p < 0.001$, $n = 19$; 4 individuals: $z = 3.270$, $p = 0.001$, $n = 15$, Figure 2b).

On a trial by trial basis, there was no overall significant effect of an individual’s barbel insertion effort on its probability of success in any group size (group size two: t = -0.742, df = 16.88, p = 0.468; group size three: t = 0.564, df = 17.95, p = 0.579; group size four: t = 0.863, df = 17.85, p = 0.400, Figure 3).

3.3.2 Level of hunting effort as a function of the number of hunters

The number of hunters had a significant effect on the hunting effort (GLM; Anova Type II: $\chi^2 = 75.3$, df = 3 $p < 0.0001$). Generally, individuals inserted their barbels with a higher proportion (mean ± se: 0.750 ± 0.0219; n = 20) when hunting alone than when hunting in groups of two (mean ± se: 0.585 ± 0.0298; n = 20), three (mean ± se: 0.602 ± 0.0357; n = 19) or four individuals (mean ± se: 0.589 ± 0.0346; n = 16) (data taken for calculations from Table S3). Indeed, pairwise comparisons between “group sizes” assessed with post-hoc Tukey test revealed that individuals made a significantly higher hunting effort when hunting alone rather than in pairs (z = 6.567, $p < 0.001$), groups of three (z = 7.285, $p < 0.001$) or groups of four (z = 6.965, $p < 0.001$), Figure 4. No significant differences in individual barbel insertion effort were found between groups of different sizes (all $z \leq 0.813$, all $p \geq 0.8481$).

3.3.3 Inter-Individual variation in barbel inserting effort

In all of the group sizes we found a strong variability between the 20 different individuals regarding their barbel insertion effort (Kruskal-Wallis: singletons: $\chi^2 = 66.5$, df = 19, $p < 0.0001$; pairs: $\chi^2 = 57.4$ df = 19, $p < 0.0001$ three: $\chi^2 = 83.8$, df = 18, $p < 0.0001$; four: $\chi^2 = 47.1$, df = 15, $p < 0.0001$, Figure 5). The 20 singleton hunters varied in their barbel insertion effort from as low as 0.556 ± 0.053 (mean ± se) (n = 24) for individual “T” (group 2), up to 0.923 ± 0.027 (mean ± se) (n = 26) for individual “H” (group 4). The 20 in pair hunting individuals varied in their barbel insertion effort from as low as 0.375 ± 0.375 (mean ± se) (n = 2) for individual “D” (group 3), up to 0.772 ± 0.059 (mean ± se) (n = 27) for individual “Q” (group 5). The 19 in groups of three hunting individuals varied in their barbel insertion effort from as low as 0.205 ± 0.09 (mean ± se) (n = 13) for individual “J” (group 4), up to 0.852 ± 0.048 (mean ± se) (n = 31) for individual “Q” (group 5). Finally, the 16 in groups of four hunting individuals varied in their barbel insertion effort from as low as 0.250 ± 0.114 (mean ± se) (n = 14) for individual “J” (group 4), up to 0.763 ± 0.048

(mean ± se) (n = 26) for individual “Q” (group 5). For all results, see Supplementary Table S3.

We could not find a link between either total length or body condition and the barbel insertion effort (LME; interaction term of: total length and group size: $\chi^2 = 5.7$, df = 3, $p = 0.1279$; body condition and group size: $\chi^2 = 0.9$, df = 3, $p = 0.8311$). No significant interactions were found in any of the four different group sizes (total length: df = 18, all $t \leq 1.028$, all $p \geq 0.3178$; body condition: df = 18, all $t \leq 2.063$, all $p \geq 0.0538$).

3.3.4 Inter-individual differences with regard to inserting the barbels first

We found significant variation between individuals regarding the probability of inserting the barbels first in three of the five groups (Chi-square tests: Group 1: $\chi^2 = 15.4$, df = 3, $p = 0.0015$; Group 2: $\chi^2 = 10.0$, df = 3, $p = 0.0189$; Group 4: $\chi^2 = 9.2$, df = 3, $p = 0.0268$, Figure 6). Further analyses revealed that in group 1 individual “N” inserted the barbels first significantly less often than the other group members ($z = -2.114$, $p = 0.0345$). In group 2 we found a tendency that individual “W” inserted the barbels first less often than the other group members ($z = -1.927$, $p = 0.054$). For group 4, no specific individual caused the overall significant effect (all $z \leq -1.211$, all $p \geq 0.226$).

The probability of first barbel insertion was significantly linked to barbel insertion effort (group size two to four combined: $\chi^2 = 7.0$, df = 1, $p = 0.0082$).

3.3.5 Associations of individual inserting effort among different group sizes

Individual barbel insertion effort when hunting alone was not significantly correlated with insertion effort in groups of any size (group size two: n = 20, t = 2.344, adj. p = 0.0923; group size three: n = 19, t = 1.897, adj. p = 0.1529; group size four: n = 16, t = 1.438, adj. p = 0.1816, Figure 7). In contrast, individual effort correlated between groups of different sizes, i.e. an individual that inserted relatively on a higher/lower effort than others in groups of two also inserted relatively on a higher/lower effort in groups of three and four (two and three: n =

19, t = 5.34, adj. p < 0.001; two and four: n = 16, t = 4.879, adj. p = 0.0013; three and four: n = 16, t = 7.159, adj. p < 0.001).

3.4 Discussion

Joint hunting in yellow saddle goatfish can be divided into two phases: In the first phase, the individual detecting a prey first, “chaser,” accelerates towards the prey, which usually escapes into a crevice of a coral block (Strubin et al., 2011). The other hunters, “blockers,” then coordinate their action in relation to their distance to the “chaser” (Steinegger et al., 2018). In this study, we investigated the second phase of the joint hunt to find out which game yellow saddle goatfish play in order to pry out the prey from the coral rock. Our results clearly indicate that irrespective of the group size (two, three or four), inserting the barbels first lead to a decreased probability to catch the prey and hence to a reduced payoff in comparison to individuals not inserting first. It is important to mention that the decrease did not reach nearly zero (see Figure 2a), which responds to the payoff matrix of a SD / VD game. Beyond the first insertion, overall insertion effort is not correlated in any way to success probability. Indeed, inserting the barbels is a necessity as touching the prey first increased prey capture. First, we explain these findings in more details and then talk about the higher effort of singleton hunters compared to when hunting in groups. Then we discuss individual variations between the different group sizes by highlighting different explanations for these findings. Finally, we discuss the continuity of the hunting effort among the different group sizes, findings that were rather unexpected.

3.4.1 Why inserting first is bad and touching first is good

At the starting point of our experiment, a crab, a rather immobile prey, was placed in the center of the round artificial reef where it normally rested. The reef was designed in a way so that yellow saddle goatfish have to insert their barbels in order to reach in with the tip of the fully extended barbels to near the center in order to harass the prey. This action produces a public good. There is literally no other option for the hunters to pry out the prey. We observed that a nearby barbel triggers a prey-reaction (e.g. caused by the water pressure of the barbel movement or the visual detection) typically in the opposite direction of where the barbel was inserted. Group-hunting yellow saddle goatfish lineup around an obstacle with hidden prey in a way to keep the maximal distance from the hunting partners (Strubin et al., 2011), resulting in a scenario in which the escaping prey ends up in a spatial position closer to the hunting group members, which now have a better prey-access. Hence, not being the first to insert the barbels has a benefit, which is also clearly supported by our data. However, we could not find an increased success for the individuals that inserted on a general lower probability, indicating that inserting does not necessarily reduce the benefit. In fact, touching the prey first significantly increases the probability of catching the prey. Prey-touching prior to capture also seems to be linked (occurred in 768 trials) compared to capturing without prior touching the prey that occurred three times less (252 trials). Touching the prey with the chemosensory barbels provides information about the quality (as a food source) and potential escape-direction of the prey. Probably most importantly, touching the prey gives information about the prey's precise location, triggering the suction movement caused by a rapid mouth opening that allows capture if the prey is near the mouth (Supplementary Video). One or a combination of the above explanations can be a reason why touching the prey the first time translates into a significant higher capture success. Collectively said, to insert the barbels first is costly and contributes to the public good, while inserting at a later moment is beneficial and self-serving.

Freeriding (i.e. not to insert the barbels during the hunt) is a strategy that can most likely be excluded in the hunting yellow saddle goatfish, that eat their prey (i.e. under natural conditions small fish (Randall, 1983)) wholly and at once and leave no carcass that is shareable as known from other group hunting species (e.g. lions (Schaller, 2009); african wild dog (Creel and Creel, 1995); chimpanzees (Boesch, 1994)). The fact that complete freeriding without a sharable prey is not an option has been demonstrated in a game theoretical model by Packer & Ruttan (1988) and can be observed, for example, in some bird species that group hunt on fish or invertebrates (Erwin et al., 1985; Gotmark et al., 1986; Scott, 1984).

3.4.2 Singleton hunters vs. group hunts

For the case that a delayed barbel insertion is beneficial, we expected that individuals would insert with a lower effort when hunting in groups than as singletons. Our results clearly support this assumption with groups of two to four individuals inserting on a significantly lower base. Inserting the barbels seems invariably the only method to startle the prey towards the edge of the system where it becomes available for capture, which does not leave many other options to a singleton hunter than following a strategy of maximal effort. However, for situations with two or more players, the hunting effort does not seem to translate directly into success. One possible explanation is that yellow saddle goatfish bring their “learned rules” to the lab. In their natural habitat, corals are highly structured and of variable size. Therefore, conditions might be such that any barbel insertion may mostly benefit the other group members (in contrast to our experimental set-up where only the first insertion was a public good). This would lead to a scenario in which later insertions still conform to a SD / VD game, resulting in individuals learning to reduce insertion effort when hunting in groups.

However, inserting is also beneficial in terms of touching the prey first, which increases the probability of catching the prey. This, however, just for the cases in which the prey is near the edge, meaning that beforehand it was startled by another hunter that inserted earlier. When individuals are unsure about how others are likely to behave in a non-linear Public Goods game such as the VD, the best strategy is to cooperate probabilistically (where the probability depends on the cost to benefit ratio of cooperating and group size, (Archetti, 2009a; Archetti, 2009b; Archetti and Scheuring, 2011; Archetti and Scheuring, 2012). This probability to “volunteer” increases in small groups when the costs for “volunteering” are low, or the common benefit from the achieved public good is high, respectively (Archetti, 2009a; Archetti, 2009b; Archetti and Scheuring, 2011; Goeree et al., 2017). This is partly applicable to our experimental set-up in which we had rather small groups with a size of a maximum of four individuals and rather low costs of volunteering (i.e. inserting first does not reduce probability of catching the prey nearly zero, as previously discussed) compared to the possible benefit an individual gets by catching the prey. Apparently, yellow saddle goatfish adjust their behavior to whether they are single hunters or hunt in a group.

3.4.3 Individual variations

For individuals hunting as singletons as well as when hunting in groups of two to four, we found variations in the proportion of hunting effort. However, we found no evidence that variation in individual hunting effort is linked to total length or body condition. One possible explanation for these results is that yellow saddle goatfish perform similarly to what has been observed in the field during ontogeny and keep the frequency of barbel insertion constant in the laboratory. A way to test, whether yellow saddle goatfish perform in a similar way in the field would be to observe them for a certain period prior or after laboratory testing. Dridi and Lehmann (2014) showed how individuals can learn how to behave in a Snowdrift game, yielding consistent variation in behavior between individuals. Variation in barbel insertion effort fits the logic of coexistence between producers and scroungers (Barnard and Sibly, 1981) as known from studies on finches in which individuals had to find profitable patches (Giraldeau et al., 1990; Giraldeau et al., 1994).

In accordance to our expectations, the proportion of first barbel insertion associated with barbel insertion effort. We see it as the logical conclusion when individuals do not specifically time their barbel insertion.

3.4.4 Consistency of hunting effort over different group sizes

Interestingly, we could not find any correlation in hunting effort between an individual as a single hunter to when hunting in groups. In their natural habitat, yellow saddle goatfish almost exclusively hunt in groups (Strubin et al., 2011) and therefore we rather expected that individuals would behave similar in the new / unknown situation as singleton hunters. During the early stage of their ontogeny, yellow saddle goatfish are often observed to hunt with fish of different species such as bird wrasses (*Gomphosus varius*) or klunzinger wrasses (*Thalassoma rueppellii*) (personal observations) and potentially behave differently compared to the intra-specific group hunts in which they participate later. Whether this has an impact on our results remains unclear.

Quite surprising are the findings regarding the consistency of individual effort over all different group sizes tested, which stands in contrast to our predictions which assumed a constant decrease from group size two to four. At the moment we only have one possible explanation, the circumstances that each individual has to participate in the group hunt in order to catch prey, since freeriding seems to be no option.

3.4.5 Conclusion

With our study on the yellow saddle goatfish we demonstrated how group hunting can be explained partly by a payoff distribution similar to SD/VD games, but mostly by self-serving behaviours. To our current knowledge, this system is unique and has not been found in any other species, including humans, and leaves many open questions. We therefore encourage researchers to continue studying the cooperative hunting behaviour of yellow saddle goatfish, dedicating a special focus on species, including humans, which might cooperate in a similar way.

3.5 Author contributions

MS and RB designed the study. MS collected and analysed the data. MS and RB wrote the paper.

3.6 Acknowledgements

We thank Hanaa Sarhan, Claire Meugnier and Moustafa Elfar for their help conducting the experiments and on the data collection. We also thank Radu Alexandru Slobodeanu statistical support and Rebekka Lützelschwab Nordmann for English corrections on our manuscript. Finally, we thank Tom Ruthenberg and Salem Hassan for their help in catching yellow saddle goatfish.

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3.8 Figures

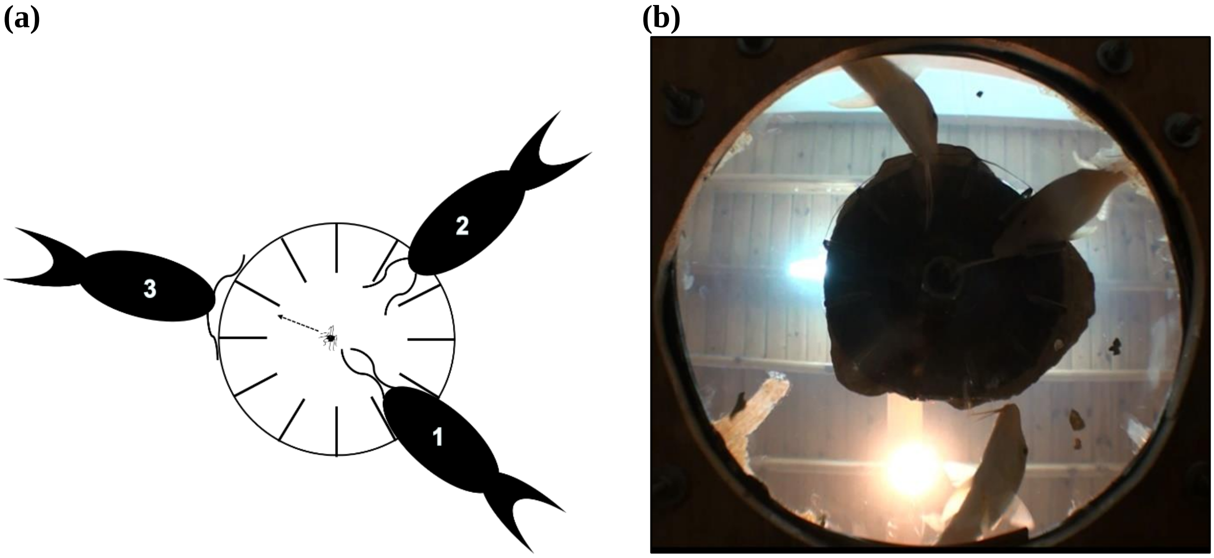


Figure 1. (a) Round artificial coral reef, with 12 similarly sized slots, a prey in the center and three hunting fish. The size of the slots was adjusted in a way so that experimental fish could reach to the center by entering part of their bodies and fully extended barbels (fish 1) in order to startle the prey. The prey reacts by escaping towards the opposite direction (arrow indication). In this scenario it would end up in a spatial position closer to fish 3. (**b)** Bottom-up screen-shot of three hunting individuals. Two fish (on top and on the right side) are inserting the barbels. The fish on the right side startles the prey in the center without touching it (Supplementary Video).

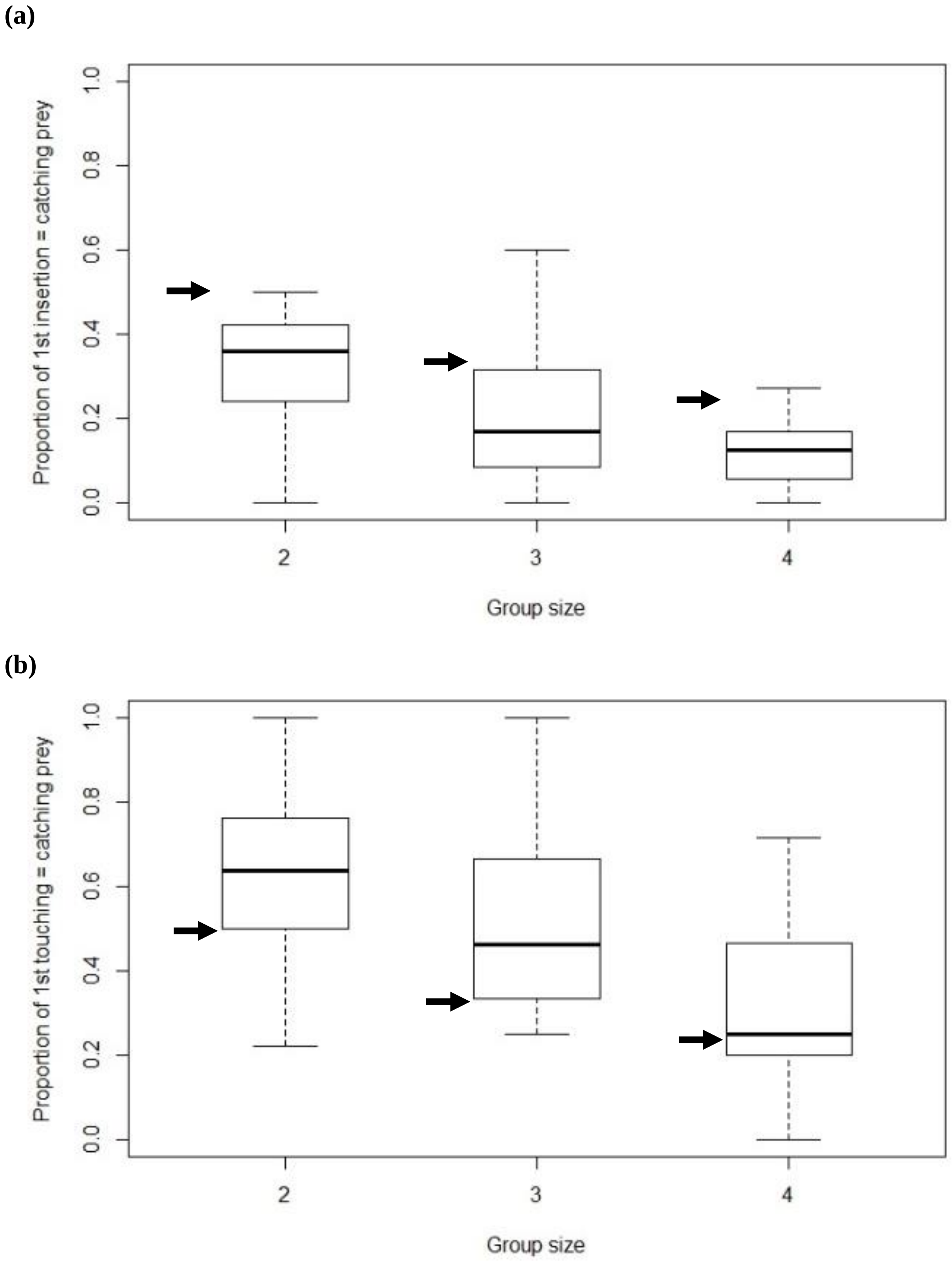


Figure 2. Proportions indicating whether the individual first inserting the barbel **(a)**, or first touching the prey **(b)**, respectively caught the prey. Arrows indicate the expected proportions for the corresponding group sizes: two = 0.5; three = 0.33; four = 0.25.

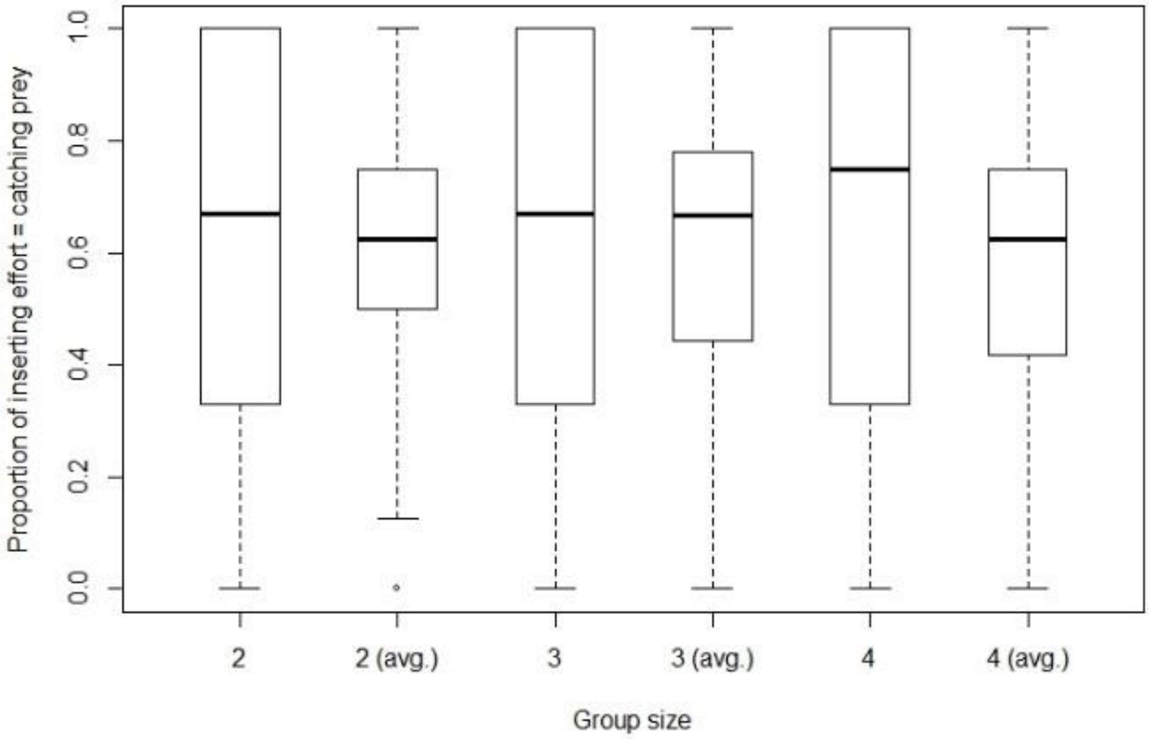


Figure 3. Proportions of individual barbel insertion effort necessary to catch the prey in relation to the average proportion of effort by the hunting group. On a trial to trial base for the group sizes two (n = 251), three (n = 202) and four (n = 111).

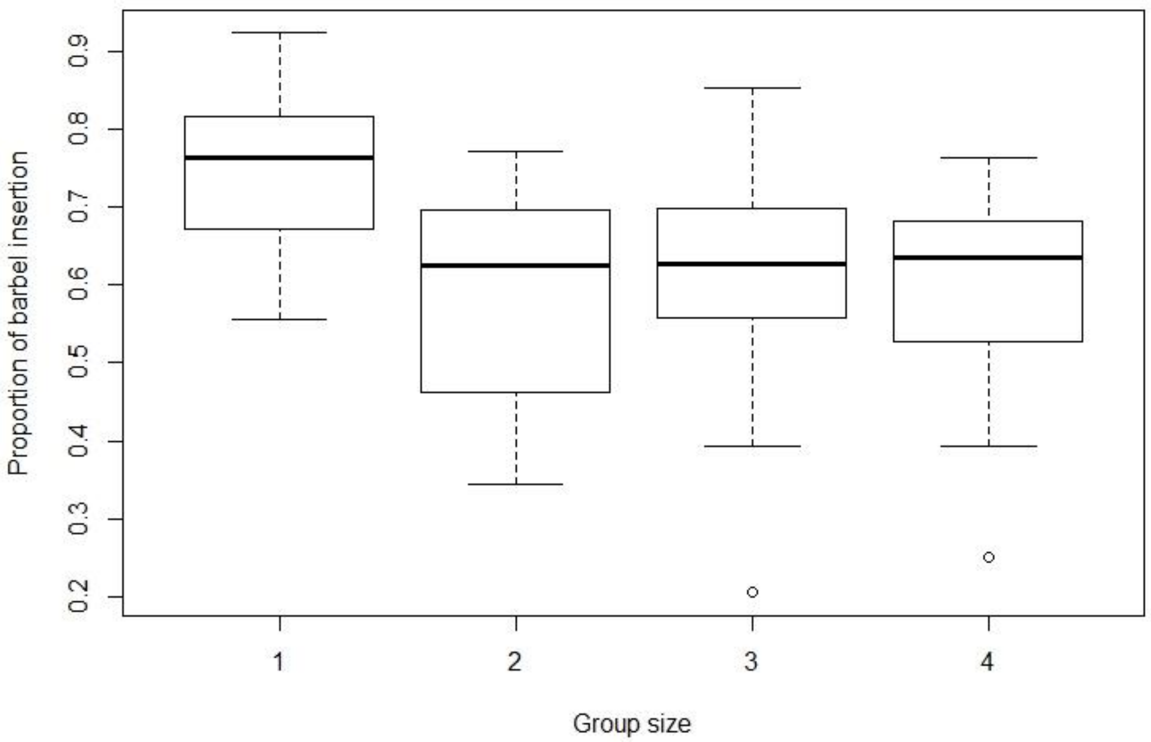
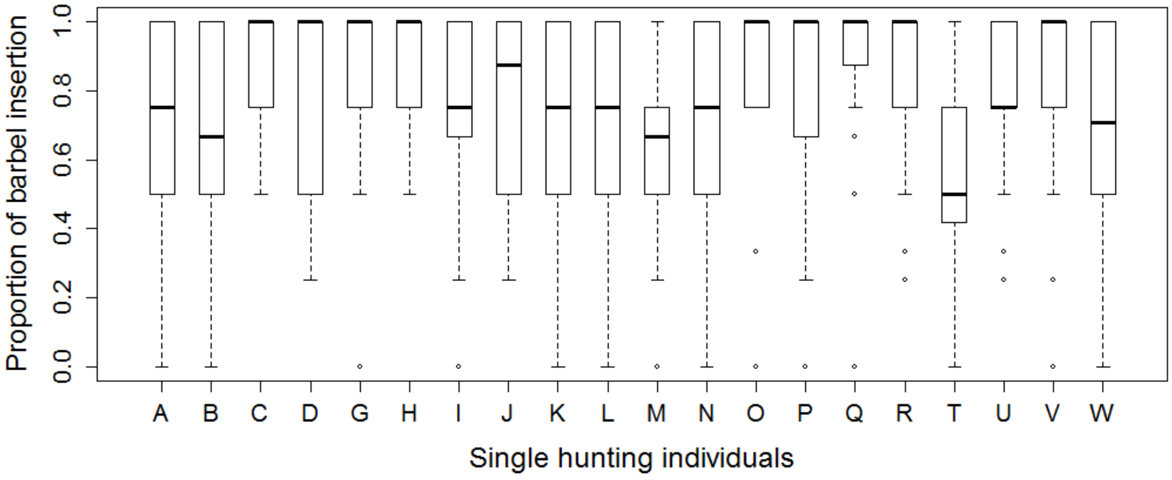
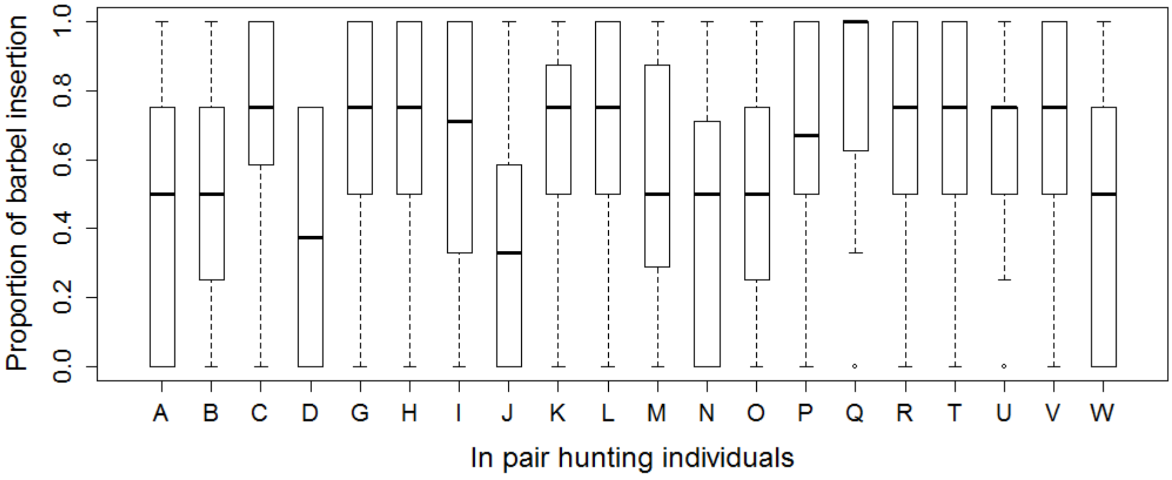


Figure 4. Proportions of individual barbel insertion for different group sizes (Data taken for calculations from Table S3). The upper and lower whiskers show 1.5 times interquartile range, the box shows median and upper and lower quartile. Individual dots indicate outliers.

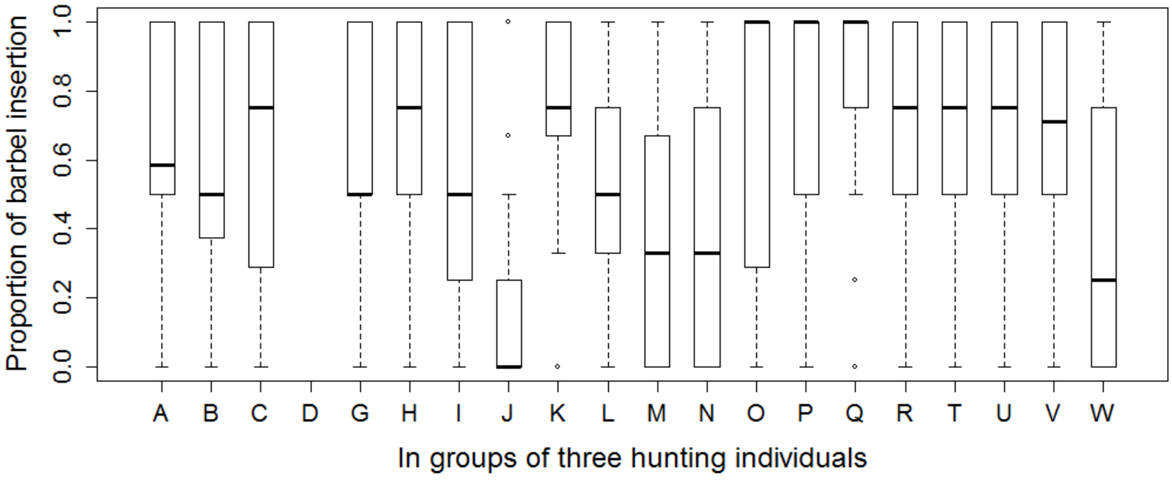
(a)


Proportion of barbel insertion
0.0
0.2
0.4
0.6
0.8
1.0
A B C D G H I J K L M N O P Q R T U V W
Single hunting individuals

(b)


Proportion of barbel insertion
0.0
0.2
0.4
0.6
0.8
1.0
A B C D G H I J K L M N O P Q R T U V W
In pair hunting individuals

(c)


Proportion of barbel insertion
0.0
0.2
0.4
0.6
0.8
1.0
A B C D G H I J K L M N O P Q R T U V W
In groups of three hunting individuals

(d)

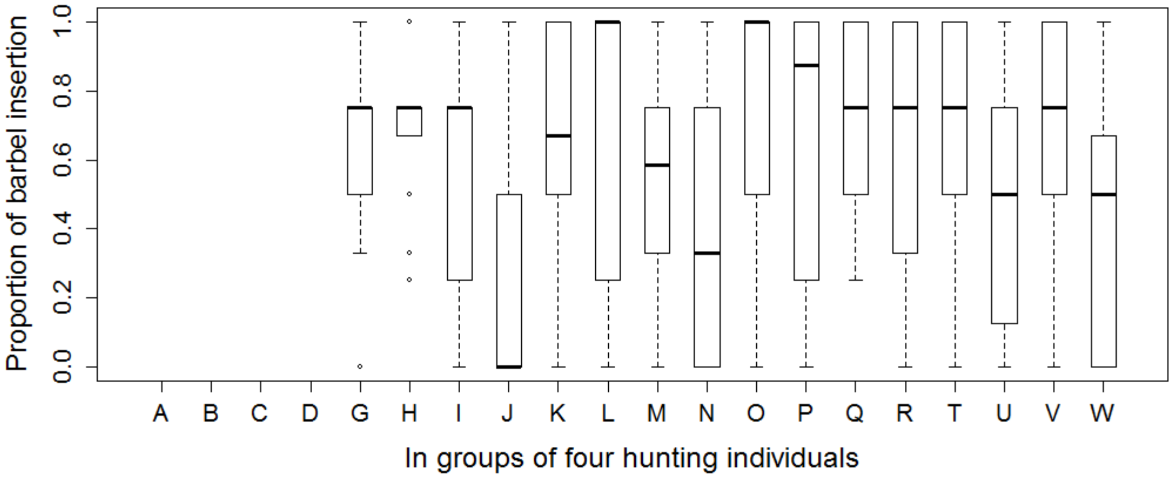


Figure 5. Boxplots of proportions of barbel insertion for all individuals (capital letters) of the different groups when hunting as singletons **(a)**, in pairs **(b)**, groups of three **(c)** and four **(d)**. Note, for Individual “D” in group size three **(c)** and individuals “A” – “D” in group size four **(d)**, no data is available. The upper and lower whiskers show 1.5 times interquartile range, the box shows median and upper and lower quartile. Individual dots indicate outliers. The sample sizes (n) for each singleton hunter are given in Table S3.

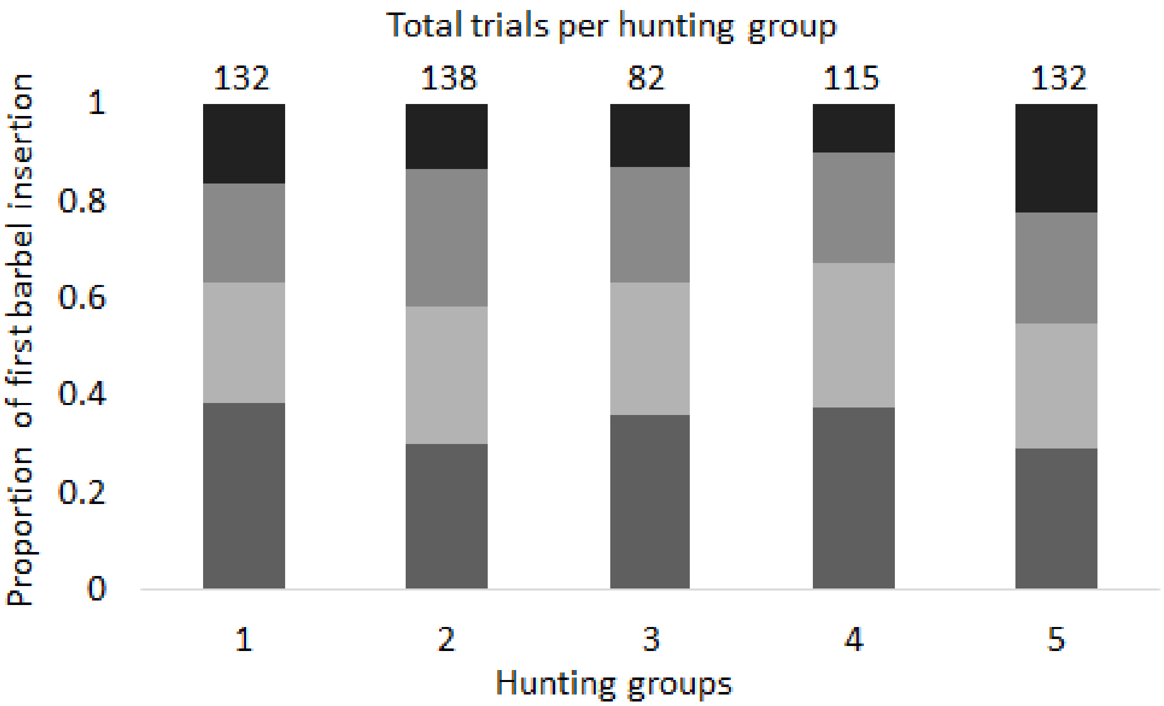
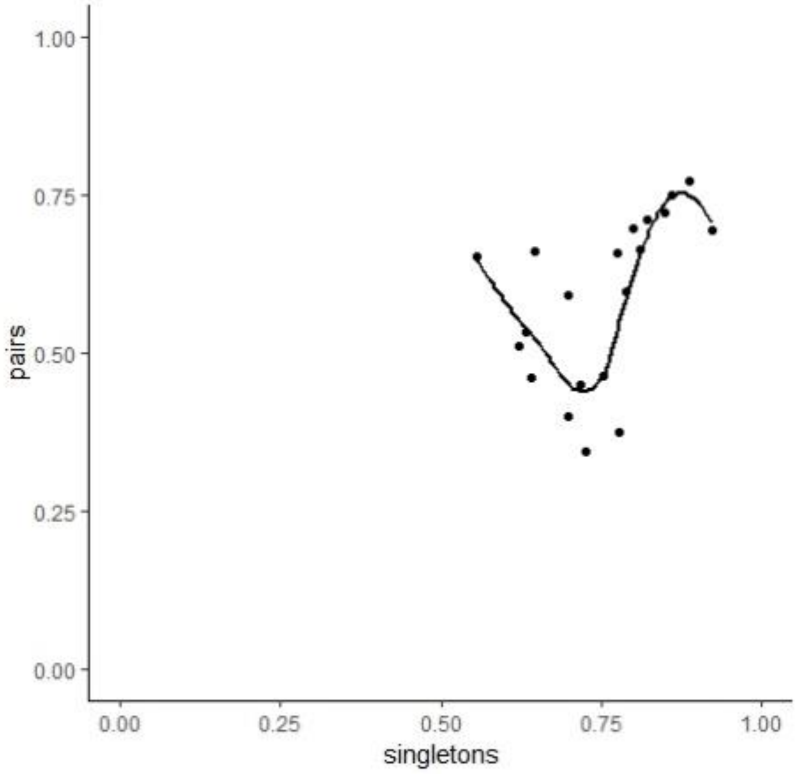


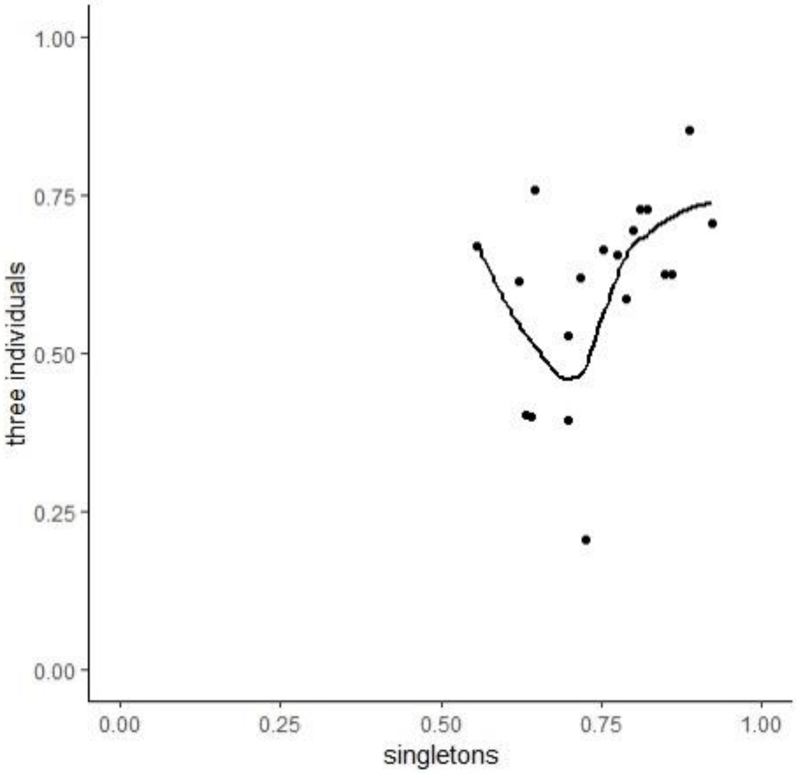
Figure 6. Individual-proportions of inserting the barbels first for each of the five groups. Individual-proportions are combined from the group size two, three and four. The bottom part of the bar of each hunting group represents the individual that performed the first insertion of barbels most often, followed by the individual performed the first insertion of barbels the second most often and so on, giving the following list for each of the five groups: Group 1: L, K, M, N; Group 2: V, U, T, W; Group 3: B, A, D, C; Group 4: H, G, I, J; Group 5: R, P, Q, O. Note, in hunting group 3 there is no data for group size four and no data from Individual "D" in group size three, which explains the lower sample size.

(a)



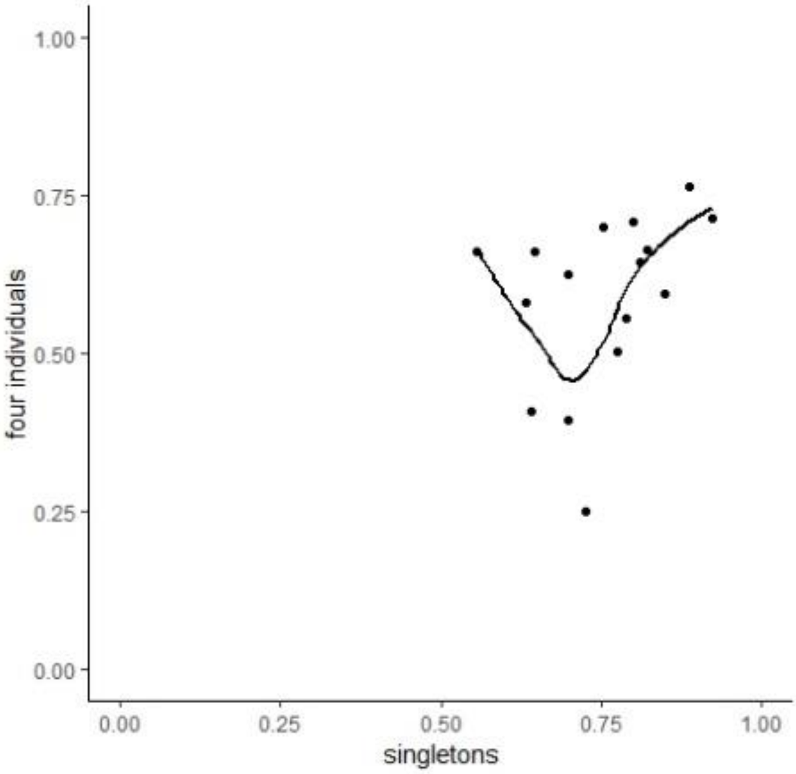
pairs
1.00
0.75
0.50
0.25
0.00
0.00
0.25
0.50
0.75
1.00
singletons

(b)

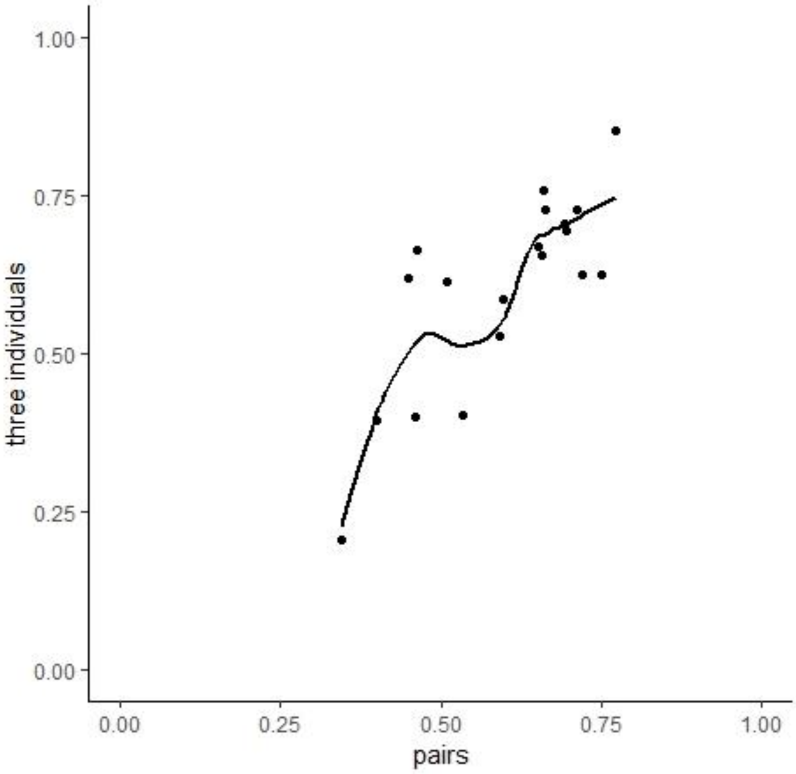


three individuals
1.00
0.75
0.50
0.25
0.00
0.00
0.25
0.50
0.75
1.00
singletons

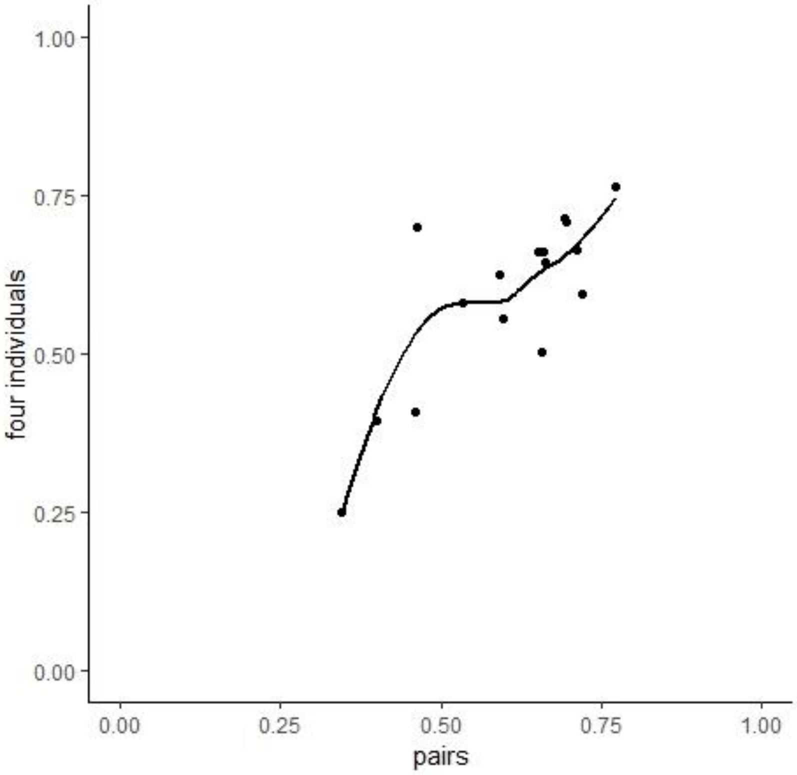
(c)


1.00
0.75
0.50
0.25
0.00
four individuals
0.00
0.25
0.50
0.75
1.00
singletons

(d)


1.00
0.75
0.50
0.25
0.00
three individuals
0.00
0.25
0.50
0.75
1.00
pairs

(e)



(f)

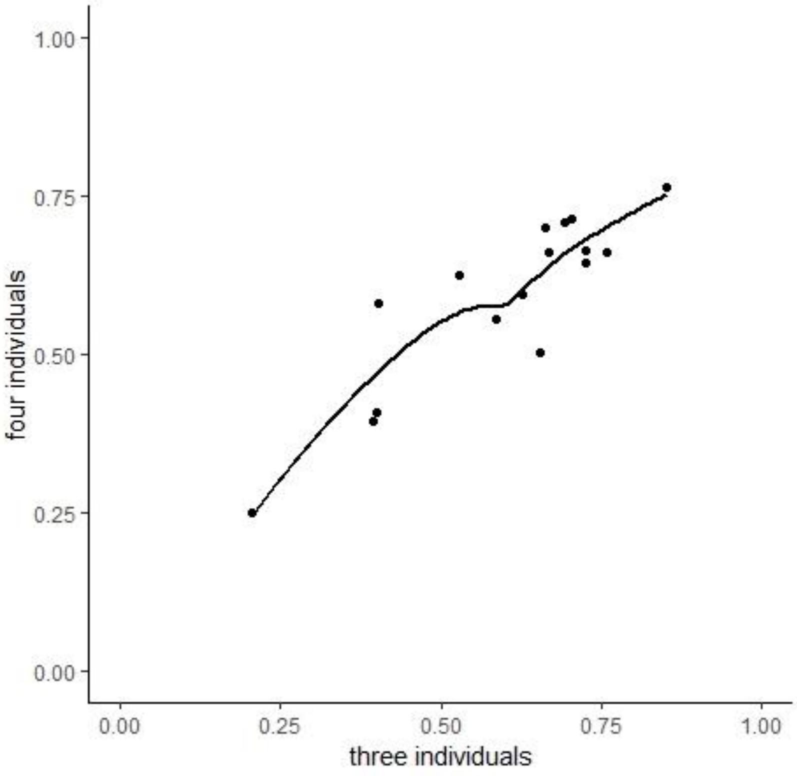


Figure 7. Graphs show the relations of the proportions of individual inserting effort between different group sizes (varying from singletons (n = 20) to four (n = 16)). Each dot represents

one out of 20 different individuals of the five groups. The line fits the prediction of the linear mixed effect model (LMM).

3.9 Supplementary materials for chapter 3

Table S1. Measurements (total length to nearest 1.0 mm and weight to nearest 1.0 g) were taken on the day after the experiments before the fish were released to the site of capture. The fish were between 162 and 238 mm TL and weighed 30 to 92 g. The Fulton's condition factor (K) was calculated additionally.

Group	FISH-ID	TL (mm)	W (g)	K*
1	K	170	38	1.93
1	L	162	30	1.75
1	M	180	53	2.30
1	N	175	47	2.20
2	T	171	34	1.70
2	U	177	56	2.54
2	V	184	52	2.12
2	W	210	70	1.96
3	A	187	54	2.10
3	B	194	62	2.17
3	C	219	88	2.19
3	D	238	92	1.81
4	G	205	70	2.10
4	H	190	58	2.16
4	I	182	51	2.14
4	J	179	41	1.80
5	O	190	65	2.42
5	P	173	50	2.42
5	Q	182	55	2.31
5	R	192	70	2.53
Ø		188	56.8	2.15
s.d.	±	18.26	16.05	0.25
median		183.00	54.50	2.15

: Fulton's condition factor as (W / TL^b) 100'000 where b is the slope of the body length (TL) – body weight (W) relationship (logW = a + blogTL)

Table S2. Originally, a total of 1200 trials were obtained by the Latin Square Model and then assigned to the five different groups. 1121 trials were considered valid: In 1039 trials, the prey was caught either inside (1015 trials) or outside (24 trials) the artificial reef. In a few trials (4), the crab swam outside of the artificial reef and was caught prior to a yellow saddle goatfish inserting the barbels, and in one trial the crab was caught outside without an individual inserting barbels to the system and without being touched by barbels. In 77 trials, the prey was not caught within the 180 seconds trial-time. 11 trials were repeated (italic) because the experimenter mistakenly disturbed the hunt or because the prey did not leave the tube or escaped back into it, respectively. 79 trials were considered non-valid: 12 trials due to poor video quality that did not allow identifying the crab. In four trials the hunt was mistakenly not recorded. In 13 trials the crab swam out of the experimental system prior to the fish arrival. In 50 trials no individual participated in the hunt.

Total of trials originally assigned to the experiment	**1200**
Valid trials	
Prey was caught inside of artificial reef (normal case)	1015
Prey was caught outside of artificial reef (normal case)	24
Caught outside prior to an individual inserting barbels into the artificial reef	4
Caught outside prior to an individual inserting barbels into the artificial reef and without touching the prey	1
Prey was not caught within 180 seconds	77
Total	**1121**
(Repeated trials)	
Prey escaped back into the tube	*1*
Prey got stuck into the tube	*7*
Experimenter mistakenly disturbed hunt at beginning	*3*
Total	***11***
Non-valid trials	
Prey was not visible because of low video quality (too dark)	12
Trial was mistakenly not recorded by camera	4
Prey swam out of artificial reef before fish arrived above visible acrylic window	13
Fish never appeared over acrylic window for 180 sec	50
Total	**79**

Table S3: Contains the mean proportion ± standard error to which an individual inserted the barbels into the system during the beginning of the hunt. We calculated the mean proportion per individual using all trials (*n*) in which an individual (given as capital letter) was either hunting as a singleton, in pairs or groups consisting of three or four individuals. For each trial we calculate the proportion by taking the average of one up to a maximum of four observations. The observations were made exactly one, two, three and four seconds after an individual first inserted the barbels into the system. For each observation we calculated the proportion of an individual inserting the barbels while it was present (inserting the barbels / present). For cases in which the prey was caught within 4 seconds or less after the first individual inserted the barbels, we have less than four observations accordingly. For cases in which the prey was caught within less than one second, we do not have any observation and expelled these cases from this analysis.

Group	Group size	FISH ID		SE	*n*	FISH ID		SE	*n*	FISH ID		SE	*n*	FISH ID		SE	*n*
3		**A**				**B**				**C**				**D**			
	1	**0,719**	±	0,054	30	**0,622**	±	0,051	45	**0,861**	±	0,039	21	**0,778**	±	0,097	9
	2	**0,449**	±	0,066	28	**0,510**	±	0,057	32	**0,750**	±	0,041	40	**0,375**	±	0,375	2
	3	**0,619**	±	0,067	28	**0,613**	±	0,062	28	**0,625**	±	0,076	28	--			0
	4	--			0	--			0	--			0	--			0
4		**G**				**H**				**I**				**J**			
	1	**0,850**	±	0,05	25	**0,923**	±	0,027	26	**0,790**	±	0,053	25	**0,725**	±	0,102	10
	2	**0,721**	±	0,051	35	**0,694**	±	0,057	33	**0,598**	±	0,059	34	**0,344**	±	0,091	16
	3	**0,626**	±	0,054	39	**0,704**	±	0,055	38	**0,586**	±	0,062	33	**0,205**	±	0,09	13
	4	**0,595**	±	0,08	14	**0,714**	±	0,06	14	**0,554**	±	0,102	14	**0,250**	±	0,114	14
1		**K**				**L**				**M**				**N**			
	1	**0,647**	±	0,058	26	**0,698**	±	0,059	24	**0,633**	±	0,049	27	**0,698**	±	0,054	24
	2	**0,661**	±	0,049	29	**0,591**	±	0,076	22	**0,534**	±	0,062	32	**0,399**	±	0,086	19
	3	**0,759**	±	0,049	38	**0,528**	±	0,065	33	**0,403**	±	0,057	37	**0,393**	±	0,056	42
	4	**0,661**	±	0,064	28	**0,625**	±	0,082	28	**0,580**	±	0,059	28	**0,393**	±	0,068	28
5		**O**				**P**				**Q**				**R**			
	1	**0,754**	±	0,084	23	**0,810**	±	0,061	21	**0,889**	±	0,049	24	**0,823**	±	0,052	25
	2	**0,464**	±	0,076	21	**0,663**	±	0,066	24	**0,772**	±	0,059	27	**0,712**	±	0,064	22
	3	**0,664**	±	0,082	27	**0,726**	±	0,065	31	**0,852**	±	0,048	31	**0,726**	±	0,059	31
	4	**0,699**	±	0,076	26	**0,644**	±	0,08	26	**0,763**	±	0,048	26	**0,663**	±	0,073	26
2		**T**				**U**				**V**				**W**			
	1	**0,556**	±	0,053	24	**0,774**	±	0,046	24	**0,800**	±	0,054	25	**0,642**	±	0,064	24
	2	**0,652**	±	0,07	23	**0,657**	±	0,053	26	**0,696**	±	0,057	26	**0,460**	±	0,079	23
	3	**0,669**	±	0,058	35	**0,654**	±	0,061	33	**0,694**	±	0,053	34	**0,400**	±	0,066	36
	4	**0,661**	±	0,058	43	**0,502**	±	0,058	43	**0,707**	±	0,051	43	**0,409**	±	0,054	43

GENERAL DISCUSSION

D.1 Summary

The primary aim of this thesis was to identify whether collaboration in yellow saddle goatfish hunting can evolve via simple decision rules to reconcile their behaviour with the initial beliefs of several scientists that collaborative hunting should be restricted to large brain-animals.

In my first chapter, which was based on the functionality of the collaborative chase during the first phase of the hunt in which yellow saddle goatfish accelerate after a fleeing prey, I could demonstrate that a simple distance-based rule triggered whether to collaborate or not. While the initiator of the hunt always directly pursued towards the prey, the follower adapted its decision whether to follow the initiator or to deviate around the coral according to the distance lagging behind. Initiators as well as followers tried to self-servingly maximise their direct benefits by doing so, hence assortments such as relatedness or reciprocity are not needed in the collaborative chase of yellow saddle goatfish.

The second chapter showed that for the second stage of a hunt – the aim to pry hiding prey out of its shelter – overall hunting efficiency increased as a function of group size. The experiment could not test whether group hunting increases per capita success, because the task was so simple that even singletons succeeded with 85% probability. Important additional results were that capture was quite evenly distributed among partners, and that individual performance as singleton hunters did not correlate with hunting success in a group. The latter result suggested that joint hunting may involve some producer-scrounger dynamics and negative frequency dependent payoffs.

In my third chapter I tested explicitly for producer – scrounger dynamics. I investigated how individuals coordinate their barbel inserting effort during the second phase of the hunt in order to extract the cornered prey from underneath the shelter. The results indicate that yellow saddle goatfish mainly follow a self-serving strategy. Regarding the first insertion of the barbels, which produces a public good and leads to a reduced success to the actor, the payoff matrix is similar to the Snowdrift game (2 players) (Sugden, 1986) or the Volunteer's

Dilemma game (N-players) (Diekmann, 1985), respectively. Besides this very first insertion of the barbels, insertions are self-serving, as touching prey increases personal hunting success. This leaves seemingly no option for a freeriding strategy, because the prey is swallowed immediately by the successful hunter and hence there is no carcass to be shared. Inter-individual differences in insertion-effort exist for all group sizes tested (including singletons), indicating that individuals seem to follow different strategies. Further I found that singleton hunters insert with a higher effort than hunters of groups of any size, which suggests that the subjects perceive the task as a Public Goods game. Interestingly, the hunting effort from group size two to four remained the same.

D.2 The big picture

D.2.1 General

Recently, intraspecific collaborative hunting has been discovered for the first time in a fish species (Strubin et al., 2011). These findings were of particular interest because: i) many researchers had previously thought that intraspecific collaborative hunting, classified as the most sophisticated form of cooperative hunting (Boesch and Boesch, 1989), is cognitively demanding and therefore restricted to large-brained vertebrates (Boesch and Boesch, 1989; Melis et al., 2006); ii) using yellow saddle goatfish as subjects has a great advantage over other collaboratively hunting species such as chimpanzees, dolphins or lions because goatfish are much smaller, easier to handle and therefore suitable to conduct group hunting experiments in the laboratory. To my knowledge, this has never been done up to date for any collaboratively hunting species and the findings of my thesis are therefore relevant for several study fields, i.e. cooperative hunting, fish cognition and evolutionary game theory.

D.2.2 Experimental approach to cooperation and evolutionary game theory

Group hunting is believed to be one of the key factors in the evolution of social living (Krause and Ruxton, 2002; Macdonald, 1983). Group hunting indeed provides potential benefits on different phases in a hunt. More individuals are more likely/faster to detect the prey (Kenward, 1978), to pursue (Creel and

Creel, 1995) and to catch/kill the prey (MacNulty et al., 2014; Packer and Ruttan, 1988; Schaller, 2009). The findings of my second chapter showed that overall hunting success (likelihood and speed of prey capture) is a function of group size and therefore fits with former correlational evidence which states that the capture of prey/prey size positively correlates with group size (Creel and Creel, 2002; Packer et al., 1990; Stander, 1992). This raises the question of how group hunting evolved, especially in non-kin groups.

The underlying processes of group hunting in unrelated individuals might be much simpler than formerly assumed and might work in the absence of sophisticated cooperation strategies i.e. invoking reciprocity, namely via immediate benefits (Brown, 1983). Cooperation can often lead to immediate benefits for the cooperating partners that exceed the costs from the assistance provided (Brown and Vincent, 2008; Kokko et al., 2001) (e.g. cooperative manoeuvres in foraging pelicans (McMahon and Evans, 1992) or cooperative hunting in golden jackals (Lamprecht, 1978). This hypothesis goes along with my findings in the group hunting yellow saddle goatfish where I propose that cooperation is maintained by self-serving by-product benefits (Brown, 1983) to all the participants.

The findings of my second chapter demonstrate that prey capture (the final step of the hunt) lasted a shorter amount of time when more hunters were present and was not simply a product of the participation of the best individual hunters. The group benefit can rather be explained by the coordination, i.e. to allocate around the obstacle to maximise the distance to the conspecifics (Strubin et al., 2011) in order to minimise the prey’s chances of escape, which self-servingly increases the success rate of the participants and thus leads to a quicker prey capture or to a reduced prey-escape probability, respectively. The only action that reduced the immediate benefits (i.e. contributes to the public good) was performed by the individual inserting the barbels firstly.

The circumstances that prey capture could basically result at any stage of the hunt, potentially promotes group hunting in the previous phases as well. In this context I want to address two subjects: First, the prey in yellow saddle goatfish is consumed entirely by a single individual and leaves no carcass from which potential free riders could profit, as known in many cooperatively hunting carnivoran species (Stander, 1992; Creel and Creel, 1995). Freeriding is seemingly no option at any stage of the hunt in yellow saddle goatfish. Not during the initial phase, where the results from my first chapter show that the initiator always ended up ahead of the follower (potential free rider strategy) and was thus more likely to catch prey before it found shelter, unless the prey turned around an obstacle towards a deviating follower goatfish. Not during the second phase of the hunt, where the findings of my third chapter demonstrate that touching the prey firstly clearly increased the probability of catching the prey and freeriding individuals (i.e. inserting at a later stage / not inserting at all) would most likely end up with lower benefits.

Second, because the prey of yellow saddle goatfish is not shareable, there is competition among the group hunting individuals (Packer and Ruttan, 1988). Under the conditions of direct competition, cooperation can, however, only evolve when the disadvantage (more competitors) is overcompensated by the per capita success and/or a decrease of the energetic costs (Packer and Ruttan, 1988), facts that I could not demonstrate with the findings of my second chapter.

Larger individuals are potentially more competitive and therefore avoided by smaller ones resulting in the formation of groups of similar sized individuals. This as an additional possibility to the assumptions made by Strubin et al. (2011) that yellow saddle goatfish form their groups by individuals of similar size, for reasons such as hydrodynamic advantages as known from shoal of fishes (Pitcher et al., 1985) or advanced coordination (Theodorakis, 1989).

D.2.3 Cooperation in yellow saddle goatfish

We can only then speak of cooperation when all participants (actor & recipient) increase their direct fitness (Lehmann and Keller, 2006) on average. Many species, including humans, cooperate and, as has already been described in the general introduction, researchers aimed to explain cooperation with game theoretical models and conditionally cooperative strategies (e.g. Iterated Prisoner’s Dilemma (Luce and Raiffa, 1957); Snowdrift game (Sugden, 1986); Stag-Hunt (Skyrms, 2004); Tit-for-Tat (Axelrod and Hamilton, 1981); Win-Stay, Lose-Shift (Nowak and Sigmund, 1993)). Humans are outstanding co-operators and have been widely tested in this context (Axelrod and Hamilton, 1981; Fehr and Gächter, 2000; Wedekind and Milinski, 2000). However, in many cases the outcomes of the empirical studies differ from theoretical predictions (Fehr and Fischbacher, 2003; Kümmerli et al., 2010) which raises questions regarding the underlying decision-making processes (Hagen and Hammerstein, 2006). Such deviations from theoretical models in humans and non-humans particularly occur in novel situations (e.g. experiments) and lead to irrational behaviour (El Mouden et al., 2012).

With my group hunting experiments on yellow saddle goatfish (second chapter), I was not able to test whether real cooperation is employed, i.e. whether there is an increased direct benefit to all participants (Lehmann and Keller, 2006). I strongly suggest that in group hunting, yellow saddle goatfish gain benefits that augment the benefits from singleton hunters. First, in my experimental set-up, the task to solve (small artificial reef with invertebrate) was potentially too easy for singleton hunters compared to the natural habitat of yellow saddle goatfish, where they hunt for fish in a highly structured environment. This deviation from the natural habitat could explain why pairs as well as groups of three and four could de facto not increase the *per capita* success in my experiments.

Second, we have to consider that the formation of groups might go beyond food-intake-maximisation. Relevant factors such as inclusive fitness (increased mating options), predator avoidance or dilution-effect should be considered whenever grouping patterns are investigated (Hamilton, 1971). While the former can be most certainly excluded, as previously discussed, the latter two have to be firmly considered since yellow saddle goatfish, as mesopredators, certainly have potential enemies (e.g. groupers) in their natural habitat. This, however, would require further research on the ecology of *P. cyclostomus*.

D.2.4 Fish - ideal subjects to test cooperation and cognition

Fish provide ideal subjects to conduct experiments on cooperation and cognition. First, fish often live in groups of non-kin (e.g. coral reef fish (Avise and Shapiro, 1986; Kolm et al., 2005) and second, some of them can be easily kept under laboratory conditions (Bergmüller and Taborsky, 2005; Bshary and Grutter, 2006; Milinski, 1987). Up to date, several interesting studies, of which I will highlight some, on cooperation have been conducted by using fish as model organisms.

Groupers (*Plectropomus pessuliferus)*, for example, have been observed to coordinate their hunting behaviour in the field with giant moray eels

(*Gymnothorax javanicus*) (Bshary et al., 2006). Groupers have then been brought to the lab where it was shown that they use referential gestures for communication (Vail et al., 2013).

Further, a recent field study on sailfish (*Istiophorus platypterus*) showed how individuals coordinate their action (attacks on schooling sardine prey (*Sardinella aurita*)) in time, but not in space, a strategy that the authors consider as proto-cooperation (Herbert-Read et al., 2016), a seemingly early form in the evolution of cooperative hunting. Another study shows that black hamlets maintain cooperation by parcelling their investments (*Hypoplectrus nigricans*) (Connor, 1992). Guppies (*Poecilia reticulata*), as a further example, stabilize cooperation with specific, i.e. more familiar partners (Granroth-Wilding and Magurran, 2013). There is even strong evidence that partner sticklebacks (*Gasterosteus aculeatus*) reciprocate by approaching a partner (Milinski et al., 1990), a cooperation concept that is expected to be found rarely, particularly in non-human animals (Bshary, 2010; Clutton-Brock, 2009). Furthermore, Bshary and collaborators (2014) conducting several studies on the cooperative behaviour on the cleaner wrasse *(Labroides dimidiatus*) and thus provided evidence for cooperation concepts that were mainly developed to explain cooperation in humans.

Furthermore, fish are also ideal subjects to study cognition. Even if associative learning (i.e. classical and operant conditioning) is most likely the standard form of learning in fish (Brown et al., 2011), recently a multitude of studies have demonstrated that some fish species have the ability to solve complex problems that require precise memory and cognitive processes superior to conditioning (Bshary et al., 2014). Guppies (*Poecilia reticulata*) have been shown to be able to perform counting tasks similarl to the ones found in mammals (Piffer et al., 2012; Piffer et al., 2013). Counting, as a cognitive task, was also discovered in other fish species (e.g. angelfish (*Pterophyllum scalare*) (Gómez-Laplaza and Gerlai, 2011), redtail splitfin (*Xenotoca eiseni*) (Stancher et al., 2013), mosquitofish (*Gambusia holbrooki*) (Agrillo et al., 2008)). In another study it was shown that the tanganyikan cichlid *Astatotilapia burtoni* can infer the social rank by only observing fights between males (Grosenick et al., 2007). These findings of transitive inference are further evidence for higher cognitive abilities in fish. Interestingly, fish did extremely well in certain laboratory-based specific cognition experiments, especially then when experiments were designed in a way that mirrored their ecology. For example, in a complex foraging task that was primarily based on the ecology of cleaner fish (*L. dimidiatus*), it was demonstrated that the cleaner fish even outperformed three primate species: chimpanzees, orang-utans and capuchin-monkeys (Salwiczek et al., 2012). This example shows how research on fish cognition can provide results that generate hypotheses about what abilities may warrant a larger brain (fish do not solve the task) or not (fish solve the task).

In my first chapter I constructed a set-up to mimic the first phase of the hunting scenario in a simple way and in accordance to the natural behaviour of yellow saddle goatfish. In this phase, the first fish to detect the fleeing prey chases towards it, while the hunting partner choses its strategy to either chase behind or deviate around the obstacle (i.e. to collaborate) via a simple distance-based decision rule. These findings show first, that collaboration, at least in yellow saddle goatfish, can evolve in a much simpler context than has been previously argued (Boesch and Boesch, 1989; Melis et al., 2006) and second, highlights, as a further example, the importance of the ecological approach to cognition in which animals cognitive abilities are bound to their evolutionary history and therefore their ecology (Bshary et al., 2007; Kamil, 1998; Salwiczek et al., 2012).

D.3 Conclusion

Although much has already been discovered on the evolution of cooperation in the past decades, decision-rules are not known as animals do not seem to play theoretical strategies (e.g. Tit-for-Tat (Axelrod and Hamilton, 1981)). Yellow saddle goatfish provided a rare opportunity to study individual strategies in N-player cooperation games in a non-human animal, using an experimental approach in an ecologically relevant context. The results of my thesis demonstrate that the cooperative behaviour in yellow saddle goatfish predominantly underlie simple decision rules rather than sophisticated cooperative strategies. Generally, I assume that many “small brained” unrelated species coordinate their cooperative behaviour and decision-making via “cheap solutions,” i.e. rules of thumb which should be incorporated more in the design of theoretical models or during data analysis of empirical research. Saying this, I want to encourage present and future researchers to continue conducting research in the fields of cooperation, cognition and game theory by using fish as study subject.

D.4 Future research

This PhD thesis provides a solid basis for future investigation on the cooperative hunting behaviour in yellow saddle goatfish. Yet many unanswered questions and further research opportunities result from this thesis. For example, comparing earlier and later trials within the same experimental set could provide us with information regarding learned decision-rules, i.e. the potential of flexible strategies in yellow saddle goatfish. In certain contexts, this has been analysed, but much has still to be done. The behaviour of a specific individual during a trial could further be compared with the outcome of the previous trial in order to check for potential Winner-Loser effects (Dugatkin, 1997; Oliveira et al., 2011) or strategies such as Win-Stay, Loose-Shift (Nowak and Sigmund, 1993).

Furthermore, various field observations demonstrated that during ontogeny, juvenile yellow saddle goatfish coordinate their hunts by following similar-sized fish of other species, such as bird wrasses (*Gomphosus varius*) or klunzinger wrasses (*Thalassoma rueppellii*) (personal observations). During various field seasons I have collected video material on different size classes. Initial video analysis showed that juvenile yellow saddle goatfish seem to adapt their coordination, i.e. angle and distance, to the individual followed, according to their own development (length). Further video analyses are required for this study area.

D.5 References

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APPENDIX

A.1 Stomach content analysis

A.1.1 Date and Place

This study was conducted between the May 10-13, 2010, in Dahab, Egypt at the Dahab Marine Research Center (DMRC)

A.1.2 Study purpose

According to the literature, the diet of yellow saddle goatfish consists mainly of fish and smaller amounts of invertebrates such as crustaceans and small cephalopods (Randall, 1983). In order to verify my assumption that yellow saddle goatfish in the local area of Dahab feed off a similar diet, a qualitative analysis of the stomach content was necessary. This knowledge was relevant, as, due to ethical reasons, it was planned to use only invertebrates for the experiments conducted with live prey.

A.1.3 Capturing, handling and stomach content analysis

Adult yellow saddle goatfish were caught during daytime (between 6 a.m. and 5 p.m.) using a large barrier net while snorkeling in the Dahab lagoon. During transportation from the sea to the lab and back, fish were kept in opaque water tanks to minimize stress. Analyses were conducted within 20min after capturing in order to minimize digestion of stomach contents. Before flushing the stomach, fish were anesthetized with Tricaine methane-sulfonate (MS-222), which is commonly used on fish (Munday and Wilson, 1997).

To obtain the stomach contents of the yellow saddle goatfish, the fish's stomachs were flushed using the gastric lavage apparatus (Figure 1), which is considered to be a very effective method that is not harmful to the fish (Hartleb and Moring, 1995). For a detailed description on the procedure, see Hartleb and Moring (1995). During the procedure, a tape measure that was included in the apparatus (Figure 1) was used to measure the total length of the individual.

Immediately after flushing, stomach contents were analyzed and determined. On the same day, fish were marked with the fin clipping method in order to avoid recapturing the same individuals, and released to the location of capture. Fin clipping is a widely used method in marking fish and has no measurable effect on mortality or swimming ability (Ward, 2003).

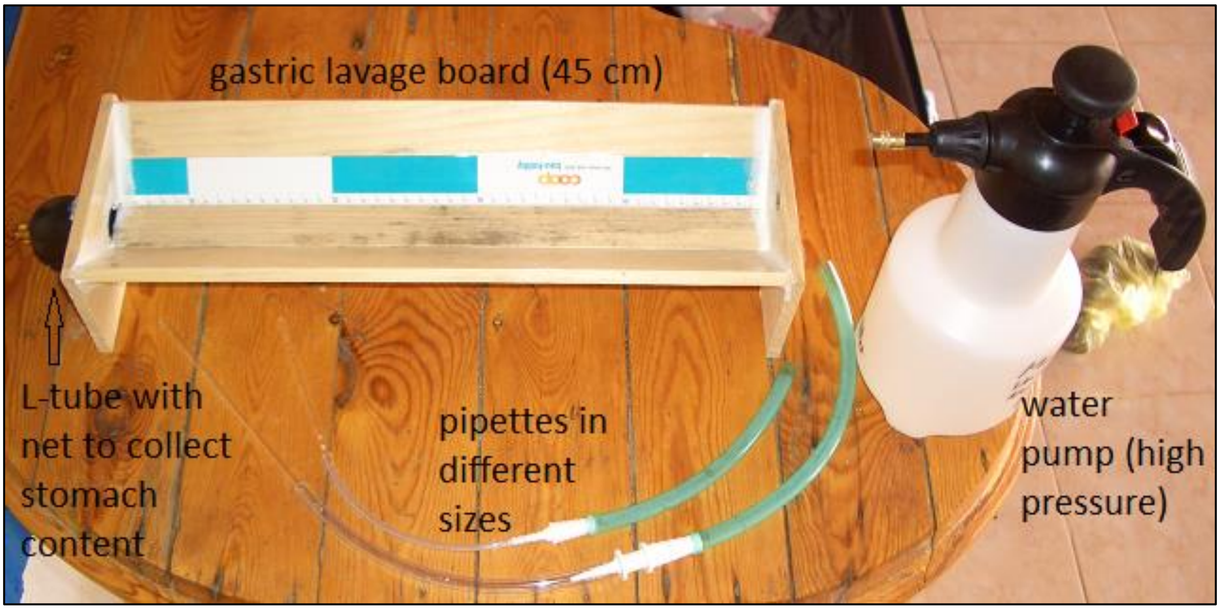

Figure 1. The gastric lavage apparatus. The apparatus, containing a tape measure, was constructed to fit yellow saddle goatfish up to a total length of a maximum of 40 centimeters. On one side of the apparatus, there was an opening to screw on a PVC tube that contained a fine net (mesh size < 100 µm) to collect the stomach content. On the other side there was an opening to facilitate the insertion of the pipette into the fish. Different sizes of pipettes served to sample different sizes of fish. The ends of pipettes were tapered, to minimize a potential injury of the fish’s esophagus. A water pump was connected to the pipette with adjustable water pressure.

A.1.4 Results

Ten yellow saddle goatfish were caught. In seven individuals, stomach contents were found, while in three individuals the stomach was completely empty (5, 8 and 9, Table 1). Six individuals contained fish in their stomach; the species of the fish in the stomach content was deteremined for three of the individuals (1, 3 and 4): Lyretail anthias (*Pseudanthias squamipinnis*). In the remaining three individuals, the advanced digestion made it impossible to identify the fish species obtained from their stomach.

In two fish (2 and 10) crustacean parts were found. One individual's content (2) was determined as *Stenopus hispidus*, that of the other individual could not be determined.

Table 1. Stomach content of ten yellow saddle goatfish caught in the Dahab lagoon.

Individual	Date of capture	Total length (mm)	Stomach content
1	10.05.2010	270	*P. squamipinnis* (3)
2	10.05.2010	256	*S. hispidus* (2)
3	11.05.2010	309	*P. squamipinnis* (1)
4	11.05.2010	286	*P. squamipinnis* (3)
5	11.05.2010	294	empty
6	12.05.2010	329	not identified fish (2)
7	12.05.2010	329	not identified fish (1)
8	12.05.2010	370	empty
9	13.05.2010	306	empty
10	13.05.2010	261	crustacean sp. (several parts)

A.1.5 References

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