Ecological constraints and benefits of philopatry promote group-living in a social but non-cooperatively breeding fish

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Why non-breeding subordinates of many animal societies tolerate group-living remains a pertinent question in evolutionary biology. The ecological constraints and benefits of philopatry hypotheses have the potential to explain the maintenance of group-living by specifying the ecological conditions favouring delayed dispersal over independent breeding by subordinates. In this study, I used field and laboratory experiments to investigate the role of ecological and social factors on the dispersal decisions of non-breeding subordinates in the coral-dwelling fish, *Paragobiodon xanthosomus* (Gobiidae). Subordinate dispersal was strongly influenced by ecological constraints (habitat saturation and risks of movement) and benefits of philopatry (relative coral size). Social factors, namely social rank and forcible eviction, did not affect the occurrence of subordinate dispersal. These results suggest that selection has favoured subordinate *P. xanthosomus*, which employ a mixed strategy—switching tactics in response to three ecological factors—despite having low mobility and extreme habitat-specific requirements. Furthermore, this study demonstrates the generality of the ecological constraints and benefits of philopatry hypotheses as explanations for group-living in species where subordinates are unrelated to breeders, provide no help and do not strictly delay dispersal.

Keywords: ecological constraints; benefits of philopatry; group-living; dispersal; habitat quality

1. INTRODUCTION

In many animal societies, subordinate group members are excluded from reproduction and gain no indirect fitness benefits from group-living (e.g. Emlen 1991; Queller *et al.* 2000; Gardner *et al.* 2003). To fully understand how these societies are maintained, a fundamental question needs to be addressed: why do non-breeding subordinates tolerate group-living as opposed to dispersing to breed independently elsewhere?

The ecological constraints and benefits of philopatry hypotheses provide two complimentary perspectives on how costs of missed reproductive opportunities may be compensated and thus how group-living is maintained (Emlen 1982; Stacey & Ligon 1987). The ecological constraints model emphasizes the role of external constraints on dispersal and independent breeding (Koenig *et al.* 1992). In particular, if other habitats are saturated (Selander 1964) or if dispersal entails energetic or survival costs (Emlen 1982), then individuals may benefit from delayed dispersal and group-living. Conversely, the benefits of the philopatry model emphasize the internal benefits of remaining within a group (Koenig *et al.* 1992). In particular, if individuals reside in a high-quality habitat that they can eventually inherit, they may gain long-term fitness benefits from delaying dispersal if alternative habitats are of inferior quality (Woolfenden & Fitzpatrick 1978; Stacey & Ligon 1987).

Besides ecological factors, pay-offs from group-living may also relate to social factors (Pasinelli & Walters 2002). In particular, there has been growing theoretical

and empirical emphasis on the importance of social rank in mediating subordinate dispersal decisions in species that form queues to inherit breeding status (Field *et al.* 1999; Kokko & Ekman 2002; Buston 2004). Moreover, the occurrence of dispersal may not necessarily reflect a voluntary decision by subordinates, but forcible eviction from the group (Cant *et al.* 2001; Buston & Cant 2006; Wong *et al.* 2007). The potential contribution of such individual-specific social factors highlights the possibility that pay-offs from dispersal and group-living may not solely reflect a generalized outcome of ecological conditions.

Most empirical tests of the ecological constraints and benefits of philopatry hypotheses have focused on co-operatively breeding species in which subordinates associate in kin groups, provide helpful cooperation and, by definition, are philopatric and delay dispersal. Opportunities to test these hypotheses in species where kinship is absent, subordinates provide no help and are not strictly philopatric are rare (see Gardner *et al.* 2003). In fact, such investigations are vitally important for assessing the generality of these hypotheses as explanations for group-living in species exhibiting a diverse range of social and genetic structures. Here I investigated the role of ecological and social factors in the occurrence of group-living in the obligate coral-dwelling goby, *Paragobiodon xanthosomus* (Gobiidae). Within coral colonies, gobies form groups in which only the largest male and female breed monogamously with each other ('dominant breeders'), with all other group-members being smaller non-breeding females ('subordinate non-breeders') (Wong *et al.* 2008a). The mating system is likely to be genetically monogamous given that the gonads of subordinate non-breeders contain no mature

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oocytes (Wong in preparation) and subordinates are reproductively suppressed by dominant breeders (Wong et al. 2007). Subordinate non-breeders are organized into size-based hierarchies that function as queues to inherit breeding status (Wong et al. 2007). While subordinates cooperate by regulating their growth to maintain threshold size ratios of 0.9–0.95 (standard length (SL) subordinate/SL dominant) in response to conflict over rank with dominants (Wong et al. 2007, 2008b), subordinates do not help in the manner exhibited by cooperatively breeding fishes (Taborsky 1985; Balshine-Earn et al. 1998). Subordinate non-breeders are unlikely to gain any indirect fitness benefits from remaining within their group because hatched larvae are washed off the reef and spend an extended period of time in a well-mixed pelagic environment before eventually settling back onto coral colonies (Sale 1991). Therefore, social groups are unlikely to be composed of relatives, and subordinates are neither philopatric nor do they delay dispersal in the strict sense. This combination of reproductive and social characteristics makes *P. xanthosomus* an excellent model for testing the importance of ecological and social factors on subordinate dispersal and group-living decisions, and provides a rare opportunity to test the ecological constraints and benefits of philopatry models beyond the scope of their usual application.

Three specific aims were addressed in this study. Firstly, the role of ecological constraints was investigated using a multi-factorial experiment manipulating coral saturation, distance to alternative coral colonies and both. If coral saturation and risks of dispersal influence subordinate dispersal, both a reduction in coral saturation and inter-coral distance should have positive effects on subordinate dispersal. Secondly, the role of benefits of philopatry was investigated by manipulating the relative sizes of coral colonies and allowing subordinates the choice of dispersing to: (i) a larger coral containing dominant breeders versus (ii) a smaller coral containing a single male. If the benefits of group-living are positively related to the size and hence quality of corals, subordinates should increasingly choose group-living as a subordinate in the larger coral over immediate breeding as a dominant in the smaller coral, as the difference between coral sizes increases. Thirdly, the effects of dominance rank and conflict with dominants were investigated by assessing the occurrence of subordinate dispersal in relation to their size rank within the hierarchy and the likelihood of eviction by dominants.

2. MATERIAL AND METHODS

(a) *General methods*
The study was conducted at Lizard Island (14°40′ S, 145°28′ E) on the northern Great Barrier Reef, Australia, between March 2004 and November 2005. Field activities were conducted in the Lizard Island lagoon and laboratory experiments conducted at Lizard Island Research Station. Details of collection, measurement, tagging and sexing procedures are given in Wong et al. (2007, 2008a).

(b) *Habitat saturation and risks of movement*
A total of 62 coral colonies (mean average diameter (cm) ± s.e.= 27.48 ± 0.56) each containing between five and 17 gobies were collected from the reef. Each coral

colony was paired with another that did not differ in group size by more than two individuals, such that a total of 31 'coral pairs' were created. Both corals of a pair were placed on rubble platforms adjacent to one another in a sandy lagoon, and separated from other coral pairs by at least 3 m to prevent movement between coral pairs.

Four experimental treatments were established: (i) low saturation + low risks of movement (LS + LR), (ii) low saturation + high risks of movement (LS + HR), (iii) high saturation + low risks of movement (HS + LR), and (iv) high saturation + high risks of movement (HS + HR) (figure 1). To create treatment 1 (LS + LR), 10 of the 31 coral pairs were randomly selected and all subordinate non-breeders permanently removed from one randomly selected coral of each pair. Dominant breeders were tagged the same colour using fluorescent elastomer and placed back into their coral. In this way, a low-saturation coral was set up. All gobies from the other coral of each pair were measured and tagged a different colour to the breeding pair from the low-saturation coral, and all placed back into their original coral. In this way, a high-saturation coral was established. The low- and high-saturation corals of each coral pair were then positioned so that the dispersal distance between them was 10 cm (simulating a low risk of movement) (figure 1). Distance is likely to be a suitable proxy for dispersal costs given the high risks of predation mortality outside of coral colonies (Lassig 1981).

To create treatment 2 (LS + HR), eight of the 31 coral pairs were randomly selected. The same procedure for treatment 1 was repeated except that the low- and high-saturation corals were placed 100 cm apart (figure 1). To create treatment 3 (HS + LR), eight of the 31 coral pairs were randomly selected. The procedure for treatment 1 was repeated except that no subordinate non-breeders were removed from either coral of each coral pair so that both corals were of high saturation (figure 1). To create treatment 4 (HS + HR), five of the 31 coral pairs were randomly selected. The same procedure for treatment 3 was repeated except that both high-saturation corals of the pair were placed 100 cm apart (figure 1). The mean average diameter (cm) ± s.e. of low-saturation corals was 27.58 ± 0.65, and of high-saturation corals was 27.35 ± 0.85.

The following day, the occurrence of subordinate dispersal between the two corals of each pair was detected by noting the presence of any gobies of the opposing tag colour. The proportion of gobies that dispersed from their original group, the social rank of gobies that dispersed and the social rank these dispersers achieved in their new group were recorded. The occurrence of any further movement was re-scored after 7 days to confirm the stability of dispersal events. To assess whether social rank and conflict with dominants influenced the occurrence of subordinate dispersal, dispersal data from treatments 1 and 3 (LS + LR and HS + LR) were analysed.

(c) *Habitat quality*
A binary choice experiment was conducted in which a subordinate female was given the choice of becoming a non-breeding subordinate on a larger coral versus breeding immediately on a smaller coral. Coral size was considered a proxy for coral quality because habitat or territory size correlates with individual growth, survival and reproductive success for other coral-dwelling fishes (Kuwamura et al. 1996; Hobbs & Munday 2004). A small coral colony was
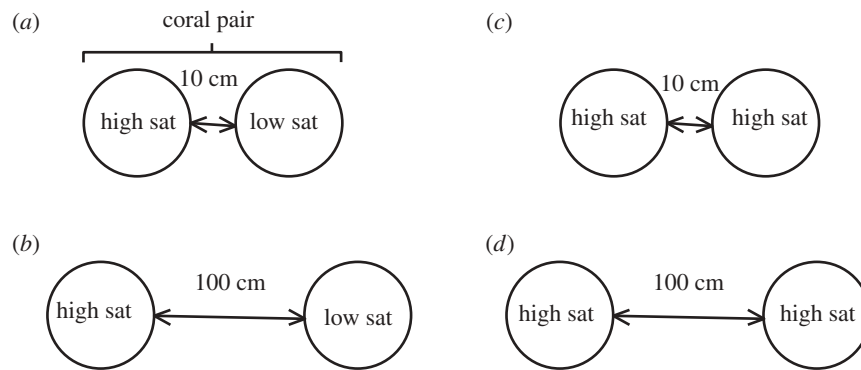
Figure 1. Multi-factorial field experiment testing the relative effects of coral saturation and dispersal distance on subordinate dispersal. (*a*) Treatment 1 (LS + LR); (*b*) treatment 2 (LS + HR); (*c*) treatment 3 (HS + LR); (*d*) treatment 4 (HS + HR).

paired with a larger coral colony (both removed of gobies) and both placed 20 cm apart in a circular aquarium. As coral size is positively correlated with group size (Thompson *et al*. 2007), coral colonies were defined as 'small' if they contained the minimum group size i.e. a breeding pair. The size of both small and larger corals was measured (average diameter: $(L + W + H)/3$; Kuwamura *et al*. 1993), and the size difference between them expressed as the coral size ratio (average diameter of smaller coral/average diameter of larger coral).

Mature males and females were then collected from the reef and uniquely tagged. A single mature male was introduced into the small coral and a breeding pair introduced into the larger coral. Breeding pairs were established by introducing size-matched mature males and females together. To control for male size on the dispersal decisions of subordinate females, the size of the single male in the small coral was matched to the size of the paired male in the larger coral such that size ratio between them was never less than 0.95.

A subordinate female was then collected from the reef. The size ratio between this choosing subordinate female and the mature males and females was always less than 0.9 to prevent eviction of the subordinate (Wong *et al*. 2007). The subordinate female was placed into a transparent plastic pipe placed an equal distance between the choice corals. Holes were cut into the pipe to allow circulation of olfactory cues. The subordinate female was allowed to acclimatize for 10 min, whereupon the pipe was gently lifted by pulling an attached piece of string. The immediate habitat choice of the subordinate female was recorded as well as the choice after 24 h. The latter was scored as the subordinate's choice because a pilot study found that choices remained stable after a 24 h period (M. Y. L. Wong 2004, unpublished data).

A total of 16 coral size ratios ranging from 0.435 to 0.947 were established. For each coral size ratio, the binary choice experiment was replicated four times using a new subordinate female each time. To create different coral size ratios, the larger coral was swapped with a new larger coral, with the smaller coral remaining the same. For each new trial: (i) a new subordinate female was tested, (ii) the breeding male and female partners were re-matched such that in no two trials were the same breeding male and female paired together, (iii) each breeding male and female was never used more than once in the same coral colony, and (iv) each single male was used in a different small coral colony.

(**d**) *Statistical tests*
To determine the relative effects of coral saturation and dispersal distance on the occurrence of subordinate dispersal, a two-way ANOVA was conducted with level of saturation (low; high) and distance (10 cm; 100 cm) as categorical predictor variables and the proportion of subordinates that moved from their original groups as the response variable. To determine the effects of social rank and size ratio on the dispersal behaviour of subordinates, a logistic regression was performed with dispersal as the binary response variable (0, no dispersal; 1, dispersal). The significance of each variable and interaction were assessed with a likelihood ratio test. A Spearman rank correlation was used to assess the relationship between the proportion of subordinates that chose group-living on the larger coral and coral size ratio.

3. RESULTS
(**a**) *Habitat saturation and risks of movement*
The proportion of subordinates dispersing was dependent on the level of saturation in the alternative coral ($F_{1,30} = 5.34$, $p = 0.03$) and the distance between corals ($F_{1,30} = 27.2$, $p < 0.01$) (figure 2). Specifically, a higher proportion of subordinates dispersed when the alternative coral was of low saturation and when it was close by. Despite there being only a trend towards a significant interaction between saturation and distance ($F_{1,30} = 3.24$, $p = 0.08$), a *post hoc* test revealed that the proportion of subordinates dispersing to low-saturation corals was significantly greater than to high-saturation corals when corals were 10 cm apart (Fisher's LSD test, $p < 0.01$) (figure 2).

(**b**) *Habitat quality*
There was a significant negative relationship between coral size ratio and the proportion of subordinates that chose group-living as a non-breeder on the larger coral (Spearman's rank correlation: $R = -0.65$, $n = 16$, $p = 0.01$) (figure 3). Thus, as the coral size ratio decreased, i.e. the difference in coral size increased, subordinate females increasingly settled on the larger corals as non-breeding group members rather than settling as dominant breeding females on the smaller corals.

(**c**) *Social factors*
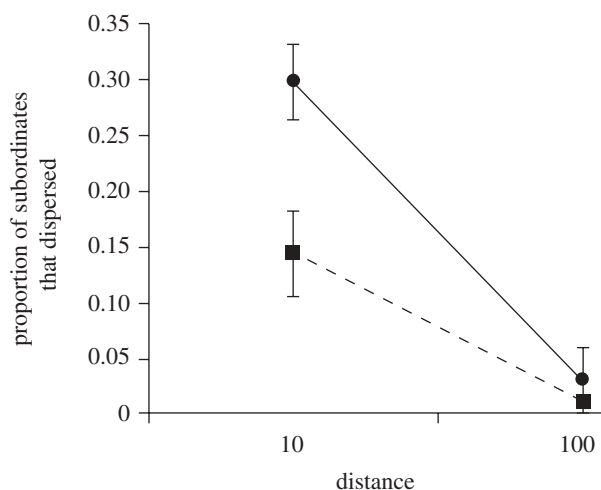The occurrence of dispersal was independent of a subordinate's rank in its original group (logistic regression:

Figure 2. Mean proportions ($\pm$s.e.) of subordinates that dispersed to high-saturation (dashed line) and low-saturation (smooth line) coral colonies that were placed either 10 or 100 cm away from their original coral.
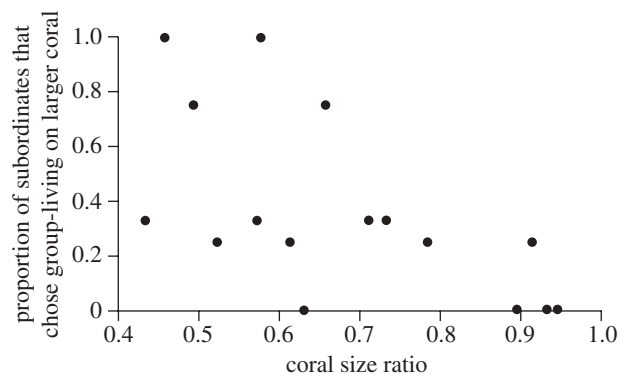

Figure 3. Relationship between the difference in coral size (expressed as coral size ratio) and the proportion of subordinate females that chose group-living as a non-breeder on the larger of two corals.

$X^2 = 0.48$, d.f. $= 1$, $p = 0.49$), the size ratio between dispersing subordinates and their immediate dominant in their original group ($X^2 = 0.36$, d.f. $= 1$, $p = 0.55$) and an interaction between social rank and size ratio ($X^2 = 0.46$, d.f. $= 1$, $p = 0.50$). Furthermore, there was no significant difference in the social rank that dispersing subordinates achieved in their new versus original group (paired t-test: $N = 23$, $T = 0.08$, d.f. $= 22$, $p = 0.94$).

4. DISCUSSION

Determining the ecological and social factors influencing the pay-offs of dispersing is essential for assessing why subordinates tolerate group-living when they are excluded from reproduction and gain no indirect or direct benefits via helping within the group. Dispersal and grouping decisions of subordinate *P. xanthosomus* were affected by coral saturation and dispersal distance, with the effects of saturation being greater at short dispersal distances. In addition, coral quality influenced grouping decisions. These results support both the ecological constraints and benefits of philopatry hypotheses, and suggest that subordinate *P. xanthosomus* tolerate non-breeding positions owing to a combination of high coral saturation, high risks of movement and a high quality of current corals (which they stand to inherit) relative to other corals in the immediate environment. Even so, the fact that facultative dispersal played out in a manner predicted by theory suggests that individuals are selected to disperse whenever suitable ecological opportunities arise.

Experimental support for the influence of habitat saturation on subordinate dispersal decisions has also been generated for the cooperatively breeding cichlid, *Neolamprologus pulcher* (Bergmüller *et al*. 2004). In *P. xanthosomus*, however, dispersal distance explained more variation in the occurrence of subordinate dispersal than habitat saturation, suggesting that risks of dispersal have a greater influence on the maintenance of group-living in *P. xanthosomus*. Costs of dispersal have been shown to constrain the dispersal decisions of subordinates in various other species, including cooperative breeders (Du Plessis 1992; Russell 2001; Heg *et al*. 2004) and

non-cooperative breeding but group-living species (Gardner *et al*. 2003), suggesting that high costs of dispersal is a key factor promoting delayed dispersal and group-living across taxa exhibiting different social and genetic systems.

The dispersal and group-living choices of subordinates were also influenced by relative coral size. Specifically, subordinate females showed an increasing preference for group-living as a non-breeder on larger corals over immediate breeding as a dominant female on smaller corals as the size difference between coral colonies increased. Although the relationship between coral size and individual fitness was not measured in this study, positive relationships between habitat size, habitat quality and reproductive success of individuals have been documented in many animal species (e.g. Goldschmidt & Bakker 1990; Oring *et al*. 1991; Kuwamura *et al*. 1994; Brooker & Rowley 1995). Results from the current study therefore suggest that subordinates face a trade-off between immediate reproduction on lower quality habitats versus delayed reproduction and group-living on higher quality habitats, with the latter being favoured as variation in habitat quality increases.

How might females benefit from group-living in larger corals? As non-breeding subordinates stand to inherit breeding status in the future (Wong *et al*. 2007), residing in and eventually inheriting a larger coral may benefit females in terms of greater lifetime fecundity. This is likely because the size of coral-dwelling gobies is often positively correlated with the size of their host coral (Kuwamura *et al*. 1996; Hobbs & Munday 2004) and female size is correlated with female fecundity, at least in the congeneric species *P. echinocephalus* (Kuwamura *et al*. 1993). Additionally, survival rates of *P. xanthosomus* could be enhanced within larger corals, as demonstrated for *P. echinocephalus* (Kuwamura *et al*. 1996), enabling longer periods of reproductive attempts. Finally, because group size is positively correlated with coral size (Lassig 1977; Thompson *et al*. 2007), females could benefit from residing in larger corals if the presence of more group members reduces predation risk owing to dilution effects or increases vigilance (Krause & Ruxton 2002). Further testing of these hypotheses would be required to confirm how exactly females benefit from residing in and eventually breeding in larger corals.

Contrary to expectations, subordinate dispersal was unrelated to social rank. Firstly, many subordinates that did not disperse from their original groups could have improved their rank by doing so. This may reflect constraints on the ability to assess social conditions in alternative groups, or potential benefits of remaining within their home group, such as familiarity effects (e.g. Griffiths *et al.* 2004). Secondly, subordinates that dispersed did not always improve their rank by doing so, as has also been documented in another habitat-specialist reef fish (Mitchell 2005). Furthermore, subordinates that did not improve their rank did not switch back to their original group. Despite their reduced ranking, staying in their new group may have been more profitable than returning, because attempting to return would have involved another costly dispersal as well as escalated conflicts over rank (Cant *et al.* 2006). Finally, subordinate dispersal was unrelated to their rank within the hierarchy. Larger and thus more dominant group members are generally expected to employ dispersal strategies to enhance their rank, owing to their reduced probability of ascending in rank by queuing relative to smaller, more subordinate group members (Buston 2004; Bergmüller *et al.* 2005). Further studies would therefore be important for elucidating the social complexities underlying dispersal in relation to rank.

Subordinate dispersal was also independent of the size ratio between the dispersing subordinate and its immediate dominant, indicating that dispersal was unlikely to have occurred as a result of forcible eviction. This result may not be surprising given that subordinates only stand to be evicted at ratios above 0.95 and they regulate their growth to avoid breaching this size ratio (Wong *et al.* 2007, 2008*b*). Nevertheless, increasing reports of subordinate evictions by dominants in social animal suggests that forcible eviction may play an important role in subordinate 'dispersal' behaviour in general (Balshine-Earn *et al.* 1998; Cant *et al.* 2001; Young *et al.* 2006). All in all, the lack of social effects in this study might imply that while social factors are known to govern within-group social interactions in *P. xanthosomus* (Wong *et al.* 2007, 2008*a*,*b*) and other social fishes (e.g. Heg *et al.* 2004; Mitchell 2005; Buston & Cant 2006), their importance in governing between-group dispersal decisions may be limited.

In conclusion, habitat saturation, costs of movement and habitat quality influence the pay-offs to non-breeding subordinates from dispersal and group-living. These results suggest that *P. xanthosomus* has been under selection for facultative dispersal in relation to ecological factors, despite having low mobility and extreme habitat-specific requirements. This study lends weight to the idea that the theory of cooperative breeding can provide a useful framework for understanding why subordinates tolerate group-living even when unrelated and unhelpful subordinates are excluded from current reproduction. Elucidating the physiological mechanisms enabling site-attached individuals to perceive and evaluate the ecological characteristics of their local environment would be an area of fascinating future research.

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