



Queue selection and switching by false clown anemonefish, *Amphiprion ocellaris*

JEREMY MITCHELL

Behavioural Ecology Research Group, Simon Fraser University

(Received 30 April 2003; initial acceptance 4 November 2003;
final acceptance 11 May 2004; published online 29 December 2004; MS. number: A9600)

Social groups of false clown anemonefish have been described as queues because, following settlement, fish acquire social rank passively by outliving more dominant groupmates. Within each queue, reproduction is restricted to the dominant pair. Therefore, individuals should adopt tactics that maximize their likelihood of attaining social dominance. Field observations indicated that, independent of an anemone's size, postlarval false clowns are more likely to settle to an anemone if the resident group is smaller, suggesting that settlers prefer shorter queues. Some individuals (switchers) moved postsettlement. There was no indication that false clowns use switching as a tactic to enhance rank: characteristics of switching and nonswitching false clowns did not differ, and switching rarely resulted in improved social rank within the new group. Some high-ranked switchers acquired larger partners. Thus, while settlement preferences increased the likelihood of acquiring social dominance, switching may function, in part, to increase the benefit associated with social dominance once it has been acquired.

© 2004 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

In group-living species, the distribution of reproductive success among group members is often highly skewed towards a socially dominant individual. A group member's lifetime reproductive success is then dependent on the social rank it achieves. A 'queue' analogy has been used to describe systems in which social rank, and the reproductive opportunities associated with rank, are acquired passively (Wiley 1981; Wiley & Rabenold 1984; Ens et al. 1995; Kokko & Johnstone 1999; Ragsdale 1999). In queue-structured groups, individuals do not attempt to displace more dominant group members through direct competition. Instead, subordinates wait, and move up their group's social hierarchy as more dominant individuals die. After joining a group as its least dominant member, an individual only achieves dominant social rank in that group if it outlives all those that arrived before it. Therefore, individuals living in queue-structured groups should adopt tactics that maximize their probability of acquiring dominant social rank. To that end, individuals recruiting into a population may seek to join shorter queues. Likewise, if some degree of intergroup movement remains possible for an individual after the initial joining decision, then the relative probabilities of achieving social

dominance in two groups should influence the decision to move from one group to the other.

Social groups in many species have queue-like elements, but only recently have the implications of queuing begun to be considered. Often, the role of queuing is difficult to assess because groups cannot be treated exclusively as queues. For example, cooperatively breeding family groups are queues, in that the offspring of a breeding pair may inherit the parent's territory (e.g. Wiley & Rabenold 1984; Lucas et al. 1997; Balshine-Earn et al. 1998; Field et al. 1999). Theoretical models that incorporate queuing have been developed with just such groups in mind (Lucas et al. 1997; Kokko & Johnstone 1999; Ragsdale 1999; Pen & Weissing 2000a; Kokko et al. 2002; Shreeves & Field 2002). But in most cooperatively breeding groups, patterns of relatedness among group members and the presence of separate male and female queues within each group complicate interpretations of subordinates' options and behaviours. Moreover, because the groups result from delayed dispersal, there can be a causal connection between a queue's length and the quality of the resource (a breeding territory) for which the queue formed. Queuing's role in postdispersal acquisition of territories and social rank has also been studied (Zack & Stutchbury 1992; Herrera & Macdonald 1993; Ens et al. 1995; Poston 1997; Bried & Jouventin 1998; Kokko & Sutherland 1998; Kokko et al. 1998; Pen & Weissing 2000b; Kokko & Ekman 2002). In these cases, it can be difficult to determine whether individuals are in line for a single territory or for

Correspondence: J. Mitchell, Behavioural Ecology Research Group, Department of Biological Sciences, Simon Fraser University, Burnaby, BC V5A 1S6, Canada (email: jmitchel@sfu.ca).

any of a set of contiguous territories. The extent to which social ranks correspond to order of arrival (i.e. the degree of queue discipline) and the mechanism through which queue discipline is enforced can also be unclear.

Anemonefish (*Amphiprion* spp.) are particularly well suited to studies of queuing's implications because many of the complexities associated with queues in other taxa do not apply. Individuals occur in small groups occupying various species of tropical Indo-Pacific sea anemones. Groups are queues for social dominance and, with dominance, the opportunity to reproduce. Anemonefish ecology and life history have been extensively reviewed (Allen 1972; Fautin 1991; Fautin & Allen 1992): a fish is not stung by its host anemone, and relies on its host for its own protection and to protect clutches of eggs laid adjacent to the anemone. An anemone is occupied exclusively by a single anemonefish group, typically consisting of a large dominant female (α), a smaller functional male (β), and a series of increasingly smaller, subordinate, sexually immature fish (γ , δ , ϵ , ζ): a strict, size-based, linear dominance hierarchy. (I use α - ζ to indicate social rank, not reproductive status. Thus, members of a group consisting of three sexually immature fish would still be labeled α , β , and γ .) Subordinates do not act as reproductive helpers (Mitchell 2003a). Juvenile fish settle individually to anemones following a planktonic dispersal period, and join existing groups as the smallest, least dominant members. Therefore, group members are not relatives, and a breeding pair's reproductive success cannot directly affect group size. Within each group, aggression directed by more dominant individuals towards their subordinates suppresses growth and sexual maturation of the latter. If the female is removed, the male (the new α) grows and changes sex, and the largest of the immature fish (formerly γ) matures as the new male. Ross (1990) termed this 'female-control protandrous hermaphroditism'. Sex change and social inhibition of maturation greatly simplify the interpretation of social group structure: a group can be treated as a single queue with a terminal reproductive reward. Within a queue, social inhibition of growth enforces queue discipline. The risk of eviction offers a convincing explanation for subordinates' willingness to accept their circumstances. The result is that a new settler's only prospect for reproduction is to outlive more dominant groupmates. The longer the queue, the longer a settler's expected wait, and the lower its likelihood of surviving to maturity.

Under these circumstances, one might expect settling anemonefish to prefer shorter queues. Previous studies, though, have argued or implied that postlarval anemonefish settle indiscriminately to any anemone from which residents do not evict them. 'Natural' settlement events are rarely observed, but postlarval fish experimentally released near an anemone are attracted to chemical cues from that anemone independent of its occupancy (Elliott et al. 1995). New settlers are typically seen only at anemones where a resident has recently disappeared, such that group size is small relative to anemone size (Fautin 1992; Elliott et al. 1995; Elliott & Mariscal 2001). Both observations are consistent with the argument that a settler's only objective is to locate an anemone before being

located by a predator. But from an evolutionary perspective, the objective must be survival to sexual maturity, and in that case, settlers should be willing to incur an appreciable predation risk in order to locate a shorter queue (cf. Martinez & Marschall 1999).

Following settlement, one might also expect anemonefish to move opportunistically between anemones. Length frequency distributions for different social ranks often overlap (Moyer & Nakazono 1978; Ochi 1989; Hattori & Yanagisawa 1991; Hirose 1995). Therefore, such movements might allow a fish to advance in social rank. However, a switcher incurs a predation risk while in transit between anemones, and successfully reaching a new anemone does not ensure successful integration into the new social group. Intergroup movement, or 'switching', has been best described for temperate populations of *A. clarkii*, and attributed to high anemone densities, low predation risk, and the species' relatively strong swimming ability (e.g. Moyer 1980; Ochi 1989; Hattori 1994; Hirose 1995).

In this study, I describe patterns of settlement to and movement among social groups of false clown anemonefish (*A. ocellaris*). I ask whether those patterns are consistent with the hypothesis that individuals seek to minimize the queuing-imposed delay between settlement and sexual maturity. False clown group size varies appreciably (J. S. Mitchell & L. M. Dill, unpublished data). I predicted that postlarval false clowns would settle preferentially at anemones occupied by fewer fish (i.e. to shorter queues). I then looked at movements between anemones. False clowns are poor swimmers, but switching does occur (Nelson et al. 1998; this study). I predicted that switchers would improve their social rank and that they would be large relative to their original rank (because such individuals are more likely to improve in rank by switching.) I also examined general characteristics of switching events.

METHODS

I collected data on settlement and intergroup movement of false clown anemonefish during 7 months (26 August 1997–28 March 1998) of observations at Bunaken Island, North Sulawesi, Indonesia. The study site ('Site 1' in Mitchell 2003a, b) spanned 500 m of shoreline, and extended from nearshore seagrass to the reef face. Occupied anemones were patchily distributed within the site, with an average nearest-neighbour distance of 12.7 m. No occupied anemones were located within approximately 100 m to either side of the study site. Over most of the monitoring period, I visited each of 70 anemones at least weekly, and more often twice or three times weekly, recording the number of fish present on each visit. At approximately 2-month intervals, I caught all individuals and measured total body length (± 1 mm). Most individuals longer than 30 mm were also given a unique tag the first time that they were captured, by injecting coloured acrylic paint (Thresher & Gronell 1978). On three occasions in February and March, I measured each anemone's diameter using a tailor's tape measure held above the expanded oral disc at its widest point (long axis) and again

perpendicular to that measure (short axis). Under the assumption that oral discs are roughly elliptical, I defined the anemone's diameter as the geometric mean of the two measures. I used the largest of the three geometric means as my measure of an anemone's expanded oral disc diameter.

Settlement

I used two types of regression analysis to determine whether the probability of settlement was correlated with anemone size, with measures of anemonefish social group composition, or with prior disappearance of a resident. I defined a settler as an individual less than 15 mm total length when first observed at an anemone. (Juveniles were generally 7–8 mm long when first observed.) I only included juveniles that remained at an anemone for at least 1 week. This requirement excluded individuals that arrived at an anemone but were either evicted or elected not to remain.

I began with a logistic regression. I examined variation in the probability of replacement settlement events, defined as settlement events that followed the death or disappearance of an established resident from an anemone. Previous studies have reported that settlement to an anemone is typically preceded by a resident's disappearance (Fautin 1992; Elliott et al. 1995; Elliott & Mariscal 2001). Furthermore, correlations between group size and anemone size are common in anemonefish species, and have been taken as indirect evidence that anemones' carrying capacities differ (Allen 1972; Ross 1978; Fricke 1979; Fautin 1992). A resident's disappearance is an unambiguous indication that the anemone is below its carrying capacity. Elliott et al. (1995) reported that, within *A. polynus* and *A. clarkii* social groups, juvenile residents are more aggressive towards would-be settlers than are larger, more dominant individuals. Therefore, I included the length of the smallest remaining resident as a predictor in the regression model. Additional predictors were anemone size and the number and summed lengths of remaining group members. In separate regressions, I used 1- and 2-lunar-month settlement windows. In both cases, I asked whether anemone size and false clown group composition influenced the probability that settlement would occur during the time window. I used the first disappearance at an anemone and excluded cases in which either a second individual disappeared from the anemone or a nonsettler arrived at the anemone during the settlement window and prior to a settler's appearance.

The logistic regression approach had limitations. First, the lag between a disappearance and subsequent settlement could not be considered. Second, because each anemone was only used once, many settlement events were excluded. Settlement events that were not preceded by a group member's disappearance were also not considered. Finally, I excluded cases in which group composition changed more than once before settlement.

I used a Poisson regression to surmount these difficulties. Like a logistic regression, a Poisson regression estimates the probability that an event occurs within a time

interval. It assumes a fixed daily event probability within the time interval, such that the cumulative probability of the event's occurrence within the time interval follows a Poisson distribution (Selvin 1995). Thus, a Poisson regression is potentially more sensitive than a logistic regression: it considers not only whether an event occurs, but also the rate at which events occur.

Using the Poisson regression, I asked whether the rate of settlement (the number of settlement events per anemone-days of observation) varied with anemone size or with the composition of a resident false clown group (the number and size of individuals present and the length of the smallest resident). I used a lunar month as my time interval so that, even if lunar pulses of settlement led to biased estimates, the bias should be consistent across the variables of interest. I defined group size in an interval as the group size on the first day of the interval. When possible, fish length data were taken from measurements made on a capture date within the interval, and otherwise from the capture date closest to the start of the interval. The interval ended before the end of the lunar month if group composition changed, due to mortality or host switching, or to a settler's arrival. The ability to include such 'partial' intervals increases the ability to detect settlement trends; these intervals would have been excluded from a logistic regression analysis. I assumed that settlement, mortality, and group switching occurred on the date midway between the survey date on which the change was observed and that of the preceding survey. The frequency with which each anemone was visited allowed an accurate estimation of settlement date relative to the (lunar month) duration of the time interval used. (I excluded December 1997 and March 1998 from the analysis because anemones were not visited with sufficient frequency.)

In both the logistic and Poisson regressions, I identified statistically meaningful predictors by following a forward stepwise procedure, using the partial likelihood ratio test ($P \leq 0.05$) as the basis for term inclusion (Hosmer & Lemeshow 1999). In neither model did the addition of a second main-effect predictor significantly reduce the value of the loss function (see Results), so I did not proceed to test for statistical interactions among predictors. In the Poisson regression, I did test specifically for an effect of the interaction between anemone size and group size.

Switching

I defined a host-switching event as the appearance at an anemone of a new individual that was at least 20 mm total length. The length restriction was intended to remove any possibility that a new settler would be mistaken for a host-switcher. In practice, no host-switching false clowns approached the 20-mm cut off (see Results), and the risk of confusion was negligible. I excluded individuals that had returned to their original anemone on the next survey date. This limitation distinguished host-switching fish from individuals that may have been temporarily displaced from their anemone.

For each host-switching event, I recorded the size of the individual that switched hosts, its social rank on its origin and destination anemones, and the sizes of both those anemones. I established the identity, and hence origin, of host-switching fish using either the fish's tag or from the concurrent disappearance of a like-sized fish from another anemone within the study site.

After contrasting these quantitative variables, I also assessed qualitatively whether and in what direction host-switching individuals' reproductive expectations changed following switching. Presumed fitness consequences of movement by subordinate fish were based on changes in social rank. Presumed fitness consequences of movement by α - and β -ranked fish were based on potential changes in reproductive success. Specifically, I assumed a positive fitness consequence when an α -ranked fish that had not already matured as a female moved to a new anemone and occupied a β rank. I made this assumption because those individuals' new partners are larger, and therefore have a greater potential fecundity, than do the host-switching fish themselves.

Most of the frequency distributions contrasted in the settlement analyses were non-normal. In these cases, nonparametric analyses were used. Anemone size was normally distributed, and was analysed accordingly.

RESULTS

Settlement

Following a resident's disappearance, resettlement within 2 lunar months was more likely if at least one resident remained than if the disappearance left the anemone vacant: false clowns settled to 7 of 34 occupied anemones but 0 of 10 vacant, but previously occupied, anemones within 1 lunar month (Fisher's exact test: $P = 0.18$), and to 11 of 29 occupied anemones but 0 of 9 vacant anemones within 2 lunar months ($P = 0.04$). The remaining anemones could not be analysed because either no fish disappeared, the first disappearance was followed by a second disappearance, or the disappearance was followed by a host-switching fish's arrival at the anemone. Among occupied anemones, the probability of resettlement was independent of group size (1 month: $\chi_1^2 = 0.06$, $P = 0.80$; 2 months: $\chi_1^2 = 0.09$, $P = 0.76$), group members' summed lengths (1 month: $\chi_1^2 = 0.25$, $P = 0.62$; 2 months: $\chi_1^2 = 0.05$, $P = 0.81$), the length of the smallest group member (1 month: $\chi_1^2 = 0.99$, $P = 0.32$; 2 months: $\chi_1^2 = 0.36$, $P = 0.55$), and anemone size (1 month: $\chi_1^2 = 0.32$, $P = 0.57$; 2 months: $\chi_1^2 = 0.61$, $P = 0.44$).

In contrast, Poisson regression results provided strong evidence that settlement probability declined as group size decreased (Table 1). During the 5 lunar months included in the analysis, I observed 48 settlement events. Settlement probability did not vary among months (i.e. no seasonal effect was detected), nor was settlement affected by the length of the smallest resident. The number of group members and their summed length are necessarily correlated, and the use of either variable alone (i.e. in univariate

models) significantly reduced the loss function value. The effect is best attributed to group size because group size yielded a smaller loss value than did group members' summed lengths. Note that group size may be better modelled as an ordinal, rather than continuous, variable. Thus, the loss function value associated with the group size model will be conservative, because it fails to account for qualitative differences between groups that differ in size.

The Poisson regression's use of anemone-days, rather than of anemones, as the experimental unit potentially results in a pseudoreplication problem, because values of the predictor variables in one time interval are correlated with their values in the next. Group size did vary from month to month at an anemone, but group size at an anemone in September would none the less be a good predictor of group size in October. To confirm the statistical significance of the result, I randomly selected a single lunar month interval for each anemone and calculated a new loss function value for group size using this reduced data set. Even using this very conservative approach, the effect of group size remained statistically significant ($\chi_1^2 = 4.88$, $P = 0.03$).

A multivariate model including both group size and group members' summed lengths did not reduce the loss value significantly beyond that of a model using group size alone (Table 1, iteration 3). Likewise, a model using group size, anemone size, and the statistical interaction between the two main effects, was no more effective at predicting settlement rate than was group size alone (Table 1, iteration 4). The settlement rate dropped consistently as group size increased from one to six fish (Fig. 1). While this analysis was limited to occupied anemones (group size ≥ 1), settlement rates were also calculated separately for each group size, including vacant anemones. Vacant anemones did not follow the pattern observed with occupied anemones: settlement to vacant anemones did not occur at a higher rate than settlement to anemones occupied by a single fish.

Switching

Between 26 August 1997 and 28 March 1998 I recorded 36 unambiguous instances of host switching by at least 30 different individuals (one fish switched hosts three times; three fish moved twice).

Switchers moved to 22 different hosts. Two of these hosts were actually pairs of adjacent anemones that were treated as single hosts by resident anemonefish; I excluded these host pairs from analyses of anemone size. The source anemone was identified in 28 of the 36 cases. In five cases, the source was completely unknown. In three cases, like-sized fish disappeared from several anemones, all near the destination anemone, on the same date. The 28 identifiable instances involved 23 different anemones. One source was an anemone pair. Four sources were anemones that themselves disappeared from the study site before they were measured (Mitchell 2003b). I excluded these hosts from anemone size comparisons.

The average expanded anemone diameter ($\bar{X} \pm \text{SD} = 29.0 \pm 5.7$ cm, $N = 70$) did not differ from that of the subset of anemones from which fish moved

Table 1. Results of a Poisson regression examining the utility of potential predictors of settlement, defined as the arrival of a false clown that was less than 15 mm in total length and that remained present at an anemone for a minimum of 1 week

Iteration	Model	Loss function value	χ^2	df	P
1	a + ln(days)	143.7			
2	a + ln(days) + b*GS	130.6	26.2	1	<0.001
	a + ln(days) + b*ML	143.5	0.4	1	0.53
	a + ln(days) + b*SL	131.3	24.8	1	<0.001
	a + ln(days) + b*EAD	143.1	1.2	1	0.27
	a + ln(days) + b1:b4*M1:M4	141.6	4.2	4	0.38
3	a + ln(days) + b*GS + c*ML	129.6	2.0	1	0.16
	a + ln(days) + b*GS + c*SL	130.5	0.2	1	0.65
	a + ln(days) + b*GS + c*EAD	130.2	0.8	1	0.37
	a + ln(days) + b1:b4*M1:M4	127.5	6.2	1	0.18
	a + ln(days) + b*GS + c*EAD + d*GS*EAD	130.0	0.4	1	0.53

Each iteration retained the single term associated with the greatest reduction in the loss function's value, assuming that any were statistically significant. In iteration 2, group size (GS) offered the greatest improvement compared with the null model from iteration 1; the difference was statistically significant. In iteration 3, the length of the smallest group member reduced the loss function by the greatest amount, but the effect was not statistically significant. Although anemone size (EAD) was not significant as a main effect, I also tested the interaction between EAD and GS (iteration 4). No other interactions were examined. The analysis presented used the subset of the data for which values of all variables were known. The qualitative result did not change when I reran the analysis excluding one or more variables and including data for which that variable was not known. Days: number of days in the time interval; GS: group size (1–6 fish); ML: length of the smallest group member; SL: summed lengths of all group members; EAD: expanded anemone diameter; M1–M4: dummy variables denoting lunar month time intervals (5 intervals require 4 dummy variables).

(30.4 ± 10.6 cm, $N = 18$) (t test: $t_{86} = 1.0$, $P = 0.32$), nor from the subset to which fish moved (30.2 ± 12.7 cm, $N = 20$) (t test: $t_{88} = 0.86$, $P = 0.39$). Eighteen different fish moved at least once between solitary anemones that were both identified and measured. The diameters of their origin and destination anemones were not correlated ($R^2 < 0.001$, $P = 0.95$), and there was no consistent size difference between those diameters (paired t test: $t_{17} = 0.61$, $P = 0.55$). (For fish that switched hosts more than once, I used the first instance for which both the source and destination anemones were measured. Thus, each fish was used only once in the analysis. Some

anemones were used more than once because several fish moved from or to them over the course of the field season.)

October and March lengths of α -, β - and γ -ranked false clowns were similar (Mann–Whitney U test: α : $U = 2248$, $N_1 = 67$, $N_2 = 64$, $P = 0.63$; β : $U = 1623.5$, $N_1 = N_2 = 55$, $P = 0.51$; γ : $U = 943$, $N_1 = N_2 = 42$, $P = 0.59$), as was the overall length distribution for fish of all ranks (Kolmogorov–Smirnov test: $D = 0.085$, $N_1 = 203$, $N_2 = 194$, $P = 0.47$). Likewise, the frequency distribution of group sizes, and hence of individuals occupying different social ranks, did not differ between dates (contingency test with groups of five and six members pooled: $\chi^2_1 = 1.2$, $P = 0.88$). Since population structure did not change over the course of the field season, I elected to contrast length- and rank-frequency distributions of host-switching fish with the overall population data from October measurements.

The relative frequency of α -ranked fish was greater among host switchers than among fish that were at least 20 mm long in the overall (October) population, and no ϵ - or ζ -ranked fish switched hosts. However, overall, the frequency distributions of social ranks in the two groups were not significantly different (contingency test with ranks δ – ζ pooled: $\chi^2_2 = 2.6$, $P = 0.27$; Fig. 2). Likewise, the frequency distribution for length of host-switchers ($\bar{X} \pm \text{SD} = 47.5 \pm 13.2$ mm, $N = 28$) did not differ from the overall population (43.6 ± 14.2 mm, $N = 175$) (Kolmogorov–Smirnov test: $D = 0.196$, $P = 0.28$; Fig. 3). Since few low-ranked fish switched hosts, I could only compare rank-specific lengths for α - and β -ranked fish. Within these ranks, lengths of host-switching fish ($\bar{X} \pm \text{SD}$: α : 52.5 ± 11.1 mm, $N = 11$; β : 47.4 ± 7.8 mm, $N = 5$) were not greater than in the overall population (α : 56.4 ± 13.7 mm, $N = 63$, β : 42 ± 10.2 mm, $N = 54$; one-tailed Mann–Whitney U test: α : $U = 425$, $N_1 = 63$, $N_2 = 11$, $P = 0.62$; β : $U = 110$, $N_1 = 54$, $N_2 = 5$, $P = 0.25$).

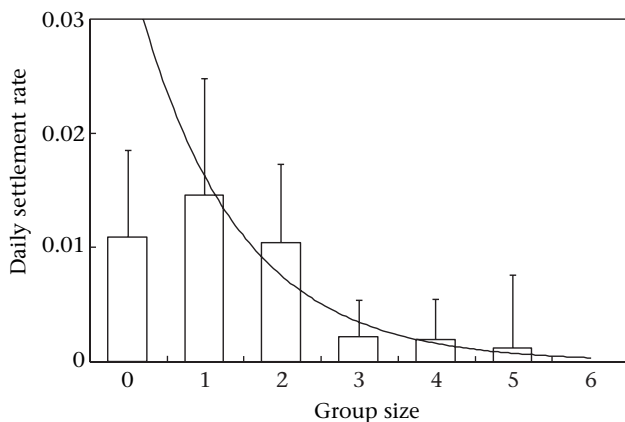


Figure 1. Daily settlement rate (average number of settlers per anemone per day) as a function of the number of existing residents at an anemone. Error bars are upper 95% confidence bounds. No settlement occurred to the single anemone at which six fish were present. The fitted curve uses coefficients generated when vacant anemones were excluded from analysis and group size was treated as a continuous variable (see text).

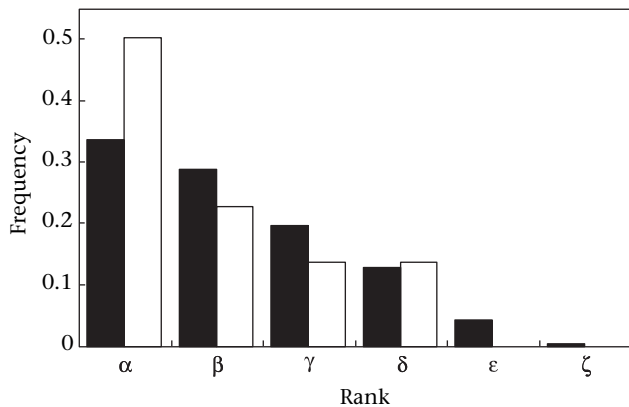


Figure 2. Frequency distributions of host-switchers' social ranks in their original groups (□; $N = 22$) and among individuals that were at least 20 mm long in the overall (October) population (■; $N = 187$). Note that ϵ - and ζ -ranked individuals are plotted separately but were pooled in the analysis.

Of 22 host-switching fish for which I knew not only the original host but also the individual's social rank on that host, in 12 cases rank did not change following host switching. In four cases, social rank improved. The six remaining fish lost social rank on switching hosts. Thus, on average, rank did not improve (one-tailed sign test: $P = 0.88$).

Lastly, I looked at each of those 22 cases individually, and at an additional case in which the host-switching individual's original rank was undefined (see Table 2). In nine cases, there was no obvious fitness cost or benefit associated with switching hosts. The host-switching fish did not lose or gain social rank, and the new partners of α - and β -ranked host-switchers were of similar size to those on their previous hosts. Two of these cases consisted of a breeding pair that moved together to a previously vacant anemone. Two host-switching fish appear to have incurred a fitness cost. One fish dropped from β to γ rank after moving. The second fish's rank increased from β to α ,

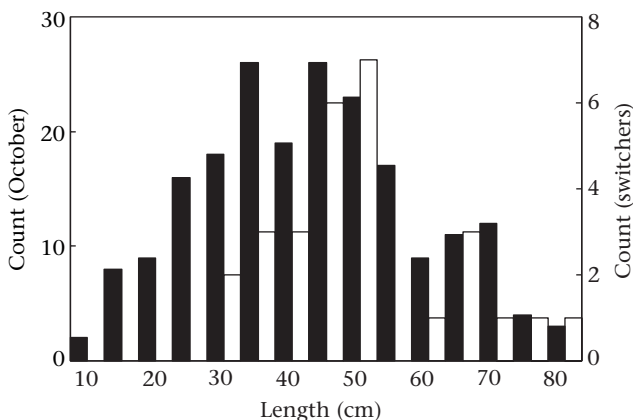


Figure 3. Length frequency distribution of false clown anemonefish from October 1997 (■; $N = 187$) and of host-switching fish (□; $N = 22$). Note that, by definition, switchers were at least 20 mm long.

Table 2. Justifications for treating as positive the fitness consequences of 12 of the 23 host-switching events for which host-switching individuals' original anemone and rank at that anemone were known

Rank at origin → rank at destination	Rationale for expecting a fitness benefit	Number of cases
$\alpha \rightarrow \gamma$ $\gamma \rightarrow \beta$ $\alpha \rightarrow \alpha$ $na \rightarrow \alpha$	Original anemone disappeared	3
$\beta \rightarrow \alpha$	Arrival of a larger individual of a different anemonefish species Arrival of larger female lowered the original female's rank; since sex change is unidirectional, the original female (now β -ranked) could not revert to a male role	1
$\alpha^* \rightarrow \beta$ ($N = 4$) $\beta^* \rightarrow \beta$ ($N = 1$)	Nonfemale α -ranked individual realizes greater reproductive success as β in a group where α is much larger, or β -ranked individual remains β -ranked but with a larger α	5
$\alpha^* \rightarrow \alpha$	β at the destination anemone is larger and is sexually mature	1
$\delta^* \rightarrow \gamma$	Social rank (and hence probability of surviving to reproductive rank) increases	1

'na' denotes a special case in which the host-switching individual was the largest false clown at its original host but was smaller than a resident of a different anemonefish species.

*Cases that could be classified unambiguously as choices.

but it lost the opportunity to breed with a much larger α at its original host. Twelve host-switching individuals appear to have realized a fitness benefit (Table 2), and seven of these cases could be characterized unambiguously as choice (i.e. the individual could have remained at its original host). When I treated as selectively neutral those cases in which neither the switcher's rank nor its partner's size changed, there was a tendency, albeit statistically nonsignificant, for host switching to have a positive fitness consequence (one-tailed sign test: $P = 0.09$). When I interpreted 'neutral' cases as costly, because switchers incurred a predation risk, there was no tendency for switching to have a positive consequence (one-tailed sign test: $P = 0.76$). Among cases in which fish appeared to benefit by switching, only one case involved rank acquisition; four cases involved fish whose social rank declined after switching groups. These results suggest that, if switching is an adaptive tactic used by some fish, then its object is not rank acquisition but rather the acquisition of a larger potential mate by fish that have already acquired either α or β social rank.

DISCUSSION

Settlement patterns suggest that false clown anemonefish discriminate against anemones at which larger social groups are present. This preference would minimize the delay between settlement and the acquisition of dominant social rank, and hence maximize the probability of surviving to attain that rank. False clowns also moved

among anemones postsettlement. These switching events rarely resulted in increased social rank, but some α - and β -ranked fish acquired larger partners through host switching. Thus, initial settlement decisions appear to be tactical responses to variation in social group composition among anemones. The same may be true of subsequent interhost movements, but not for the expected reason.

A settler preference for short queues should not be surprising. Previous studies, though, have not detected such discrimination in other anemonefish species (Fautin 1992; Elliott et al. 1995; Elliott & Mariscal 2001). Possibly, costs and benefits of discrimination differ between sites or species. Alternatively, this study's use of a more sensitive statistical approach may have allowed the detection of settler preferences that are common to all anemonefish species. Previous studies have also concluded that settlement attempts are only successful to anemones at which the resident anemonefish group is small relative to the host's carrying capacity. Anemone size has been used as a measure of carrying capacity because group size and anemone size are often correlated (Allen 1972; Ross 1978; Fricke 1979; Fautin 1992; Buston 2003). Some studies have reported stronger correlations between anemone size and group members' summed lengths, as might be expected if larger group members require more resources than their smaller subordinates (Allen 1972; Ross 1978; Hattori 1991; Fautin 1992; Elliott & Mariscal 2001; Buston 2003). Restriction of settlement to 'unsaturated' anemones, would not preclude further discrimination by settlers based on the degree of saturation. Indeed, that possibility motivated my analysis of postdisappearance settlement events. But this study's results are not consistent with that view of anemonefish settlement. Summed length was not a better predictor of settlement rate than group size was. More importantly, anemone size was not a useful predictor of settlement rate.

The preference for short queues did not extend to vacant anemones. Settlers may avoid vacant anemones because group membership reduces mortality risk (e.g. Forrester 1990; Booth 1995), or because an existing resident is a potential future mate. The presence of conspecifics may be a cue involved in anemone detection or an indicator of a potential host's suitability (cf. Sweatman 1988; but see Elliott et al. 1995). Alternatively, settlers may assess habitat attributes directly, but vacant anemones may tend to occur in marginal habitats. Such processes potentially extend to larger groups, offsetting effects of queuing. Queuing's implications do not extend to vacant anemones (because reproduction requires two group members); vacant anemones were excluded from the Poisson regression analysis for that reason.

Potential settlers might avoid or emigrate from large groups, even in the absence of long-term queuing considerations, if the immediate costs of aggressive interactions with residents increase with group size (e.g. Shima 2001, 2002; Buston 2003). (In this context, the distinction between an individual's 'decision' to search for a shorter queue and its 'eviction' by residents (sensu Buston 2003) is semantic: both descriptions refer to the same behavioural response to interactions with other group members.) This interpretation is less satisfying for two reasons.

First, it predicts high rates of settlement to vacant anemones. Second, were settlement patterns a consequence of resident aggression, the rate of settlement to groups of two should remain high, because both members of a resident pair benefit when at least one subordinate is available as a replacement mate. The observed reduced settlement rate to groups of two is more consistent with queuing.

No variable other than group size had statistically significant predictive utility. The absence of any anemone size main effect was interesting. At a mechanistic level, it suggests that a settler's ability to detect a potential host was not affected by anemone size. At an ultimate level, the result is surprising because anemone size affects not only group size, but also the size of the dominant group member (Fautin 1992; J. S. Mitchell & L. M. Dill, unpublished data). One might expect settlers to prefer hosts that offer their residents a greater potential for long-term growth. The rate of settlement was also unaffected by the length of the smallest resident. Elliott et al. (1995) found that small group members are more active in excluding potential settlers than are larger individuals. It is possible that resident false clowns do not see settlers as competitors. Alternatively, the smallest residents, those most likely to perceive a settler as a threat, may also be those least able to exclude a settler.

Settlement decisions might also be sensitive to host quality. My assumption that settlement tactics maximize the probability of acquiring dominant social rank allowed a straight forward, qualitative prediction regarding settlement decisions. In fact, though, settlement decisions should maximize expected future reproductive success. This could lead to settlement rules that generate longer queues at superior sites. For example, Ens et al. (1995) argued that queue length in oystercatchers (*Haematopus ostralegus*) should be proportional to the quality of the breeding territory for which the queue formed. Kuwamura et al. (1996) described a similar situation for *Paragobiodon echinocephalus* gobies occupying coral heads. In anemonefish, one might expect longer queues at larger anemones, because female length tends to increase with host diameter (Fautin 1992; Elliott & Mariscal 2001; J. S. Mitchell & L. M. Dill, unpublished data) and a larger fish is potentially more fecund. Queue length does increase with anemone size in this population (J. S. Mitchell & L. M. Dill, unpublished data), but not because of settlement rates. Indeed, the positive correlation between group size and host anemone size arises despite avoidance of longer queues. I have previously shown that false clown reproductive success is correlated with social group composition, rather than with female size alone (Mitchell 2003a). Thus, if a female's short-term reproductive success is used as the measure of her host's quality, then larger anemones are not necessarily superior hosts. A complete picture of settler expectations would also consider effects of anemone characteristics and queue composition on anemonefish mortality rates, rates that may also vary over time as an individual grows and as group composition changes. Such accounting is possible (e.g. Martinez & Marschall 1999) but requires more complete demographic data than are available for false clowns.

False clowns also moved between groups and hosts postsettlement. Some of these switching events did not result in any obvious fitness cost or benefit. When those cases were interpreted as costly, because they involved a predation risk, there was no tendency for false clowns to benefit by switching. When 'no benefit' switching events were treated as neutral, the tendency for switchers to benefit approached statistical significance. The results are interesting in either case because the nature of the fitness benefit was unexpected. Switchers did not improve their social rank; many were already α - or β -ranked. Individuals that benefited by moving to a new anemone did so by acquiring a larger potential mate. Implications of switching in queue-structured groups have been considered in a number of reef fish species. Switching by socially dominant anemonefish has been best described in *A. clarkii* (Moyer 1976, 1980; Ochi 1989; Fautin 1991; Hattori & Yanagisawa 1991; Hattori 1995; Hirose 1995). Some authors have proposed that switching opportunities have led to the evolution of alternate pathways of sexual maturation in that species (Yanagisawa & Ochi 1986; Ochi 1989; Hattori & Yamamura 1995). Switching's implications have also been considered in reef fish that change sex from female to male (*D. aruanus* humbug damselfish: Coates 1982; *Centropyge ferrugatus* angelfish: Sakai 1997; Hamaguchi et al. 2002; *Labroides dimidiatus* cleaner wrasse: Sakai et al. 2001). In these species, subordinate group members are females within a harem and therefore realize some reproductive success. But females breeding within a harem are also queuing to become the dominant (male) group member, whose reproductive success will be qualitatively greater.

Smaller, lower-ranked fish did move between anemones, but voluntary, adaptive switching was restricted to socially dominant group members. Why? First, risks may be lower for larger, higher-ranked individuals. Small fish may either not switch (voluntarily), or may be eaten while in transit. Second, the size structure of most groups may preclude joining at an intermediate social rank. A would-be immigrant that is large enough to supplant one resident may be too large to be tolerated by the next higher-ranked resident (Coates 1982). In this view, groups can be likened to lanes of 'tail-gating' traffic: individuals cannot change lanes because the distances (size differences) between residents in the adjacent lane are too small. A third interpretation stems from the observation that the probability of a higher-ranked resident dying declines as one moves up a queue. A γ -ranked individual improves its social rank if α or β dies but an ε -ranked individual improves its rank if any of α , β , γ , or δ dies. Thus, switching may not benefit individuals at the tails of queues because they expect to advance up their current queues relatively quickly.

Opportunities to switch at intermediate ranks discourage discrimination during settlement: the initial settlement decision is not binding, and other individuals may later 'chisel' into a queue ahead of the settler. In contrast, when high-ranking fish switch, a preference for short queues is more easily understood. A settler's goal is then to acquire dominance, anywhere, and then (possibly) transfer that dominance elsewhere. When individuals use such

a strategy, queue length will not necessarily be correlated with a site's (reproductive) quality. Both settlers and host-switching individuals may still prefer sites that are associated with higher survival if a reduced risk of mortality increases a subordinate's probability of outliving more dominant groupmates. This effect is possible even when dominant groupmates also experience reduced mortality risks (Kokko & Johnstone 1999; but see Shreeves & Field 2002). A reduced risk of mortality in larger groups may then offset, or reverse, a preference for shorter queues. Identifying the factors that affect survival within queue-structured groups should therefore be considered an important goal of future research.

Acknowledgments

This study was approved by the Simon Fraser University (SFU) Animal Care Committee (Proposal No. 572B). It was funded by a grant from the CIDA Eastern Indonesia University Development Project (EIUDP) and a Natural Sciences and Engineering Research Council (NSERC) Canada operating grant (A6869) to L.M. Dill and by grants and fellowships to the author from NSERC, SFU, the Canada-ASEAN Centre, Garfield-Weston, B.C. Packers, William and Ada Isabelle Steele and Petro-Canada. Kodak Canada and Bonica Precision donated field equipment. EIUDP and Sam Ratulangi University (UNSRAT) provided logistic support in Manado. Benny Pratasik in the UNSRAT Faculty of Fisheries and Marine Science introduced the field site to me. Members of the SFU Behavioural Ecology Research Group provided advice over the course of the study. A. Wirsing provided statistical advice. B. Crespi, L. Dill, D. Green, S. Holbrook and D. Lank offered valuable comments on the manuscript.

References

- Allen, G. R. 1972. *The Anemonefishes: Their Classification and Biology*. Neptune City, New Jersey: T.F.H.
- Balshine-Earn, S., Neat, F. C., Reid, H. & Taborsky, M. 1998. Paying to stay or paying to breed? Field evidence for direct benefits of helping behavior in a cooperatively breeding fish. *Behavioral Ecology*, **9**, 432–438.
- Booth, D. J. 1995. Juvenile groups in a coral-reef damselfish: density-dependent effects on individual fitness and population demography. *Ecology*, **76**, 91–106.
- Bried, J. & Jouventin, P. 1998. Why do lesser sheathbills *Chionis minor* switch territory? *Journal of Avian Biology*, **29**, 257–265.
- Buston, P. M. 2003. Forcible eviction and prevention of recruitment in the clown anemonefish. *Behavioral Ecology*, **14**, 576–582.
- Coates, D. 1982. Some observations on the sexuality of humbug damselfish, *Dascyllus aruanus* (Pisces, Pomacentridae) in the field. *Zeitschrift für Tierpsychologie*, **59**, 7–18.
- Elliott, J. K. & Mariscal, R. N. 2001. Coexistence of nine anemonefish species: differential host and habitat utilization, size and recruitment. *Marine Biology*, **138**, 23–36.
- Elliott, J. K., Elliott, J. M. & Mariscal, R. N. 1995. Host selection, location, and association behaviors of anemonefishes in field settlement experiments. *Marine Biology*, **122**, 377–389.
- Ens, B. J., Weissing, F. J. & Drent, R. H. 1995. The despotic distribution and deferred maturity: two sides of the same coin. *American Naturalist*, **146**, 625–650.

- Fautin, D. G. 1991. The anemonefish symbiosis: what is known and what is not. *Symbiosis*, **10**, 23–46.
- Fautin, D. G. 1992. Anemonefish recruitment: the roles of order and chance. *Symbiosis*, **14**, 143–160.
- Fautin, D. G. & Allen, G. R. 1992. *Field Guide to Anemonefishes and Their Host Sea Anemones*. Perth: Western Australian Museum.
- Field, J., Shreeves, G. & Sumner, S. 1999. Group size, queuing and helping in facultatively eusocial hover wasps. *Behavioral Ecology and Sociobiology*, **45**, 378–385.
- Forrester, G. E. 1990. Factors influencing the juvenile demography of a coral reef fish. *Ecology*, **71**, 1666–1681.
- Fricke, H. W. 1979. Mating system, resource defence and sex change in the anemonefish *Amphiprion akallopisos*. *Zeitschrift für Tierpsychologie*, **50**, 313–326.
- Hamaguchi, Y., Sakai, Y., Takasu, F. & Shigesada, N. 2002. Modeling spawning strategy for sex change under social control in harem angelfishes. *Behavioral Ecology*, **13**, 75–82.
- Hattori, A. 1991. Socially controlled growth and size-dependent sex change in the anemonefish *Amphiprion frenatus* in Okinawa, Japan. *Japanese Journal of Ichthyology*, **38**, 165–177.
- Hattori, A. 1994. Inter-group movement and mate-acquisition tactics of the protandrous anemonefish, *Amphiprion clarkii*, on a coral reef, Okinawa. *Japanese Journal of Ichthyology*, **41**, 159–165.
- Hattori, A. 1995. Coexistence of two anemonefishes, *Amphiprion clarkii* and *A. perideraion*, which utilize the same host sea anemone. *Environmental Biology of Fishes*, **42**, 345–353.
- Hattori, A. & Yamamura, N. 1995. Coexistence of subadult males and females as alternative tactics of breeding post acquisition in a monogamous and protandrous anemonefish. *Evolutionary Ecology*, **9**, 292–303.
- Hattori, A. & Yanagisawa, Y. 1991. Life history pathways in relation to gonadal sex differentiation in the anemonefish, *Amphiprion clarkii*, in temperate waters of Japan. *Environmental Biology of Fishes*, **31**, 139–155.
- Herrera, E. A. & Macdonald, D. W. 1993. Aggression, dominance, and mating success among capybara males *Hydrochaeris hydrochaeris*. *Behavioral Ecology*, **4**, 114–119.
- Hirose, Y. 1995. Patterns of pair formation in protandrous anemonefishes, *Amphiprion clarkii*, *A. frenatus* and *A. perideraion*, on coral reefs at Okinawa, Japan. *Environmental Biology of Fishes*, **43**, 153–161.
- Hosmer, D. W., Jr & Lemeshow, S. 1999. *Applied Survival Analysis: Regression Modeling of Time to Event Data*. New York: J. Wiley.
- Kokko, H. & Ekman, J. 2002. Delayed dispersal as a route to breeding: territorial inheritance, safe havens, and ecological constraints. *American Naturalist*, **160**, 468–484.
- Kokko, H. & Johnstone, R. A. 1999. Social queuing in animal societies: a dynamic model of reproductive skew. *Proceedings of the Royal Society of London, Series B*, **266**, 571–578.
- Kokko, H. & Sutherland, W. J. 1998. Optimal floating and queuing strategies: consequences for density dependence and habitat loss. *American Naturalist*, **152**, 354–366.
- Kokko, H., Lindström, J., Alatalo, R. V. & Rintamäki, P. T. 1998. Queuing for territory positions in the lekking black grouse (*Tetrao tetrix*). *Behavioral Ecology*, **9**, 376–383.
- Kokko, H., Johnstone, R. A. & Wright, J. 2002. The evolution of parental and alloparental effort in cooperatively breeding groups: when should helpers pay to stay? *Behavioral Ecology*, **13**, 291–300.
- Kuwamura, T., Nakashima, Y. & Yogo, Y. 1996. Plasticity in size and age at maturity in a monogamous fish: effect of host coral size and frequency dependence. *Behavioral Ecology and Sociobiology*, **38**, 365–370.
- Lucas, J. R., Creel, S. R. & Waser, P. M. 1997. Dynamic optimization and cooperative breeding: an evaluation of future fitness benefits. In: *Cooperative Breeding in Mammals* (Ed. by N. G. Solomon & J. A. French), pp. 171–198. Cambridge: Cambridge University Press.
- Martinez, F. A. & Marschall, E. A. 1999. A dynamic model of group-size choice in the coral reef fish *Dascyllus albisella*. *Behavioral Ecology*, **10**, 572–577.
- Mitchell, J. S. 2003a. Social correlates of reproductive success in false clown anemonefish: subordinate group members do not pay-to-stay. *Evolutionary Ecology Research*, **5**, 89–104.
- Mitchell, J. S. 2003b. Mobility of *Stichodactyla gigantea* anemones and implications for resident false-clown anemonefish, *Amphiprion ocellaris*. *Environmental Biology of Fishes*, **66**, 85–90.
- Moyer, J. T. 1976. Geographical variation and social dominance in Japanese populations of the anemonefish *Amphiprion clarkii*. *Japanese Journal of Ichthyology*, **23**, 12–25.
- Moyer, J. T. 1980. Influence of temperate waters on the behavior of the tropical anemonefish *Amphiprion clarkii* at Miyake-jima, Japan. *Bulletin of Marine Science*, **30**, 261–272.
- Moyer, J. T. & Nakazono, A. 1978. Protandrous hermaphroditism in six species of the anemonefish genus *Amphiprion* in Japan. *Japanese Journal of Ichthyology*, **25**, 101–106.
- Nelson, J. S., Chou, L. M. & Phang, V. P. M. 1998. Inter-habitat migration of the anemonefish *Amphiprion ocellaris*. *Asian Journal of Tropical Biology*, **3**, 19–31.
- Ochi, H. 1989. Acquisition of breeding space by nonbreeders in the anemonefish *Amphiprion clarkii* in temperate waters of southern Japan. *Ethology*, **83**, 279–294.
- Pen, I. & Weissing, F. J. 2000a. Towards a unified theory of cooperative breeding: the role of ecology and life history re-examined. *Proceedings of the Royal Society of London, Series B*, **267**, 2411–2418.
- Pen, I. & Weissing, F. J. 2000b. Optimal floating and queuing strategies: the logic of territory choice. *American Naturalist*, **155**, 512–526.
- Poston, J. P. 1997. Dominance, access to colonies, and queues for mating opportunities by male boat-tailed grackles. *Behavioral Ecology and Sociobiology*, **41**, 89–98.
- Ragsdale, J. E. 1999. Reproductive skew theory extended: the effect of resource inheritance on social organization. *Evolutionary Ecology Research*, **1**, 859–874.
- Ross, R. M. 1978. Territorial behavior and ecology of the anemonefish *Amphiprion melanopus* on Guam. *Zeitschrift für Tierpsychologie*, **36**, 71–83.
- Ross, R. M. 1990. The evolution of sex-change mechanisms in fishes. *Environmental Biology of Fishes*, **29**, 81–93.
- Sakai, Y. 1997. Alternative spawning tactics of female angelfish according to two different contexts of sex change. *Behavioral Ecology*, **8**, 372–377.
- Sakai, Y., Kohda, M. & Kuwamura, T. 2001. Effect of changing harem on timing of sex change in female cleaner fish *Labroides dimidiatus*. *Animal Behaviour*, **62**, 251–257.
- Selvin, S. 1995. *Practical Biostatistical Methods*. Belmont, California: Duxbury Press.
- Shima, J. S. 2001. Regulation of local populations of a coral reef fish via joint effects of density- and number-dependent mortality. *Oecologia*, **126**, 58–65.
- Shima, J. S. 2002. Mechanisms of density- and number-dependent population regulation of a coral-reef fish. *Marine and Freshwater Research*, **53**, 175–179.
- Shreeves, G. & Field, J. 2002. Group size and direct fitness in social queues. *American Naturalist*, **159**, 81–95.

- Sweatman, H.** 1988. Field evidence that settling coral reef fish larvae detect resident fish using dissolved chemical cues. *Journal of Experimental Marine Biology and Ecology*, **124**, 163–174.
- Thresher, R. E. & Gronell, A. M.** 1978. Subcutaneous tagging of small reef fishes. *Copeia*, **1978**, 352–353.
- Wiley, R. H.** 1981. Lekking in birds and mammals: behavioral and evolutionary issues. *Advances in the Study of Behavior*, **20**, 201–291.
- Wiley, R. H. & Rabenold, K. N.** 1984. The evolution of cooperative breeding by delayed reciprocity and queuing for favorable social positions. *Evolution*, **38**, 609–621.
- Yanagisawa, Y. & Ochi, H.** 1986. Step-fathering in the anemonefish *Amphiprion clarkii*: a removal study. *Animal Behaviour*, **34**, 1769–1780.
- Zack, S. & Stutchbury, B. J.** 1992. Delayed breeding in avian social systems: the role of territory quality and 'floater' tactics. *Behaviour*, **123**, 194–219.