

Forcible eviction and prevention of recruitment in the clown anemonefish

Peter Buston

Cornell University, Department of Neurobiology and Behavior, Seeley G. Mudd Hall, Ithaca, NY 14853, USA

How big an animal group will be depends on how the group's size is regulated and on the costs and benefits of living in the group. To determine which individuals regulate group size of the clown anemonefish, *Amphiprion percula*, I investigated the strategies involved in the formation, maintenance, and dissolution of its groups. Groups composed of a single breeding pair and of zero to four nonbreeding subordinates occupied individual sea anemones (*Heteractis magnifica*), which provided the fish with oviposition sites and protection from predators. Group size increased linearly with anemone size. I used the residuals of this relationship as a measure of the degree of saturation of each anemone. Residents evicted low-rank subordinates and prevented the recruitment of additional subordinates at anemones with a high degree of saturation, but not at anemones with a low degree of saturation. These strategies indicate that residents control group membership of their subordinates, and suggest that residents might incur costs from the presence of subordinates in more saturated anemones. In general, whenever residents can control group membership, the prevention of recruitment and the eviction of subordinates will set an upper limit on group size. *Key words*: density dependence, group size, habitat saturation, habitat selection, migration, settlement. [*Behav Ecol* 14:576–582 (2003)]

A central question of animal behavior is, how big will a group be? Theoretical models of group living (see Fretwell, 1972; Giraldeau, 1988; Higashi and Yamamura, 1993; Johnstone and Cant, 1999; Reeve and Emlen, 2000; Sibly, 1983) have indicated that the answer depends on how group size is regulated and on the costs and benefits of living in the group. Determination of which individuals regulate group membership is thus a vital step toward gaining a complete understanding of any animal group; group size should reflect the best interests of whichever individuals have control over group membership. It is possible to determine which individuals regulate group size, and shed light on the economics of group living, by investigating the strategies involved in the formation, maintenance, and dissolution of groups (Danchin and Wagner, 1997). For example, in the cooperative mongoose, *Suricata suricatta*, the dominant female may evict subordinates when she is about to give birth (Clutton-Brock et al., 1998). This eviction indicates three things: (1) that the dominant female controls group membership, (2) that her costs and benefits of retaining subordinates shift as her pregnancy progresses, and (3) that subordinates would benefit from remaining in the group, because they are persistent in their attempts to re-enter.

Group dynamics are influenced by four strategies, two that govern joining groups and two that govern leaving groups. Joining depends on the settler's decision of whether to join a group or continue searching for another group (Martinez and Marshall, 1999), and on each resident's decision of whether or not to let the settler join the group (Higashi and Yamamura, 1993). Leaving depends on each resident's decision of whether to stay with or voluntarily leave the group, and on each resident's decision of whether or not to

evict other residents from the group (Johnstone and Cant, 1999; Reeve and Emlen, 2000).

Coral reef fishes make excellent subjects for studies both of the strategies underlying group dynamics and of the costs and benefits associated with living in groups (Booth, 1992, 1995; Clifton, 1990; Sweatman, 1983, 1988). Most coral reef fishes have a bipartite life cycle, with a dispersing pelagic larval phase and a relatively sedentary reef resident phase (Sale, 1980). At the end of the pelagic phase, larvae settle on the reef and attempt to recruit to the resident population (Williams and Sale, 1981). The smallest fish found on the reef can be defined as settlers, whereas individuals that survive some arbitrary time after larval settlement and successfully join the resident population can be defined as recruits (Caley et al., 1996; Keough and Downes, 1982; Sale, 1991; Victor, 1991; Williams and Sale, 1981). Because the resident phase is relatively sedentary, the decisions made at the time of recruitment (joining) greatly affect the future success of both settlers and current residents.

The 28 species of anemonefish (Family Pomacentridae) are a common sight on Indopacific coral reefs (Fautin and Allen, 1992). Groups of anemonefish form obligate associations with sea anemones that provide the fish with oviposition sites and protection from predators (Allen, 1972). There often is a positive correlation between anemone size (e.g., diameter, area, or number of anemones) and anemonefish group size (e.g., number of individuals, or the sum of the standard lengths [SLs] of individuals) (Allen, 1972; Elliott and Mariscal, 2001; Fautin, 1992; Fricke, 1979; Hattori, 1991; Ross, 1978). Typically, groups are composed of a dominant breeding pair and of zero to four nonbreeding subordinates (Allen, 1972; Elliott and Mariscal, 2001). Within each group, a size-based dominance hierarchy exists; the female is largest, the male is second largest, and the smaller fish are nonbreeders (Allen, 1972; Fricke, 1979). *Amphiprion* are protandrous hermaphrodites (Fricke and Fricke, 1977; Moyer and Nakazono, 1978); if the female of a group dies, then the male changes sex, and a large nonbreeder from the population becomes male (Fricke, 1979; Hattori, 1994; Ochi, 1989).

Of the four strategies that could influence anemonefish group dynamics, Elliott et al. (1995) investigated the settler's

Address correspondence to P. Buston, who is now at the National Center for Ecological Analysis and Synthesis, University of California, 735 State Street, Suite 300, Santa Barbara, CA 93101-5504, USA. E-mail: buston@nceas.ucsb.edu.

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strategy in detail. Their field experiments indicated that settlers attempted to recruit at anemones irrespective of the presence or absence of conspecifics (*A. polymus*, *A. clarkii*) and did not leave anemones voluntarily (*A. sandaracinos*, *A. clarkii*). Using the clown anemonefish, *Amphiprion percula*, I investigated the three remaining strategies that could influence group dynamics and determined the extent to which these strategies were contingent on the degree of saturation of each anemone (a measure of the density of fish within each anemone). Specifically, I tested three hypotheses: (1) residents will only allow settlers to recruit at anemones with a low degree of saturation, (2) residents will not voluntarily depart from their anemones, and (3) residents will evict subordinates, but only from anemones with a high degree of saturation. Results indicate that residents have control over the group membership of their subordinates and suggest that some residents might incur costs from the presence of their immediate subordinates in highly saturated anemones.

METHODS

Study population

I studied the clown anemonefish, *Amphiprion percula*, for 12 months (January 1997–December 1997), in Madang Lagoon, Papua New Guinea (5°09' S, 145°48' E). All fieldwork was conducted by using scuba equipment, at depths of up to 13 m. I located 97 groups on three reefs: Sinub (reef 1), $n = 40$; Wongad (reef 2), $n = 31$; and Masamoz (reef 3), $n = 26$ (Buston, 2002; see Jebb and Lowry, 1995, for a description of Madang Lagoon and its reefs). This study utilized 71 groups, located on reefs 1 and 2. (The 26 groups on reef 3 were not used for this study because they could not be regularly censused). Each group occupied a single anemone *Heteractis magnifica*, and anemones were an average of 30 m apart. Groups consisted of a breeding pair and zero to four nonbreeders (mean number of individuals in each group \pm SD = 3.5 ± 0.9 , $n = 71$).

In January 1997, all fish ($n = 248$) were captured by using hand nets and were taken to the surface in plastic bags. There, the SL of each individual was measured to 0.1 mm by using calipers (Caillet et al., 1986). All fish 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 (one to six) based on their size relative to other individuals within their group, with the largest being ranked one. I considered an individual of rank N to be dominant to all individuals with ranks greater than N . Although fish of rank N were larger than fish of rank $N + 1$ within each group, this did not always hold true across groups (Buston, 2002).

Group dynamics

I monitored 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). Following the logic of previous investigators (Keough and Downes, 1982; Williams and Sale, 1981), individuals were assigned to one of five classes: (1) settlers, if they were less than 18 mm in SL when they were first observed in an anemone; (2) recruits, if they reached 18 mm or more in SL after settling in an anemone; (3) residents (rank, one through six), if they were 18 mm or more in SL and were present in the anemone at the beginning of the study; (4) migrants, if they were 18 mm or more in SL and moved between anemones; or (5) 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 marked the point (18 mm SL) at which a settler was deemed to have joined a group. Although the 18-mm SL transition point was arbitrary, it was chosen for two reasons: (1) fish greater than 18-mm SL could be recognized individually on the basis of natural variation in their color markings, when regularly censused (Nelson et al., 1994); and (2) fish greater than 18-mm SL could be reliably censused without continual disturbance of the anemone (Elliott and Mariscal, 2001). Duration of residency was not used as the criterion to distinguish between settlers and recruits, because very small individuals could not be identified individually, and could not be reliably censused without disturbing the anemone. Although my definitions of settlers and recruits are slightly different from those of some other authors (see Elliott et al., 1995; Elliott and Mariscal, 2001; Holbrook and Schmitt, 1997; Schmitt and Holbrook, 2000), these differences do not affect the major conclusions of the study.

Anemone saturation

I used the mean diameter of each anemone's oral disc (Fautin and Allen, 1992) as a measure of anemone size (mean anemone diameter \pm SD = 50 ± 8 cm, $n = 71$). The diameter of the anemone was measured to the nearest 5 cm, and the mean was calculated from 15 separate measures of the oral disc taken throughout 1997. Each anemone was measured multiple times over the year because anemones varied slightly in size from day to day. No anemone growth was detected over the year.

I used the group SL (GSL) as a measure of group size (mean GSL \pm SD = 140.1 ± 37.6 mm, $n = 71$). The GSL was calculated as the sum of the SLs of all residents (individuals \geq 18-mm SL). I used GSL as a measure of group size rather than the number of individuals, for two reasons. First, GSL incorporated the sizes as well as the number of individuals in the group and, thus, might be a better measure of the resource requirements of the group (Elliott and Mariscal, 2001; Robertson, 1998). Second, the correlation between GSL and anemone diameter was stronger than that between number of individuals and anemone size (see also Elliott and Mariscal, 2001; Fautin, 1992; Hattori, 1991; Ross, 1978).

The observation that anemone size and GSL were related suggested that there could be a point at which anemones of a given size would be saturated (sensu Holbrook et al., 2000; Schmitt and Holbrook, 2000), or at carrying capacity (Ross, 1978). Individuals were expected to be gained at undersaturated patches of habitat, whereas individuals were expected to be lost from oversaturated patches of habitat (Holbrook et al., 2000). Because there was no a priori way of determining the actual point of habitat saturation, and because patches of habitat were likely to span a continuum of saturation, I estimated the relative degree of saturation of each anemone.

The degree of anemone saturation was calculated as the residual from the significant second order polynomial regression of GSL on mean anemone diameter (regression: $y = 0 + 4.709x - 0.037x^2$; Buston, 2002). Negative residuals indicated a smaller GSL than expected for the size of the anemone (i.e., low degree of saturation), and positive residuals indicated the opposite (i.e., high degree of saturation). I used the term saturation, rather than density, because density is most commonly used to mean the number of individuals per unit of suitable habitat (see Schmitt and Holbrook, 2000).

RESULTS

Hypothesis 1

I tested the hypothesis that residents will only allow settlers to recruit at anemones with a low degree of saturation. Elliott et

al. (1995) observed that residents often drove settlers from anemones within minutes of the latter's arrival, but the relationship between this behavior and the degree of anemone saturation was not investigated. I predicted that the degree of saturation of anemones in which recruitment occurred would be lower than that of anemones in which there was no change in the number of subordinate individuals.

Observational test

I recorded settlement events as they were observed, as well as every recruitment event in 57 anemones for the entire study period. To rule out the possibility that the recruitment pattern was the product of settlement preferences alone, I tested the hypothesis that residents modify the initial settlement pattern, by comparing the settlement pattern to the recruitment pattern. I predicted that the proportion of anemones in which recruitment occurred would be lower than the proportion of anemones in which settlement was observed. The lowest-rank residents were observed attempting to drive settlers from anemones twice, providing a mechanism that could modify the pattern of settlement. Settlement was observed in 30 of 57 anemones (53%), whereas recruitment was observed in only nine of 57 anemones (16%). This difference was highly significant (χ^2 test: $df = 1$, $\chi^2 = 17.2$, $p < .005$).

I compared the degree of saturation of anemones for groups in which there was no change in the number of subordinate individuals with those in which recruitment of a new subordinate occurred. The degree of anemone saturation was measured at the beginning of the study, except in five cases in which the recruitment of a subordinate was preceded by the disappearance of a resident breeder (resulting in a drop in saturation). The degree of saturation of these five anemones was estimated at the time of the recruitment event, by determining their residual from the regression of GSL on anemone diameter after the breeder's disappearance. No anemone was included in the analysis more than once. The degree of saturation of anemones at which recruitment occurred (mean \pm SE = -59.0 ± 10.8 , $n = 9$) was lower than the degree of saturation of anemones at which no change in the number of subordinate individuals occurred (mean \pm SE = -3.8 ± 5.3 , $n = 38$; Kruskal-Wallis test: $p < .0001$; see also the test of hypothesis 3) (Figure 1). Multiple comparisons between samples (following the Kruskal-Wallis test; Zar, 1984) indicated that this difference was significant (Q test: $p < .01$).

All recruitment events occurred at anemones with one to three 3 individuals, raising the possibility that group dynamics were related to the number of individuals rather than to the degree of anemone saturation per se. To evaluate this possibility, I repeated the comparison of the degree of saturation, restricting the analysis to small groups (those with one to three individuals). The degree of saturation of anemones at which recruitment occurred (mean \pm SE = -59.0 ± 10.8 , $n = 9$) was still significantly lower than that of anemones at which no change in the number of subordinate individuals occurred (mean \pm SE = -23.8 ± 4.9 , $n = 23$; Mann-Whitney test: two-tailed: $U = 168.0$, $p = .007$).

Experimental test

I tested hypothesis 1 experimentally by artificially decreasing the degree of saturation of 13 anemones. I removed all resident nonbreeders from these anemones, four lunar months after the beginning of the study. Manipulated groups were randomly selected from the pool of groups of three or four individuals that had bred in the first four lunar months of the study. Unmanipulated control groups ($n = 37$) were those from which there was neither experimental removal nor natural disappearance for the entire study period. I recorded

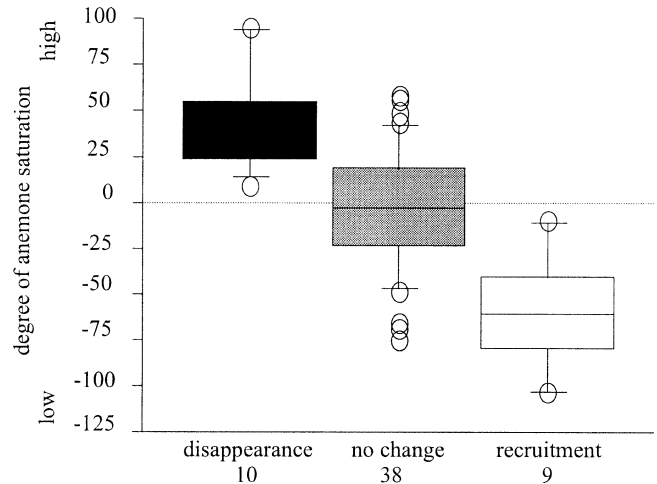


Figure 1

The degree of saturation of anemones in which recruitment occurred, no change in the number of subordinate individuals occurred, and low-rank disappearance occurred, (Kruskal-Wallis test: H [no ties] = 25.9, $p < .0001$; $Q_{\text{recruitment versus no change}} = 3.14$, $p < .01$; $Q_{\text{disappearance versus no change}} = 3.30$, $p < .01$).

all anemones at which recruitment occurred for the next six lunar months. I predicted that the proportion of manipulated groups, (groups with an artificially reduced degree of saturation), in which recruitment occurred would be greater than the proportion of unmanipulated groups in which recruitment occurred. Recruitment occurred at 13 of 13 manipulated anemones (100%) that had an artificially reduced degree of saturation. In contrast, recruitment occurred in only two of 37 unmanipulated anemones (5.4%) during the same observation period. These proportions were significantly different (Fisher exact test: $p < .0001$) (Figure 2).

To eliminate the possibility that recruitment was a product of the settler's preference alone, I repeated the comparison of the proportion of groups in which recruitment occurred, this time restricting my analysis to groups in which settlement was observed. I predicted that the proportion of settled groups in which recruitment occurred would be greater for manipulated groups than for unmanipulated groups. Recruitment occurred at all 13 manipulated groups in which settlement took place (100%). In comparison, recruitment occurred in only two of 16 unmanipulated groups in which settlement was observed (13%). This difference was still highly significant (Fisher exact test: $p < .0001$).

Hypothesis 2

I tested the hypothesis that residents will not voluntarily depart from their anemones. Ross (1978) and Fricke (1979) suggested that tropical anemonefish rarely moved between anemones, but these observations were not quantified. I predicted that there would be few migrations among anemones within the study population, and little immigration from other populations.

Observational test

I recorded every resident that vanished from, and every new immigrant that arrived at, 57 anemones for the 10 lunar month study period. A total of 23 out of 248 residents vanished from their anemones. Of these, none were sighted at any of the other 71 anemones within the study population, indicating that individuals did not migrate between anem-

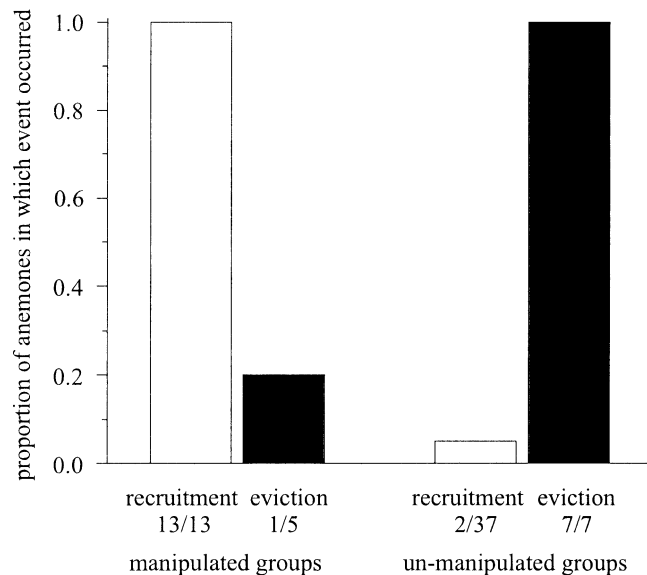


Figure 2

The proportion of manipulated and unmanipulated groups in which recruitment occurred, (white bars, Fisher exact test: $p < .0001$); and from which introduced nonbreeders were evicted, (black bars, Fisher exact test: $p = .010$). Manipulated groups had had their degree of anemone saturation artificially reduced by the removal of resident nonbreeders.

ones. Further, no new immigrants entered the study population, indicating that individuals did not migrate between reefs.

Experimental test

I tested hypothesis 2 experimentally, by taking advantage of the manipulation performed to test hypothesis 1 (above). To test hypothesis 1, I removed all nonbreeders from 13 groups, creating vacancies within groups. I predicted that residents would not voluntarily migrate, despite the existence of the experimental vacancies. No residents migrated from unmanipulated groups into groups where vacancies had been created. Further, no residents migrated from manipulated groups.

Hypothesis 3

I tested the hypothesis that residents will evict subordinates from anemones with a high degree of saturation. Allen (1972) and Ochi (1985) observed that anemonefish sometimes evicted subordinate residents from anemones, but these observations were not quantified and the relationship between this behavior and the degree of anemone saturation was not investigated. I predicted that the degree of saturation of anemones from which disappearance of subordinates occurred would be higher than that of anemones at which there was no change in the number of subordinates.

Observational test

I recorded every disappearance event at 57 anemones for the entire 10-month study period. I divided the disappearances into two groups, high rank (one to three, $n = 12$) and low rank (four to six, $n = 11$), on the basis of the observation that the probability of disappearance was significantly higher for low-rank subordinates than for high-rank individuals (χ^2 test: $df = 1$, $\chi^2 = 14.1$, $p < .001$; Buston, in press), and I further investigated low-rank disappearances as putative evictions.

I compared the degree of saturation of anemones at which there was no change in the number of low-rank subordinates

with those at which there was the disappearance of a low-rank subordinate. No anemone was included in the analysis more than once. The second to lowest-ranked resident was observed attempting to evict the lowest-ranked resident from three anemones (e.g., rank 4 attempted to evict rank 5, from a group of five). In each case, this involved the larger individual aggressively driving the smaller individual beyond the periphery, and the smaller individual persistently trying to re-enter the anemone. Eleven low-rank residents disappeared from 10 anemones. The degree of saturation of anemones at which no change in the number of subordinates occurred (mean \pm SE = -3.8 ± 5.3 , $n = 38$) was significantly lower than the degree of saturation of anemones at which disappearance of a low-rank subordinate occurred (mean \pm SE = 47.5 ± 9.1 , $n = 10$; Kruskal-Wallis test: $p < .0001$; see also the test of hypothesis 1) (Figure 1). Multiple comparisons between samples (following the Kruskal-Wallis test; Zar, 1984) indicated that this difference was significant (Q test: $p < .01$).

All disappearances of low-ranked subordinates occurred at anemones with four to six individuals. Once again, this raises the possibility that group dynamics were related to the number of individuals rather than the degree of anemone saturation per se. I repeated the comparison of the degree of saturation, this time controlling for the number of individuals, by restricting the analysis to large groups (those with four to six individuals). In this restricted analysis, the degree of saturation of anemones from which a low-rank subordinate disappeared (mean \pm SE = 47.5 ± 9.1 , $n = 10$) was higher than the degree of saturation of anemones at which there was no change in the number of subordinate individuals (mean \pm SE = 27.1 ± 4.6 , $n = 15$), though the difference is not quite significant in a two-tailed test (Mann-Whitney U test: $U = 106.0$, two-tailed $p = .086$).

Experimental test

I tested hypothesis 3 experimentally, by introducing nonbreeders to five manipulated groups and seven unmanipulated groups, after 5 December 1997, and conducting focal observations. Manipulated groups were randomly selected from the groups that had had their degree of saturation artificially decreased to test hypothesis 1 (above), by the removal of all resident nonbreeders at the end of lunar month 4. The new recruits that had arrived at these anemones since that time (see Hypothesis 1) were removed on 5 December. Unmanipulated controls were randomly selected from groups of three individuals that had not changed in composition during the study period. Introduced nonbreeders came from other anemones on the same reef, and were at least 5 mm smaller than the resident male. The introduced nonbreeder was scored, each day, as either admitted to the anemone (within the periphery and not being attacked) or evicted (beyond the periphery and being attacked), until either disappearance occurred or until the experiment was terminated after 4 days. I predicted that introduced nonbreeders would be evicted from a greater proportion of unmanipulated groups (natural degree of saturation) than of manipulated groups (artificially reduced degree of saturation). Focal observations revealed that introduced nonbreeders were evicted from seven out of seven unmanipulated (natural degree of saturation) anemones (100%). In contrast, only one out of five introduced nonbreeders was evicted from manipulated (artificially reduced degree of saturation) anemones (20%) (Fisher exact test: $p = .01$) (Figure 2).

All eight fish that were evicted were aggressively driven beyond the periphery of the anemone. All residents participated in these evictions, unlike the observations of eviction under natural conditions. All evictees were persistent in their attempts to re-enter the anemone. When the experiment was

terminated, six of the eight fish had vanished, and two remained outside the periphery of the anemone. Of the six fish that vanished, five disappeared and were never seen again, and one successfully migrated to a group 10 m down reef from which a similar-sized individual had been removed in the previous week.

DISCUSSION

A. percula residents do not voluntarily move between anemones, indicating that it is always beneficial for residents to stay at their current anemone, rather than move among anemones. This is consistent with the results of Elliott and Mariscal (2001), who found that *A. percula* residents did not move between anemones during an 11-week study. This is a particularly challenging result to understand from the perspective of the nonbreeding subordinates, but it is plausible for three reasons: (1) there is a high probability of being preyed on when attempting to move between anemones, because *A. percula* are poor swimmers and predators are abundant (Elliott et al., 1995; Mariscal, 1970); (2) there is a low probability of obtaining a better living situation in another anemone, because every anemone is occupied by territorial residents (Buston, 2002; Elliott and Mariscal, 2001); and (3) there is a chance of outliving the dominants and inheriting the breeding position at the current anemone (Buston, 2002).

I did not test the hypothesis that *A. percula* settlers exhibit a preference for anemones with a particular degree of saturation for two reasons. Firstly, the results of Elliott et al. (1995) suggest that anemonefish settlers do not exhibit such a preference, because settlers (*A. polymnus*, *A. clarkii*) were attracted to anemones irrespective of the presence or absence of conspecifics. Secondly, my data were collected at intervals of 1–2 days, a time period in which the *actual* settlement pattern could be modified to give rise to the *observed* settlement pattern (Booth, 1992; Elliott et al., 1995; Elliott and Mariscal, 2001; Holbrook and Schmitt, 1997; Schmitt and Holbrook, 1999b; Sweatman, 1988). Regardless of any settlement preference that might exist in *A. percula*, the pattern of settlement was modified to give rise to the pattern of recruitment under both natural and experimental conditions. A number of processes could cause this modification (Caley et al., 1996), but the most likely candidate process is that residents prevent recruitment.

A. percula residents prevent the recruitment of settlers at anemones with moderate or high degrees of saturation, and evict low-rank subordinates from anemones with high degrees of saturation. This generates a pattern of recruitment consistent with the results of Elliott and Mariscal (2001), who found that recruitment of *Amphiprion clarkii* to *Heteractis crispa* was related to the total length of resident fish, when anemone size was controlled. A small number of observations suggest that individuals were primarily driven from the anemone by their immediate dominant, under natural conditions. This is consistent with observations of conflict within groups of other anemonefishes, which indicate that aggression is primarily directed from a more dominant individual toward its immediate subordinate (Allen, 1972; Fricke, 1979; Fricke and Fricke, 1977). The observations suggest that residents might incur costs from the presence of their immediate subordinates in more saturated anemones. This cost may be related to competition for food, if the diets of similar sized individuals overlap extensively (Jones, 1991). Alternatively the cost may be related to competition for rank, which determines access to reproduction, if the rank of

similarly sized individuals is still under dispute (Buston, 2002).

This study demonstrates that resident *A. percula* can control the group membership of their subordinates, corroborating similar observations in other *Amphiprion* sp. (Allen, 1972; Elliott et al., 1995; Ochi, 1985). Further, this study establishes that the control of group membership is contingent on the degree of anemone saturation. Because individuals can control the residency of their subordinates, I predict that the presence of subordinates will be closely linked to the costs and benefits that higher-rank individuals incur or accrue from them. Further, because subordinates can be evicted, I predict that they will pay to stay in some way, either by minimizing the costs they inflict or by conferring some benefits on the dominants (Balshine Earn et al., 1998; Emlen, 1991; Fricke, 1979). The precise costs and benefits of the association, from the perspective of both the dominants and subordinates, have yet to be established.

Eviction and the prevention of recruitment may be widespread phenomena influencing the group dynamics of other reef fishes. The ecological context in which natural selection might favor these strategies is common (Sale, 1991): patchy habitat (e.g., anemones, coral heads, patch reefs); inhospitable terrain between patches, which makes subordinates reluctant to leave; and competition within patches, which provides dominants with an incentive to evict. A decrease in recruitment with increasing competitor density has been widely documented among reef fishes (Behrens, 1987; Forrester, 1995; Sale, 1976; Shulman, 1984; Shulman et al., 1983; Stimson, 1990; Sweatman, 1985; Tupper and Hunte, 1994), and evidence is accumulating that this can be owing to the antagonistic actions of residents (Elliott et al., 1995; Schmitt and Holbrook, 1999a). Eviction of residents from groups has been well documented in the East African cichlids (Balshine-Earn et al., 1998; Taborsky, 1985). In the marine environment, direct evidence for eviction comes from observations of individuals attempting to exclude conspecifics from shelter (e.g., *Dascyllus* sp., Schmitt and Holbrook, 1999a; *Dascyllus aruanus* and *D. reticulatus*, Sweatman, 1983; *Tautoglabrus adspersus*, Tupper and Boutillier, 1995). Indirect evidence for eviction comes from observations that subordinate residents of some fishes have strategies that apparently help them to avoid eviction (Doherty, 1983; Itzkowitz, 1977; Sale, 1980; Thresher, 1978). Such strategies would only be expected to evolve if eviction was an important process leading to differential survival and reproduction in these fishes.

Theoretical models of group living generally make an assumption about which individuals are in control of group membership (see Fretwell, 1972; Giraldeau, 1988; Higashi and Yamamura, 1993; Johnstone and Cant, 1999; Reeve and Emlen, 2000; Sibly, 1983). This study tests this assumption in *A. percula* and suggests that models in which dominant individuals are assumed to have control over group membership (Higashi and Yamamura, 1993; Johnstone and Cant, 1999; Reeve and Emlen, 2000) might provide the most insight into the lives of these fish. Observations and experiments such as those presented here are vital for the evaluation of theoretical models of group living, and will ultimately lead to a better understanding of why animals form groups.

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