

Territory inheritance in clownfish

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Recd 28.10.03; Acctpd 17.12.03; Published online 20.02.04

Animal societies composed of breeders and non-breeders present a challenge to evolutionary theory because it is not immediately apparent how natural selection can preserve the genes that underlie non-breeding strategies. The clownfish *Amphiprion percula* forms groups composed of a breeding pair and 0–4 non-breeders. Non-breeders gain neither present direct, nor present indirect benefits from the association. To determine whether non-breeders obtain future direct benefits, I investigated the pattern of territory inheritance. I show that non-breeders stand to inherit the territory within which they reside. Moreover, they form a perfect queue for breeding positions; a queue from which nobody disperses and within which nobody contests. I suggest that queuing might be favoured by selection because it confers a higher probability of attaining breeding status than either dispersing or contesting. This study illustrates that, within animal societies, individuals may tolerate non-breeding positions solely because of their potential to realize benefits in the future.

Keywords: cooperative breeding; disperse; contest; queue; inherit; reproductive skew

1. INTRODUCTION

Many animal societies are composed of breeders and non-breeders. Such societies have generated enormous interest among evolutionary biologists because it is not immediately apparent how natural selection can preserve the genes that underlie non-breeding strategies. Non-breeders may benefit from the association in one of three ways. First, they may, in fact, accrue present direct benefits by obtaining a small share of the current reproduction. Second, they may accrue present indirect benefits by helping to raise additional non-descendant kin (Emlen & Wrege 1989). Third, they may accrue future direct benefits by inheriting the territory following the death of the breeders (Wiley & Rabenold 1984). Most investigations of these societies have been conducted in terrestrial organisms, and the conceptual framework for understanding them has developed in parallel (Emlen 1991). There is a real need to extend the taxonomic and environmental base of empirical studies to test the robustness of the current theory and provide new insights.

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In Madang Lagoon, Papua New Guinea, groups of the clownfish, *Amphiprion percula*, inhabit sea anemones that afford protection from predators (Fautin 1992; Buston 2003a). Each group is composed of a breeding pair and 0–4 non-breeders (Fricke 1979; Fautin 1992). Within each group, there is a size-based dominance hierarchy; the female is largest, the male is second largest and the non-breeders get progressively smaller as the hierarchy is descended (Fricke 1979; Buston 2003b). Non-breeders accrue neither present direct nor present indirect benefits from being in a group; non-breeders do not have functional gonads (Fricke 1979) and they do not enhance breeder fitness (Buston 2004). Non-breeders might, however, accrue direct benefits in the future: in other *Amphiprion* spp., if the female of a group dies, the male changes sex to become the breeding female, and a large non-breeder from the reef becomes the breeding male (Fricke 1979; Ochi 1989; Hattori 1994).

2. METHODS

I studied *A. percula* that occupied the anemone *Heteractis magnifica*, in Madang Lagoon, Papua New Guinea (5°09' S, 145°48' E), from January 1997 to December 1997 (see Buston (2003a) for a more detailed description of methods). I located 97 groups on three reefs: reef 1, $n = 40$; reef 2, $n = 31$; reef 3, $n = 26$. Each group occupied a single anemone, and anemones on the same reef were an average of 30 m apart. Groups were composed of a breeding pair and 0–4 non-breeders (mean number of individuals in each group \pm s.d. = 3.4 ± 0.9 , $n = 97$).

In January 1997, I captured all fishes ($n = 334$) and took them to the surface. There, I measured the standard length (SL) of each individual to within 0.1 mm. All individuals survived this procedure without any sign of harm, and they were returned to the anemone from which they were captured within 3 h, where they remained. Individuals were ranked (1–6) based on their size relative to other individuals within their anemone, with the largest being ranked 1. Within an anemone, I considered an individual of rank x to be dominant to all individuals with ranks of greater than x , and subordinate to all individuals with ranks of less than x .

I monitored the settlement, recruitment, migration and disappearance of individuals by conducting a thorough census of each group every 1–2 days, for 10 lunar months (7 February–5 December 1997). Individuals were assigned to one of five classes: (i) larval settlers, if they were less than 18 mm in SL when they were first observed in an anemone; (ii) recruits, if they reached 18 mm or more in SL after settling in an anemone; (iii) residents (rank of 1–6), if they were 18 mm or more in SL and were present in the anemone at the beginning of the study; (iv) migrants, if they were 18 mm or more in SL and moved between anemones; or (v) disappearances, if they had been 18 mm or more in SL but could not be found in their anemone or any of the other anemones on the reef after a thorough search. The transition from settler to recruit marks the point (18 mm SL) at which a settler was deemed to have joined a group. This transition point was chosen because fish greater than 18 mm SL could be individually recognized on the basis of natural variation in their markings.

I monitored the reproductive activity of individuals over the same time period. Breeding was readily detectable because, in the week after spawning, the male spent a large proportion of his time tending the eggs.

3. RESULTS

(a) Natural occurrence of territory inheritance

I investigated the natural pattern of territory inheritance by monitoring 33 groups on reef 1 and 24 groups on reef 2. I excluded 14 groups on these reefs from the test because they were experimentally manipulated for another study (Buston 2004). I monitored each group for (i) the appearance of new individuals; (ii) reversals of rank; and (iii) the disappearance of one of the breeding pair. In the event of a breeder disappearance, I recorded which individual from the reef filled the breeding vacancy.

I observed nine individuals joining groups, and in every case the newcomer was a larval settler and joined at the

Table 1. Pattern of territory inheritance.

the fate of breeding vacancies	natural vacancies	experimental vacancies
non-resident usurped the vacancy	0/9	0/16
resident non-breeder filled the vacancy	7/9 ^a	16/16
largest resident non-breeder inherited the vacancy	1/1	7/7
new pairing successfully bred	5/9 ^b	16/16

^a In the remaining two cases, breeding vacancies arose in groups that did not have non-breeders, and in each of these cases the vacancy was filled by a larval settler that recruited at the anemone.

^b In the remaining four cases, breeding did not recommence successfully before the end of the study period, but natural vacancies occurred only a few months before the end of the study, and breeding should have recommenced successfully in early 1998.

bottom of the hierarchy (Buston 2003a). I observed no reversals of rank, out of 144 pairwise interactions. I observed nine natural disappearances from breeding positions (five female and four male), which created nine breeding vacancies. In seven out of nine cases, a non-breeder present in the anemone filled the vacancy (table 1); in no case did a resident migrate from another anemone and usurp the vacancy (table 1). In one case, there was more than one non-breeder present in the anemone, and in this case the largest non-breeder inherited the vacancy (table 1). In two cases, there was no non-breeder present in the anemone when the vacancy arose, but a larval settler recruited at the anemone (joined the group) and filled the vacancy. In five out of the nine cases, the new pairing bred successfully before the end of the study period (table 1); in the remaining four cases, the vacancy arose only a few months before the end of the study.

(b) Experimentally induced territory inheritance

I investigated the pattern of territory inheritance experimentally by removing males from 16 groups on reef 3. I removed males one lunar month after the beginning of the study, from groups that had bred during the first lunar month of the study. The 10 remaining groups on reef 3 provided a source of non-breeders (11 individuals) that could potentially usurp breeding vacancies. In the months that followed male removal, I recorded which individual from the population filled the breeding vacancies that I had created.

A non-breeder from within the anemone filled the vacancy in 16 out of 16 cases (table 1); there was not a single case in which a non-breeder from another anemone usurped the vacancy (table 1). In seven out of the 16 cases, there was more than one non-breeder present in the anemone, and in each of these cases the largest non-breeder inherited the breeding position (table 1). In all 16 cases, the new pairing bred successfully before the end of the study period (table 1).

4. DISCUSSION

Amphiprion percula lives in groups composed of a breeding pair and 0–4 non-breeders (Fricke 1979; Fautin 1992; Buston 2003a,b). Non-breeders accrue neither direct nor indirect benefits from this association (Fricke 1979; Buston 2004). In light of this, I predicted that they must stand to inherit territories in the future. I show that non-breeding *A. percula* inherit the territory within which they reside. Moreover, they form a strict queue for breeding positions; individuals only ascend in rank as those ahead

of them disappear, and newcomers always join the bottom of the hierarchy—the back of the queue (table 1).

Territory inheritance by queuing is well documented in a wide variety of animal societies (McDonald 1993; Creel & Waser 1994; Field *et al.* 1999; East & Hofer 2001), but social queues are puzzling because it is rarely clear why subordinates wait peacefully. To understand why queuing is favoured by selection, two questions must be addressed (Wiley & Rabenold 1984; Emlen 1991; Field *et al.* 1999; Kokko & Johnstone 1999): (i) why do subordinates stay rather than disperse; and (ii) why do subordinates queue rather than contest? Simply, queuing can be favoured if it confers a greater probability of attaining breeding status than the alternative strategies (Kokko & Johnstone 1999; Ragsdale 1999). This probability will be maximized by pursuing the strategy that conveys the highest probability of ascending in rank at each step in the hierarchy.

The probability of ascending in rank by queuing is equal to the probability that the individual outlives at least one of its dominants. This is because an individual will ascend in rank if any one of its dominants dies, and not just when its immediate dominant dies. Using the success runs Markov chain (Taylor & Karlin 1984), it can be shown that the probability of ascending from rank x to rank $x - 1$ is:

$$\left(\frac{q_x}{p_x + q_x} \right), \quad (4.1)$$

where, p_x is the probability of the rank x individual dying in a given time period and q_x is the probability of any individual ranked higher than x dying in the same time period. In *A. percula*, the probability of mortality is associated with rank and rank alone (Buston (2003c); probability of mortality per 10 lunar months = $1/(1 + e^{(3.69 - 0.60 \times \text{rank})})$, $\chi^2 = 4.75$, $p = 0.029$). The parameters of this logistic model can be used to estimate the mortality rate of each rank, and hence the probability that an individual ascends in rank by queuing. The probability of ascending in rank by queuing is surprisingly high (*ca.* 0.5 for rank 3), and it increases towards the back of the queue.

The probability of ascending in rank by dispersing will depend on both the probability of successfully moving between anemones and the probability of successfully entering another anemone at a higher rank. The first probability is likely to be exceptionally low, because *A. percula* are poor swimmers and are rapidly preyed upon if removed from their anemone's tentacles (Mariscal 1970; Elliott *et al.* 1995). The second probability is also likely to be very low because, in Madang Lagoon, territorial

residents occupy 100% of the anemones on the reef (Fautin 1992) and these territorial residents evict intruders (Buston 2003a). I predict that these two factors together (the low chance of successfully moving between anemones and the low chance of successfully entering another anemone) will reduce the probability of ascending in rank by dispersing to well below that for queuing.

The probability of ascending in rank by contesting depends on the subordinate's chance of winning a fight with its immediate dominant. This, in turn, depends on the relative body size of the two fishes (Rowland 1989). This probability is likely to be very low because within groups of *A. percula* well-defined size differences are maintained between individuals adjacent in rank (Buston 2003b). These size differences are maintained by the actions of dominants and subordinates. Dominants will evict subordinates that are of similar size to themselves. Evictions are, however, rare under natural conditions and occur only at the point of entry into groups when individuals similar in size are forced together (Buston 2003a). Once subordinates have joined the group, they modify their growth rate to maintain a size difference with respect to their immediate dominant that does not elicit eviction. I predict that the relatively large size differences maintained between individuals adjacent in rank will reduce the probability of ascending in rank by contesting well below that for queuing.

5. CONCLUSION

In *A. percula*, non-breeders stand to inherit the territory within which they reside following the disappearance of higher-ranked individuals. Non-breeders form a perfect queue for breeding positions—a queue from which nobody disperses and within which nobody contests. Queuing is probably favoured by selection because it confers a higher probability of ascending in rank than either dispersing or contesting. This study provides support for the idea that, when ecological constraints are harsh and there is a real threat of eviction, individuals may tolerate non-breeding positions in a society purely because of their potential to realize benefits in the future (Emlen 1991; Kokko & Johnstone 1999; Ragsdale 1999).

Acknowledgements

This work comprises a portion of the author's doctoral dissertation requirements (Cornell University). The author thanks his PhD advisors, S. T. Emlen, P. W. Sherman, H. K. Reeve, A. R. McCune and A. H. Bass, for valuable support; M. Andrade, M. Cant, J. Dale, E. Tibbetts, R. Warner, C. Webb and Cornell's 'Behavior Lunch Bunch' for helpful comments and discussion; J. Mizeu, M. Black, C. Norris, M. Moore, and the staff of the Christensen Research Institute and the Jais Aben Resort for their assistance in Papua New Guinea; the landowners of Riwo Village, the Madang Provincial Government and Papua New Guinea Government for permitting his fieldwork.

Supported by D. Christensen and the Christensen Fund, a National Science Foundation Doctoral Dissertation Improvement Grant, the Andrew W. Mellon Fund of the Cornell College of Agriculture and Life Sciences, the Cornell and National Chapters of Sigma Xi, the International Women's Fishing Association and the Cornell University Department of Neurobiology and Behavior. The author is currently a Postdoctoral Fellow at the National Center for Ecological Analysis and Synthesis, a Center funded by NSF (grant DEB-0072909), the University of California, and the Santa Barbara campus.

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