THE EVOLUTION OF ANIMAL SOCIETIES: MONOGAMY, GROUP-LIVING AND CONFLICT IN A CORAL-DWELLING FISH

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ABSTRACT

One of the fundamental goals of behavioural ecology is to understand the evolution of mating systems and determine how they influence the formation, structure and stability of animal societies. Monogamous mating systems are particularly challenging to understand, since one sex generally has a higher potential reproductive rate than the other and should therefore be selected to mate multiply. In addition, monogamous mating systems often occur within the context of social groups. The presence of other group members and hence potential mates makes the evolution of monogamy even more perplexing, since an individual's immediate opportunities for polygamy are greatly enhanced. Monogamy within the context of social groups also poses problems for understanding why other group members tolerate group-living, given that they are excluded from reproduction, and how conflict over reproduction between group members is resolved if groups are to be stable. In this thesis, I investigated the ecological determinants of the evolution of monogamy and its consequences for the formation, structure and stability of social groups in a coral-dwelling goby, *Paragobiodon xanthosomus* (Gobiidae).

In chapter 2, I quantified the social structure of natural groups and determined the mating system of *P. xanthosomus*. Regardless of group size, groups consisted of one mature male and female plus several smaller immature females that were organised into a size-based dominance hierarchy. Observations of breeding behaviour confirmed that *P. xanthosomus* exhibits a monogamous mating system in which only the mature male and female breed at the expense of the other female group members. To address the evolution of monogamy despite the immediate availability of multiple females within groups, I used field and aquarium experiments to test whether competition between females over limiting nest sites, food or paternal care constrained

males to monogamy. Supplemental feeding increased the fecundity of breeding females, suggesting that food is a limited resource for reproduction. Supplemental feeding did not however result in the maturation of other female group members. This suggests that monogamy has evolved because dominant females suppress the reproduction of subordinate females because they are competitors for limited food. Finally, males in pairs that received supplemental food exhibited a diminishing ability to care for enlarged clutches laid by similarly-sized breeding females. This suggests that constraints on paternal care provide additional benefits for females from maintaining a monogamous mating system.

In chapter 3, I investigated the consequences of the monogamous mating system on the maintenance of group-living in *P. xanthosomus*. Specifically, I applied cooperative breeding theory to determine the factors promoting group-living by non-breeding subordinates given that they obtain no current reproduction within groups due to the monogamous mating system. Using field and aquarium experiments in which coral saturation, costs of movement between corals and the size of available corals was manipulated, I demonstrated that non-breeding group members tolerate group-living because of high costs of movement and benefits from inheriting a territory of high quality. In contrast, coral saturation and position in the hierarchy appeared to have no effect on the occurrence of subordinate dispersal.

In chapter 4, I investigated the mechanisms involved in resolving conflict over rank between group members, and thus promoting the stability social groups given the unequal distribution of reproduction between group members due to the monogamous mating system. Specifically, I tested whether the combination of punishment by dominants in the form of eviction from the group, and cooperation by subordinates in the form of growth regulation had evolved as a means of conflict resolution. Firstly, I conducted a removal experiment in the field and showed that non-breeding subordinate group members form size-based queues in which they

wait to inherit dominant breeding status. Conflict over reproduction should be particularly intense in queues since subordinates gain no reproduction while they wait and face the prospect of dying before inheriting a breeding position. Detailed quantification of size ratios between individuals of adjacent rank in groups revealed a prevalence of a specific size ratio between individuals, and analysis of individual growth rates in the field demonstrated that the specific size ratio is maintained over time via the regulation of subordinate growth rates. Staged contest experiments in aquaria between individuals of adjacent rank revealed that the specific size ratio represents a threshold above which subordinates can evict their immediate dominant from the group, but are much more likely to be evicted by their immediate dominant themselves. This suggest that threshold size ratios are being maintained by subordinates as a form of cooperation whereby they avoid becoming a threat to their immediate dominants, and that such cooperation arises in response to the threat of punishment by dominants. Societies in *P. xanthosomus* are therefore being stabilised as a result of punishment and cooperation acting in concert to promote the resolution of conflict over rank between group members.

Finally in chapter 5, I used a supplemental feeding and removal experiments to explicitly test whether: (1) disproportional acquisition of food resources as a result of differential competitive ability contributed to the maintenance of size differences between individuals within size-based queues, and (2) subordinates are capable of regulating their own growth to avoid inflicting costs on dominants. Supplemental feeding resulted in elevated growth rates of subordinates in both the presence and absence of the breeding female, suggesting that food limitation on subordinates due to competitive exclusion by dominants promotes the maintenance of size differences within size-based queues. Feeding of rank 4 subordinates resulted in some restraining their own growth by reducing their food intake, demonstrating that subordinates are capable of regulating their own growth to avoid breaching the threshold size ratio. The remaining

rank 4 subordinates grew in breach of the threshold size ratio and were consequently evicted from the group, suggesting that food availability may also influence the stability of queues. Taken together, both competition over food and subordinate growth restraint in response to the threat of eviction appear to be important in regulating subordinate growth rates and in maintaining well-defined size differences within size-based queues, although social regulation is likely to be the primary factor ensuring the stability of *P. xanthosomus* societies over time.

In summary, this thesis represents a quantitative and systematic investigation into the mechanisms responsible for, and the links between, the evolution and maintenance of monogamy, social groups, and conflict resolution in a monogamous, group-living fish. In so doing, it provides a comprehensive picture of the mechanisms underlying the formation, structure and stability *P. xanthosomus* societies, and contributes to a greater understanding of the processes governing the evolution and maintenance of animal societies in general.

TABLE OF CONTENTS

LIST OF FIGURES

STATEMENT OF SOURCES

DECLARATION

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