Evolutionary Ecology Research, 2003, **5**: 89–104

Social correlates of reproductive success in false clown anemonefish: subordinate group members do not pay-to-stay

Jeremy S. Mitchell*

Behavioural Ecology Research Group, Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia V5A 1S6, Canada

ABSTRACT

In group-territorial species, subordinate group members may affect the reproductive success of a dominant, breeding pair. Dominants should be choosy, evicting subordinates whose presence does not increase reproductive success in favour of those whose presence is beneficial. I examined correlations between components of reproductive success and measures of social group composition in false clown anemonefish (*Amphiprion ocellaris*), in which breeding pairs tolerate subordinates that could be expelled from sea anemone hosts. Statistical interactions between group members' lengths, including interactions with the length of a non-breeding subordinate, were significantly better predictors of clutch size than a female's absolute length. For large females, clutch size increased with the length of the largest subordinate. The relationship between laying frequency and group composition was similar to that of clutch size, except that the statistical interaction was between subordinate and male, not female, length. Hatching success was not correlated with female length or with the length of the largest subordinate. Hatching success was correlated with the interaction between male length and the total number of subordinates; on average, hatching success declined as group size increased but the effect direction reversed at larger male lengths. Because clutch size and laying frequency were not correlated with a subordinate's size directly, but rather with interactions among group members' lengths, and because hatching success on average declined with group size, I conclude that the presence of subordinates did not have a positive effect on a breeding pair's reproductive success – that is, there is no evidence that subordinate false clown anemonefish pay-to-stay. This result is surprising given the ease with which a breeding anemonefish pair can evict non-beneficial subordinates.

Keywords: *Amphiprion*, cooperative breeding, queue, reproductive success, social organization.

INTRODUCTION

In group-territorial species, reproduction is often limited to a dominant pair. Non-breeding subordinates may affect that breeding pair's reproductive success, for example by acting as reproductive helpers (Emlen, 1991). Gaston (1978) hypothesized that helping behaviour was

---

* e-mail: jmitchel@sfu.ca

'rent' paid by a subordinate to the dominant in return for continued residency on a territory. The subordinate accepts its circumstances because territory residency reduces its current mortality risk and because it may be able to breed in the future if it outlives the dominant and inherits the territory. More recently, Ragsdale (1999), Kokko and Johnstone (1999) and Kokko *et al.* (2002) have extended earlier reproductive skew models (Vehrencamp, 1983; Reeve and Ratnieks, 1993) to include the effects of territory inheritance. In the process, they have developed a more formal version of Gaston's (1978) hypothesis. Ragsdale (1999) argued that, under certain conditions, a dominant should be choosy, evicting subordinates whose presence does not increase the dominant's reproductive success in favour of those whose presence is beneficial. Gaston's (1978) pay-to-stay hypothesis referred exclusively to helping behaviour. Ragsdale's (1999) model does not specify the mechanism through which a subordinate's presence benefits a dominant breeder, although helping is an obvious candidate. Using Ragsdale's (1999) model, dominant choosiness for subordinates that increase dominant reproductive success should occur when (cf. Kokko *et al.*, 2002):

(i) ecological constraints prevent a subordinate from leaving its group, acquiring its own territory and breeding immediately;
(ii) subordinates can be readily evicted;
(iii) subordinates queue for (inherit) reproductive rank on established territories;
(iv) group members are not related.

In systems that meet these conditions, subordinates will 'bid' for the opportunity to fill a limited number of social vacancies on territories to which dominants can restrict access. Dominant breeding pairs should, therefore, realize greater reproductive success when subordinates are present (because dominants will only accept subordinates whose presence is beneficial).

Most research on the consequences of social group structure for individual reproduction has been conducted using bird and mammal species (Stacey and Koenig, 1990; Solomon and French, 1997; Cockburn, 1998). Growth in birds and mammals is determinate, resulting in small differences in size between dominant and subordinate individuals within groups. When size differences are small, the cost of expelling an uncooperative subordinate may be appreciable – that is, condition (ii) is not met. Growth in fishes, on the other hand, is indeterminate. Their dominance hierarchies often map easily onto size differences among group members and, given those size differences, it is reasonable to assume that a dominant individual could expel an unhelpful subordinate without expending too much time and without much risk of injury. Helping behaviour is rare among fish, but has been documented in several African cichlid species (Taborsky and Limberger, 1981; Yamagishi and Kohda, 1996), in particular *Neolamprologus pulcher* (Taborsky, 1984, as *Lamprologus brichardi*). Balshine-Earn *et al.* (1998) concluded that helping in social groups of *N. pulcher* could be explained using Gaston's (1978) pay-to-stay framework.

Ragsdale's (1999) criteria for the evolution of dominant choosiness are met in group-territorial anemonefish (*Amphiprion* spp.). The ecology of these fishes has been extensively reviewed (Allen, 1980; Fautin, 1992; Fautin and Allen, 1992). An anemonefish group's territory is a sea anemone. The anemone protects the fish against predators and protects clutches, laid adjacent to the host anemone's pedal disc, from egg predators. Unoccupied anemones are rare. Thus, territories are necessary for survival and reproduction and, in most anemonefish species, a subordinate that leaves its current group is unlikely to acquire its own territory – that is, ecological constraints are high (condition (i)). The anemonefish group residing on an anemone is structured as a size-based dominance hierarchy within which dominant individuals inhibit subordinates' growth. Growth inhibition maintains relative size, and hence rank, differences between group members. In the anemonefish species used in this study, the largest group member (α) is typically 2–3 times the mass of the second-largest (β) and 4–5 times the mass of the third largest (γ) (J.S. Mitchell, unpublished data). Thus, dominant individuals can dictate group membership; they can evict unwelcome subordinates (condition (ii)). Sexual maturation and sex change from male to female are also socially inhibited. In reproductively active groups, α is female and β is male. All other group members are sexually immature. If the female is removed, the male changes sex and becomes the new female, the previously third-ranking fish matures as the new male, and other group members move one step up the social ladder. Thus, an anemonefish dominance hierarchy is a queue for the opportunity to mature and breed, first as a male and later as a female, once reaching dominant social rank. Subordinates gain breeding opportunities by outliving current dominants and inheriting dominant social rank (condition (iii)). Finally, juvenile anemonefish attempt to settle on to anemones after a planktonic dispersal stage, joining resident social groups at the tails of dominance hierarchies. If a group is large relative to its host's size, its members will respond aggressively to the would-be settler, excluding it from the anemone (or eating it; Elliott *et al.*, 1995). Settlement only occurs if there is 'social space' in the resident group. Settlement contingent on acceptance by existing group members again ensures that dominants control group membership (condition (ii)). Pre-settlement dispersal also ensures that group members are not related (condition (iv)).

Although the life history and social system of several anemonefish species have been studied extensively, field measurements of reproductive success are few (see Richardson *et al.*, 1997, and references therein). Based on egg deposition areas, Ochi (1989a) concluded that, despite a reduction in laying frequency, *A. clarkii* annual fecundity increased with female length in some years. However, Ochi did not examine correlations with other group members' lengths. In the only published study to investigate hatching success in an anemonefish, Bell (1976) defined as successful any clutch from which eggs hatched; Bell did not examine correlates of variation in hatching success. On the basis of comments made by Fricke (1979), subordinate members of anemonefish social groups have been described as helpers (Krebs and Davies, 1987: 280), but Fricke himself, while he posited such a role, acknowledged the absence of supporting evidence. In-depth behavioural studies of several anemonefish species have been conducted and reproductive helping has never been reported (e.g. Moyer and Bell, 1976; Ross, 1978; Fricke, 1979; Moyer and Steene, 1979; for reviews, see Thresher, 1984; Fautin and Allen, 1992).

In this study, rather than looking again for behavioural evidence of reproductive helping by subordinate group members, I instead examined directly the consequences of their presence for the reproductive success of breeding anemonefish pairs. I monitored the reproductive behaviour of false clown anemonefish (*A. ocellaris*) and examined social correlates of three components of reproductive success. I wished to determine whether the presence and size of subordinates was associated with increases in clutch size, laying frequency or percent hatch. The answers to those questions (yes, yes and no) suggest that the presence of subordinate members of false clown anemonefish groups does not directly cause increases in a breeding pair's reproductive success, and raise questions as to why breeding pairs tolerate subordinates.

METHODS

From September 1997 to March 1998, I monitored groups of false clown anemonefish occupying *Stichodactyla gigantea* sea anemones at Bunaken Island, North Sulawesi Province, Indonesia, recording settlement, disappearance and inter-group migration. On 1–3 weekly visits to each anemone, I also checked for the presence of a clutch of eggs adjacent to the anemone's pedal disc and, when eggs were present, photographed the clutch using a submersible camera with a 1 : 2 extension tube. I then counted the eggs from developed prints. At approximately 3 month intervals, I captured all group members and measured total body lengths. Length differences among group members ensured unambiguous identification of individuals within each group. In addition, I marked most fish >30 mm using subcutaneous acrylic paint injections (Thresher and Gronell, 1978) to allow individual identification. These marks, and the frequency of visits to each anemone, allowed me to identify cases of fish movement between anemones.

I used two study sites, approximately 1.5 km apart. Monitoring was most intensive at Site 1; monitoring at Site 2 was less frequent and was carried out over a shorter period. At both sites, each group of false clown anemonefish occupied either a single *S. gigantea* anemone or, rarely, two anemones in close (<1 m) proximity on a shallow subtidal shelf extending from the shoreline to a vertical 'drop-off'. In nearshore seagrass beds, anemones occupied by false clowns were typically found in shallow depressions that retained some water when the shelf was exposed during spring tides. Anemones also occurred amidst back reef rubble and on the reef crest. *Stichodactyla gigantea* anemones did not extend down the reef's outer face. The two sites differed in current and wave exposure but were otherwise broadly similar.

Clutch size

To measure clutch size, I used egg counts from photographs of clutches laid no more than 2 days previously. I inferred clutch age from egg colour: eggs are bright yellow or orange when first laid, turn reddish brown as the embryos absorb the egg yolk and, finally, take on a silvery sheen near hatch as the eyes develop (Fautin and Allen, 1992). Clutches that were already red or brown when first photographed were excluded from the clutch size analyses. To ensure that all clutches photographed at an anemone were laid by the same female under the same social circumstances, I also excluded clutches laid following a change in the identity of α or β. Such changes typically occurred when one member of a breeding pair disappeared and was replaced either by an immigrant or through maturation of a previously subordinate resident. Following the same rationale, clutch size data collected at several anemones where a fish matured and first reproduced midway through the field season were included only if the maturing individual's mate had not been observed breeding previously. Data from several hosts at which inter-host migration led to the formation of new, reproducing pairs were also included, but only if neither member of the pair had been observed reproducing at their previous host. Clutch size was ln-transformed to approximate normality.

Before examining the correlation between social group composition and clutch size, I tested for seasonal variation in clutch size using the subset of groups ($n = 5$) for which I had data on at least five clutches spread over at least 4 months. I ran an analysis of covariance (ANCOVA) with ln-transformed clutch size as the response variable, social group as a categorical predictor and laying date as a quadratic covariate. (A quadratic Date term was included in case the usual December–January rainy season was accompanied by changes in reproductive activity. Due to the 1997–98 El Niño/Southern Oscillation event, that rainy season never arrived.) The ANCOVA established that seasonal variation in clutch size would not confound an examination of clutch size's social correlates (see Results).

I then proceeded with multiple regressions of clutch size on measures of social group composition. For some social groups, I had only a single usable photograph of a newly laid clutch. In these cases, I used group members' lengths on the measurement date closest to that of the photograph. At anemones for which I had usable photographs of more than one newly laid clutch, I averaged all (ln-transformed) clutches laid over a 4 month interval, beginning with the first clutch photographed at that anemone, and used length measurements from the date closest to midway through that time interval. Over 4 months, some α-γ group members grew 1 mm, but none grew more than 2 mm.

My approach potentially underestimates clutch size due to egg loss prior to the photograph being taken. Such an effect would be greater where the rate of egg loss was greater. The relationship between group composition and hatching success was such as to make tests for a relationship between group composition and clutch size conservative. An alternative approach would be to use each female's maximum observed clutch size. Using that alternative, effects of social group composition on clutch size could be confounded with effects on laying frequency. In practice, both approaches gave qualitatively similar results.

I first regressed average ln-transformed clutch size on female (α) and male (β) lengths and the number of subordinates in the group. I then replaced the number of subordinates with the length of the largest subordinate (γ) and re-ran the regression. I began analyses using saturated models (with all interactions among predictor variables included) and then sequentially removed non-significant terms, beginning with higher-order interactions. I re-ran analyses using only data from Site 1 because statistical interactions with Site complicated the interpretation of coefficient estimates.

Laying frequency

It proved difficult to assess and control for seasonal effects when laying frequency was measured directly as the interval between clutches. Instead, I counted the number of clutches laid over a fixed time interval. Using this approach, sample size declined with the length of the time interval because fewer and fewer groups remained unchanged as the interval length increased. The dual needs for an interval long enough to make differences in laying frequency apparent, and for an interval within which the composition of enough groups remained stable, were best met by counting clutches initiated between 20 October and 26 November 1997. I excluded from the analysis groups at which γ's identity changed during this period but ignored changes in group composition at the δ and ε social ranks. I used the number of clutches laid as the response variable in a multiple regression with Site and α, β and γ lengths as predictors. The regression model included all interactions among length variables. The sample size was too small to include interactions with Site. Thus, the model allows for site differences in baseline laying frequency, but not for site differences in effects of group composition. I did not examine effects of group size because group size was not consistent across clutches at all groups.

Hatching success

To assess variation in hatching success, I used clutches that had been photographed twice on different days. I refer to the number of eggs counted on the first and second photographs as A and B, respectively. The first regression used lnA, the number of days separating the photographs (Days), the date on which the first photograph was taken (Date) and the social group involved (Group, a categorical variable) as predictors of lnB. The data set was not large enough for me to account for a non-linear effect of Date, so I limited myself to estimates made before November 1997. A seasonal change between September and November may not be linear but should at least be monotonic. The first regression included only data from groups for which at least four hatching success estimates had been made by November. The use of ln-transformed clutch sizes accounts for the possibility that the rate of egg loss varies with initial clutch size. Were the rate unaffected by clutch size, the lnA coefficient would be 1. Date and Group were included in the regression model only as interactions with Days and with lnA. Date and Group were not used as main effects because neither could affect B directly. I did not include an interaction between Days and lnA – that is, I assumed that the rate of egg loss was constant for a given clutch. Under the same assumption, I ignored variation in the ages of clutches when first photographed.

From the coefficients estimated using the first regression (excluding the effect of Group), I calculated predicted lnB values for a larger data set, which included data from other false clown groups for which I had fewer than four egg loss estimates. I then calculated the difference between predicted and observed lnB values and, finally, the average difference (AD) for each social group. Breeding pairs in social groups with positive AD's lost fewer eggs per day than expected based on the dates they laid. A negative AD indicated that more eggs were lost per day than expected. Finally, I regressed AD on the social group composition variables. As in the analysis of laying frequency, a limited sample size precluded inclusion of interactions with Site; thus, the multiple regression allowed for between-site variation in the baseline rate of egg loss but not for site-related variation in the effects of group composition. As with the analyses of initial clutch size, I ran one regression using α and β lengths (from October measurements) and the number of subordinate group members and then a second in which the number of subordinates was replaced by γ length.

RESULTS

Clutch size

At least one clutch of newly laid eggs was found and photographed at each of 35 anemones, 22 at Site 1 and 13 at Site 2. Clutch sizes ranged from 62 to 1376 eggs (mean ± standard deviation = 491 ± 246). At five anemones, all at Site 1, photographs were taken of at least five newly laid clutches without any change in group membership taking place between clutches. Clutch size differed among groups but, within each group, variation was independent of laying date (Table 1). Therefore, I ignored laying date in subsequent analyses of clutch size variation (below).

Groups with 0, 1, 2 and 3 subordinates were found at 1, 9, 15 and 10 anemones, respectively. To facilitate comparison with analyses using γ length (see below), I excluded the anemone at which no subordinates were present. I regressed average ln-transformed clutch

Table 1. Results of an ANCOVA examining seasonal variation in clutch size at five anemones

Factor	Test statistic	P (two-tailed)
Group	$F_{4,32} = 19.8$	<0.001
Date	$F_{1,31} = 0.9$	0.35
Date^2	$F_{1,30} = 0.1$	0.74
Group*Date	$F_{4,26} = 1.0$	0.45
Group*Date^2	$F_{4,22} = 0.7$	0.60

Note: Social group (Group) is a categorical variable. Laying date (Date, Date^2) is a quadratic covariate. Clutch size was ln-transformed. Analysis was restricted to the five groups for which at least five clutch size estimates were available (37 clutches, 5–10 clutches per group). The ordering of terms in the table reflects their order of removal from the model (from bottom to top). Social group was the only statistically significant predictor; it explained 71% of clutch size variation at the five anemones.

size on α length, β length and the number of subordinate group members at Sites 1 and 2. After removing non-significant terms, the reduced model, which consisted of the four main effects and the interactions $\alpha*\beta$ and Subordinates*Site, was statistically significant ($F_{6,27} = 5.5$, $P < 0.001$, $R^2 = 0.45$). To simplify interpretation, I re-ran the regression using only data from Site 1. At Site 1, the number of subordinates was not a significant predictor of clutch size, either as an interaction with α or β ($\alpha*\beta*$Subordinates: $t_{1,13} = 1.2$, $P = 0.27$; α*Subordinates: $t_{1,14} = 0.2$, $P = 0.85$; $\beta*$Subordinates: $t_{1,15} = 0.9$, $P = 0.37$) or as a main effect ($t_{1,18} = 1.5$, $P = 0.16$). Nor was α's length a significant predictor ($\alpha*\beta$: $t_{1,16} = 1.5$, $P = 0.15$; α: $t_{1,17} = 0.5$, $P = 0.62$). The model reduced to a simple linear regression of average ln-transformed clutch size on β length ($F_{1,19} = 11.1$, $P = 0.003$, $R^2 = 0.34$).

I then replaced the number of subordinates with γ length and re-ran the regression. The saturated multiple regression of clutch size on Site and on lengths of α, β and γ was significant ($F_{15,18} = 4.3$, $P = 0.002$) and explained 49% of clutch size variation at the two sites (compared with 45% for the equivalent regression using the number of subordinate group members; see above). The highest-order interaction, $\alpha*\beta*\gamma*$Site, was statistically significant ($t_{1,18} = 2.8$, $P = 0.01$). Using only the data for groups at Site 1, the regression remained significant ($F_{4,16} = 4.0$, $P = 0.02$). The reduced model included α, β and γ lengths and the interaction between α and γ lengths. [The latter term approached statistical significance (Table 2).] Large females laid larger clutches when γ was large; small females did not (Table 2, Fig. 1). The model explained 38% of clutch size variation at Site 1. R^2 dropped to 0.28 if the $\alpha*\gamma$ interaction was not included.

Note that female length was, at best, a weak predictor of clutch size. At Site 1, linear and allometric regressions of average ln-transformed clutch size on α length explained 11% and 10% of clutch size variation, respectively.

Laying frequency

From 20 October to 26 November 1997, α, β, and γ identities remained constant at 26 reproductively active groups (Site 1 = 14 groups, Site 2 = 12 groups). Site, β and γ lengths,

Table 2. Results of multiple regressions of average ln-transformed clutch size on social group composition variables (α, β and γ lengths) at Site 1 ($n = 21$)

Factor	Coefficient	$t_{1,16}$	P (two-tailed)
Constant	23.8		
α	−0.32	2.0	0.07
β	0.11	2.3	0.04
γ	−0.57	1.9	0.08
α*γ	0.0079	1.9	0.08

Note: A saturated model was run first. Non-significant interactions were then sequentially removed. The reduced model explained 38% of clutch size variation.

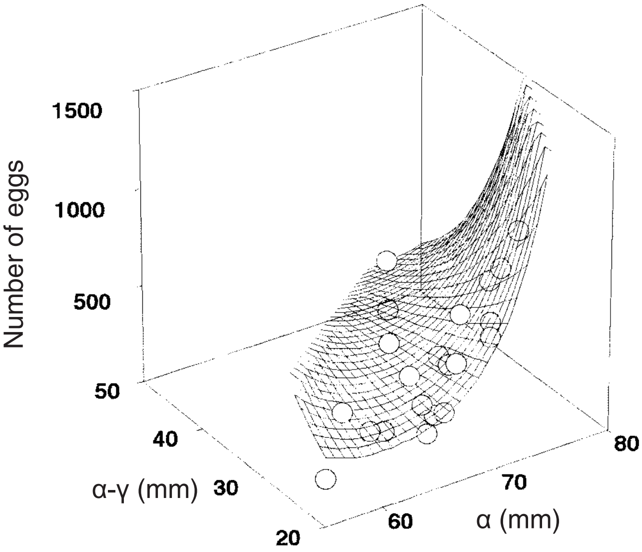

Fig. 1. Relationship between clutch size, female (α) length and γ length at Site 1. The effect of β length on clutch size was incorporated by regressing β length on α and γ lengths and then substituting the predicted β length, given α and γ. The range of possible γ lengths increases with α length because γ is, by definition, smaller than α. Therefore, to simplify presentation, γ length is plotted as α-γ. (The regression model from which the curve was developed used γ's absolute length.) Note that clutch size only increases with γ length if α is large. The left side of the surface is not plotted because no data were available for those combinations of α and γ.

and the interaction between those two lengths, explained significant variation in laying frequency ($F_{4,21} = 4.1$, $P = 0.01$, $R^2 = 0.33$). At anemones where the male was large, female laying frequency increased with γ length. Laying frequency did not increase with γ length if the male was small. Laying frequency was not affected by the female's own length. More clutches were laid at Site 1 than at Site 2 (Table 3, Fig. 2). Samples sizes were not large enough for site-specific regressions to be meaningful.

Table 3. Results of a multiple regression of the number of clutches initiated from 20 October to 26 November 1997, at Sites 1 ($n = 14$) and 2 ($n = 12$) on social group composition variables

Factor	Coefficient	$t_{1,21}$	P (two-tailed)
Constant	49.0		
Site	0.67	3.1	0.006
β	−0.91	2.3	0.03
γ	−1.2	2.6	0.02
$\beta{*}\gamma$	0.024	2.5	0.02

Note: The regression was first run using lengths of α, β and γ and interactions among those variables; Site was included only as a main effect (Site 1 = +1, Site 2 = −1). Non-significant terms were then sequentially removed, beginning with higher-order interactions. The resulting model explained 33% of the variation in laying frequency.

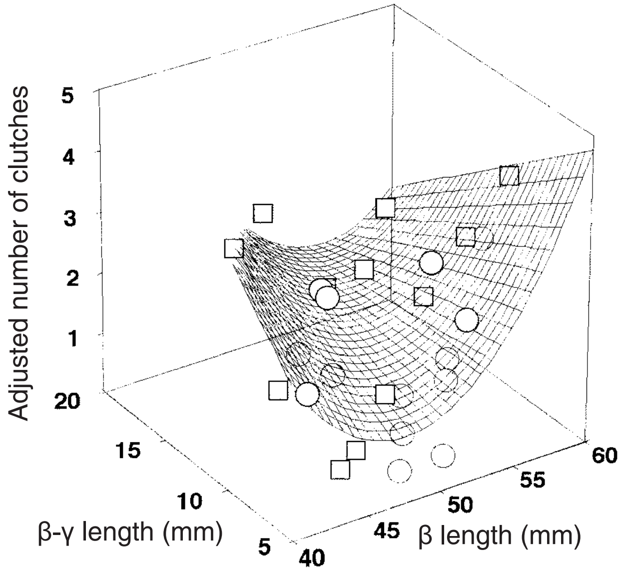

Fig. 2. Relationship between laying frequency, male (β) length and γ length at Sites 1 (○) and 2 (□). Laying frequency was estimated as the number of clutches initiated between 20 October and 26 November 1997. Gamma is plotted as β-γ because the range of possible γ lengths increases with β length (see Fig. 1 caption). The left side of the surface is not plotted because no data were available for those combinations of β and γ. The data have been adjusted using the Table 4 'Site' coefficient to control for between-site laying frequency differences.

Hatching success

Thirty pairs of clutch photographs (A: the first photograph of a clutch; B: a later photograph of the same clutch) were taken at six Site 1 anemones between September and November 1997, with at least four A–B pairs per anemonefish group. The daily rate of egg loss varied among groups but was consistently greater as the season progressed – that is, the

Table 4. Results of an ANCOVA examining seasonal variation in the rate of egg loss from 30 clutches at six anemones

Factor	Coefficient	Test statistic	P (two-tailed)
Constant	−0.87		
lnA	1.1	$F_{1,10} = 124$	<0.001
lnA*Date	0.0012	$F_{1,10} = 5.6$	0.04
lnA*Group	—	$F_{5,10} = 1.0$	0.44
lnA*Date*Group	—	$F_{5,10} = 3.0$	0.06
Days	0.067	$F_{1,10} = 2.8$	0.12
Days*Date	−0.0024	$F_{1,10} = 12.9$	0.005
Days*Group	—	$F_{5,10} = 11.8$	0.001

Note: Social group (Group) is a categorical variable. (Hence, no coefficients are given for terms involving Group.) The response variable, lnB, is the number of eggs counted on the second photograph of a clutch (ln-transformed). The (ln-transformed) number of eggs on the first photograph (lnA) and the number of days separating the first and second egg photographs (Days) are independent predictors of lnB. Laying date (Date) and social group (Group) were included as interactions with lnA and with Days. The interaction term Days*Date*Group was non-significant and was removed from the model.

Table 5. Results of a multiple regression of social group composition variables on hatching success at 22 anemones

Factor	Coefficient	$t_{1,17}$	P (two-tailed)
Constant	4.6		
Site	0.11	2.2	0.04
β	−0.091	2.5	0.02
Subordinates	−2.1	2.5	0.02
β*Subordinates	0.040	2.4	0.03

Note: Hatching success was estimated as AD, a group's average observed deviation of lnB values from values predicted based on lnA, Days and Date (see Table 4 for coefficients). The regression was first run using lengths of α and β, the total number of subordinates ('Subordinates') and interactions among those variables; Site was included only as a main effect (Site 1 = +1, Site 2 = −1). Non-significant terms were then removed sequentially, beginning with higher-order interactions. The resulting model explained 27% of the variation in AD.

coefficient of the Days*Date interaction was negative, where Days is the number of days separating photographs A and B and Date is the date on which photograph A was taken (Table 4). There was some indication of among-group variation in the seasonal effect ($F_{5,10} = 3.0$, $P = 0.06$). On average, relatively more eggs were lost from smaller clutches early in the season. Later in the season, relatively more eggs were lost from larger clutches.

Using coefficient estimates from Table 4, I calculated predicted values of lnB for clutches at five of the anemones used to estimate those coefficients (no subordinates were present at the sixth anemone, so it could not be used in the analyses that follow) and for 24 other clutches laid at 17 other anemones, for which fewer than four paired photographs were available. I then calculated AD (the average deviation from the predicted lnB value) for each social group (Site 1 = 15 groups, Site 2 = 7 groups). A positive AD indicates a higher than average hatching success. Data from one anemone, at which the AD value was more than 3 standard deviations below the mean, were excluded.

I first regressed AD on lengths of α and β and on the number of subordinate group members. Groups with 0, 1, 2 and 3 subordinates were found at 2, 5, 11 and 6 anemones, respectively. To facilitate comparison with the subsequent regression model (using γ length), I excluded the data from the two anemones at which no subordinates were present. A reduced model, which included Site, the male's (β) length, the total number of subordinates and an interaction between the latter two variables, was marginally significant ($F_{4,17} = 2.9$, $P = 0.05$) and explained 27% of the variation in hatching success (Table 5). For males >52 mm long, AD increased as the number of subordinates increased. For smaller males, AD decreased with the number of subordinates. [Male length ranged from 41 to 59 mm (mean 50 mm).] AD increased with male length when only one subordinate was present, but declined with male length if more subordinates were present. I then replaced the number of subordinates with γ length and re-ran the regression. Gamma length was not a useful predictor of hatching success either in interactions with α and β (α*β*γ: $t_{1,13} = 1.6$, $P = 0.13$; α*γ: $t_{1,15} = 1.1$, $P = 0.28$; β*γ: $t_{1,16} = 0.4$, $P = 0.69$) or as a main effect ($t_{1,19} = 1.2$, $P = 0.25$). Nor was a model that excluded γ statistically significant ($F_{4,17} = 0.8$, $P = 0.54$).

DISCUSSION

Positive correlations between γ length and both clutch size and laying frequency are superficially consistent with the hypothesis that subordinate group members provide a reproductive benefit to breeding pairs. However, the importance of interactions among group members' lengths is not consistent with the pay-to-stay hypothesis. At Site 1, the relationship between clutch size and γ length varied with female length: large females laid larger clutches when γ was large; small females did not (Fig. 1). Social inhibition of growth ensures that the smallest female is still qualitatively larger than the γ in its own social group, large enough to control group membership and to coerce her subordinates. Thus, were subordinates providing some reproductive benefit, one would expect small females, as well as large females, to realize that benefit. Moreover, the number of subordinate fish was not a useful predictor of clutch size at Site 1. When both sites were included in regression analyses, models using γ length and using the total number of subordinates yielded similar correlation coefficients. The two variables are confounded because δ- and ε-ranked subordinates could only settle in groups where γ was large. Without either a much larger sample size or, preferably, manipulation of group size, it is not possible to determine to which variable the effect should be attributed. The role of statistical interactions is unexpected in either case.

Laying frequency was also correlated with γ length and, as with clutch size, a statistical interaction was an important predictor. For most observed combinations of β and γ length, laying frequency increased with β (male) length, γ length and with γ's length relative to β's. But laying frequency did not increase with γ length when β was small (Fig. 2). As with clutch size, one would not expect a causal effect of γ length on female laying frequency to be limited to groups with large males. (For the smallest males, laying frequency appeared to decline with increasing γ length. That apparent effect occurred near the limit of the state-space range, and may be an artifact of the analytical approach.)

The relationship between group composition and hatching success further supports the conclusion that subordinates did not provide a reproductive benefit. Hatching success is the component of reproductive success that a subordinate could, potentially, influence directly. But hatching success declined, on average, as the number of subordinates increased. Statistical interactions were, again, important: whether hatching success increased or decreased with the number of subordinates depended on male size. When few subordinates were present, small males were more successful at raising clutches than were large males, even though large males should be, if anything, better parents. Conversely, when more subordinates were present, hatching success increased with male length.

These results are not consistent with theoretical predictions based on anemonefish ecology (Kokko and Johnstone, 1999; Ragsdale, 1999; Kokko *et al.*, 2002), but are consistent with previous ecological and behavioural studies of anemonefish. Helping behaviour is the most obvious mechanism through which subordinate group members might benefit a breeding pair. Subordinate members of a false clown group should be capable of acting as reproductive helpers. Helping does occur in *N. pulcher*: subordinates clean and aerate eggs and defend clutches against predators (Taborsky, 1984; Balshine-Earn *et al.*, 1998). In contrast, helping has not been reported in any anemonefish species (Moyer and Bell, 1976; Ross, 1978; Fricke, 1979; Moyer and Steene, 1979; for reviews, see Thresher, 1984; Fautin and Allen, 1992). The only published report of extra-parental care in an anemonefish is Yanagisawa and Ochi's (1986) study of stepfathering *A. clarki*: immigrant males replaced males that were removed while a clutch was present, and those immigrants cared for the clutch. Alternatively, subordinate anemonefish might assist with tasks unrelated to reproduction, thereby leaving a breeding pair with more time and energy to devote to reproduction. Specifically, subordinates might help to protect the host anemone or to repulse intruding conspecifics (Fricke, 1979; Taborsky and Limberger, 1981). However, with the exception of the apparent mutualism between the anemonefish *A. melanopus* and its host *Entacmaea quadricolor* (Godwin and Fautin, 1992), the relationship between anemonefish and host sea anemones may best be described as commensal; anemones do not require anemonefish for protection (for a review, see Fautin, 1991). At Bunaken Island, not all *S. gigantea* anemones were occupied throughout the study period, and unoccupied anemones remained apparently healthy (J.S. Mitchell, unpublished data). If false clowns, whatever their social status, do not benefit their hosts, then subordinates cannot help dominants by protecting their group's anemone. Subordinate false clowns do respond to experimental presentations of unfamiliar conspecifics (J.S. Mitchell, unpublished data), and false clowns do occasionally migrate between anemones (Nelson *et al.*, 1998; J.S. Mitchell, unpublished data). However, such events are rare. It is unlikely that conspecific incursions occur with sufficient frequency to affect the time and energy that a breeding pair has available for reproduction. Subordinates could conceivably act as sentinels, but, again, such behaviour has not been reported.

And yet, female false clowns appear to have altered both clutch size and laying frequency in response to their social context. Clutch size and laying frequency are clearly under female control, but were not fixed functions of female size. The limited predictive utility of female length in isolation was surprising. Clutch size was not a simple allometric function of female length, but could be remarkably well-predicted when lengths of β and γ were included in a regression model. Clutch size was best predicted by models that included statistical interactions: at Site 1, R^2 dropped appreciably when the $\alpha*\gamma$ interaction term was removed from the regression. Similarly, laying frequency was unrelated to female length and was best predicted by a model that included an interaction: between β and γ lengths. Hatching success followed a similar pattern, except that the number of subordinates, rather than γ length, interacted with β length.

The predictive value of such interactions suggests an underlying correlation between reproductive success and the composition of the group as a whole. Fautin (1992) argued that a group's size composition was an indicator of the amount of time its members had spent together. Although growth inhibition ensures that a subordinate never grows larger than a more dominant group member, minimum length differences will be approached over time. Relatively small differences between group members' lengths may indicate that group composition has remained unchanged for a long time. Possibly, females in well-established groups need to devote less time and energy to maintaining social rank, leaving more available for reproduction. Alternatively, a safer microhabitat may lead both to long-term group stability (because the mortality rate is lower) and to greater reproductive success (because more time is spent foraging and, hence, more energy is available). If the underlying correlation is between the long-term stability of a group and the size and frequency of its females' clutches, then one might also have expected hatching success to increase with the number of subordinates present. Instead, the reverse was true. Nonetheless, it is parsimonious to assume that the same underlying process affected all three components of reproductive success. Whatever that process may be, the pattern is not consistent with the hypothesis that subordinates increase a breeding pair's reproductive success.

I cannot rule out the possibility that correlations between social group composition and components of reproductive success reflect causal relationships between both sets of variables and an external habitat variable. Anemonefish group size and/or α length often increase with anemone size (e.g. Ross, 1978; Fricke, 1979; Fautin, 1992). In the study population, both group size and α length increased with anemone diameter (J.S. Mitchell, unpublished). Therefore, causal effects of social group composition will lead to correlations with anemone size and vice versa. Teasing apart the two possibilities would require a sample size large enough for anemone size to be included as an additional predictor. [In practice, correlations with anemone diameter are consistently lower than the R^2 values reported here (J.S. Mitchell, unpublished data).] Even if correlations between social group composition and components of reproductive success did not reflect a causal process, the conclusion would remain unchanged: subordinates do not increase a breeding pair's reproductive success.

Why not? Given the ecological conditions described earlier in this paper, why don't breeding pairs oblige subordinates to act as reproductive helpers? Reduced hatching success in groups with more subordinates may not reflect a causal process, but dominants do expend time and energy enforcing their group's social hierarchy (Fricke and Fricke, 1977). And if subordinates are capable of helping, then a dominant that does not enforce helping by subordinates is, in effect, paying a reproductive cost. The dominant could instead evict a non-helping subordinate in favour of a more helpful individual (Ragsdale, 1999) or could use punishment for non-helping as a form of coercion (Kokko *et al.*, 2002). Thus, it is not sufficient to argue that subordinates are tolerated simply because their presence is not costly.

Fricke and Fricke (1977) proposed that dominants tolerate subordinates because subordinates are future replacement mates – that is, both members of a breeding pair may view a subordinate as insurance against the death of their current partner. Were no subordinates present, a widowed individual would have to emigrate, wait for an immigrant to arrive or wait for a juvenile anemonefish to settle to the anemone and for that juvenile to grow to maturity. The more rapid return to active reproduction enabled by a resident replacement mate may compensate for the time and effort expended in dominance interactions with a subordinate. For less mobile anemonefish species living in high predation risk environments, Fricke and Fricke's (1977) hypothesis may be a sufficient explanation for the willingness of breeding pairs to share their anemone hosts with a single subordinate. But false clown groups can contain as many as seven members (the breeding pair and five subordinates) and five subordinates seems an excessive insurance premium. Moreover, equally large groups occur in *A. clarkii*, which is much more mobile and in which the formation of new breeding pairs often involves fish moving between hosts, even when hosts are sparsely distributed (e.g. Yanagisawa and Ochi, 1986; Hirose, 1995).

A more interesting explanation is that subordinates may provide dominants with non-reproductive benefits. Kokko and Johnstone (1999) argued that subordinates will be tolerated when their presence reduces a dominant's mortality risk. In this view, risk dilution alone can be a sufficient incentive for acceptance of subordinates. However, using Ragsdale's (1999) logic, passive risk dilution is not sufficient when social vacancies on territories are limiting and dominants choose who fills those vacancies. Just as a dominant may choose among subordinates on the basis of reproductive benefits, so may it choose based on variation in survival benefits. A breeding anemonefish pair should evict (Ragsdale, 1999) or punish (Kokko *et al.*, 2002) 'careful' subordinates in favour of those whose behaviour makes them the focus of a greater proportion of predators' attacks on the group. Consistent with this prediction, subordinates in *A. clarkii* occupy peripheral (presumably riskier) locations around a host anemone, with more dominant group members in central positions (Ochi, 1986, 1989b). It follows from Ragsdale's (1999) argument that subordinates should occupy those riskier locations despite the availability of more protected alternatives.

In conclusion, anemonefish meet the social and ecological conditions under which the pay-to-stay hypothesis should operate, but there is no evidence that the presence of subordinates is of reproductive benefit to a dominant, breeding pair. Dominants are not choosy even though they are in a position, ecologically, to require that subordinates provide some reproductive benefit. Thus, to the extent that rent payment is defined in terms of reproductive benefits, subordinate members of false clown anemonefish social groups do not pay-to-stay. False clowns appear to be an exception to Ragsdale's (1999) prediction. If the exception is to prove the rule, a convincing explanation for the occurrence of social groups in anemonefish is needed.

ACKNOWLEDGEMENTS

This study was funded by grants from the Eastern Indonesia University Development Project (EIUDP) and NSERC (operating grant A6869) to L.M. Dill and by grants and fellowships to the author from NSERC, Simon Fraser University, 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 at UNSRAT sponsored my work at Bunaken. The Dill laboratory and the SFU Behavioural Ecology Research Group provided useful advice over the course of the study. L.M. Dill, B. Crespi and D. Lank made insightful comments on the manuscript.

REFERENCES

Allen, G.R. 1980. *The Anemonefishes of the World*: *Species, Care, and Breeding*. Mentor, OH: Aquarium Systems.

Balshine-Earn, S., Neat, F.C., Reid, H. and Taborsky, M. 1998. Paying to stay or paying to breed? Field evidence for direct benefits of helping behavior in a cooperatively breeding fish. *Behav. Ecol.*, **9**: 432–438.

Bell, L.J. 1976. Notes on the nesting success and fecundity of the anemonefish *Amphiprion clarkii* at Miyake-Jima, Japan. *Jap. J. Ichthyol.*, **22**: 207–211.

Cockburn, A. 1998. Evolution of helping behavior in cooperatively breeding birds. *Annu. Rev. Ecol. Syst.*, **29**: 141–177.

Elliott, J.K., Elliot, J.M. and Mariscal, R.N. 1995. Host selection, location, and association behaviors of anemonefishes in field settlement experiments. *Mar. Biol.*, **122**: 377–389.

Emlen, S.T. 1991. Evolution of cooperative breeding in birds and mammals. In *Behavioural Ecology: An Evolutionary Approach,* 3rd edn (J.R. Krebs and N.B. Davies, eds), pp. 301–335. Oxford: Blackwell.

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. and Allen, G.R. 1992. *Field Guide to Anemonefishes and their Host Sea Anemones*. Perth, WA: Western Australian Museum.

Fricke, H.W. 1979. Mating system, resource defence and sex change in the anemonefish *Amphiprion akallopisos. Z. Tierpsychol.*, **50**: 313–326.

Fricke, H.W. and Fricke, S. 1977. Monogamy and sex change by aggressive dominance in coral reef fish. *Nature*, **266**: 830–832.

Gaston, A.J. 1978. The evolution of group-territorial behavior and cooperative breeding. *Am. Nat.*, **112**: 1091–1100.

Godwin, J. and Fautin, D.G. 1992. Defense of host actinians by anemonefishes. *Copeia*, **1992**: 902–908.

Hirose, Y. 1995. Patterns of pair formation in protandrous anemonefishes, *Amphiprion clarkii*, *A. frenatus*, and *A. perideraion*, on coral reefs of Okinawa, Japan. *Environ. Biol. Fishes*, **43**: 153–161.

Kokko, H. and Johnstone, R.A. 1999. Social queuing in animal societies: a dynamic model of reproductive skew. *Proc. R. Soc. Lond. B*, **266**: 571–578.

Kokko, H., Johnstone, R.A. and Wright, J. 2002. The evolution of parental and alloparental effort in cooperatively breeding groups: when should helpers pay to stay? *Behav. Ecol.*, **13**: 291–300.

Krebs, J.R. and Davies, N.B. 1987. *An Introduction to Behavioural Ecology*. Oxford: Blackwell.

Moyer, J.T. and Bell, L.J. 1976. Reproductive behavior of the anemonefish *Amphiprion clarkii* at Miyake-Jima, Japan. *Jap. J. Ichthyol.*, **23**: 23–32.

Moyer, J.T. and Steene, R.C. 1979. Nesting behavior of the anemonefish *Amphiprion polymnus. Jap. J. Ichthyol.*, **26**: 209–214.

Nelson, J.S., Chou, L.M. and Phang, V.P. 1998. Inter-habitat migration of the anemonefish *Amphiprion ocellaris*. *Asian J. Trop. Biol.*, **3**:19–31.

Ochi, H. 1986. Growth of the anemonefish *Amphiprion clarkii* in temperate waters, with special reference to the influence of settling time on the growth of 0-year-olds. *Mar. Biol.*, **92**: 223–229.

Ochi, H. 1989a. Mating behavior and sex change of the anemonefish, *Amphiprion clarkii*, in the temperate waters of southern Japan. *Environ. Biol. Fishes*, **26**: 257–275.

Ochi, H. 1989b. Acquisition of breeding space by nonbreeders in the anemonefish *Amphiprion clarkii* in temperate waters of southern Japan. *Ethology*, **83**: 279–294.

Ragsdale, J.E. 1999. Reproductive skew theory extended: the effect of resource inheritance on social organization. *Evol. Ecol. Res.*, **1**: 859–874.

Reeve, H.K. and Ratnieks, F.L.W. 1993. Queen–queen conflicts in polygynous societies: mutual tolerance and reproductive skew. In *Queen Number and Sociality in Insects* (L. Keller, ed.), pp. 45–85. Oxford: Oxford University Press.

Richardson, D.L., Harrison, P.L. and Harriott, V.J. 1997. Timing of spawning and fecundity of a tropical and subtropical anemonefish (Pomacentridae: *Amphiprion*) on a high latitude reef on the east coast of Australia. *Mar. Ecol. Prog. Ser.*, **156**: 175–181.

Ross, R.M. 1978. Reproductive behavior of the anemonefish *Amphiprion melanopus* on Guam. *Copeia*, **1978**: 103–107.

Solomon, N.G. and French, J.A. 1997. *Cooperative Breeding in Mammals*. Cambridge: Cambridge University Press.

Stacey, P.B. and Koenig, W.D. 1990. *Cooperative Breeding in Birds: Long Term Studies of Ecology and Behavior*. Cambridge: Cambridge University Press.

Taborsky, M. 1984. Broodcare helpers in the cichlid fish *Lamprologus brichardi*: their costs and benefits. *Anim. Behav.*, **32**: 1236–1252.

Taborsky, M. and Limberger, D. 1981. Helpers in fish. *Behav. Ecol. Sociobiol.*, **8**: 143–145.

Thresher, R.E. 1984. *Reproduction in Reef Fishes*. Neptune City, NJ: T.F.H. Publications.

Thresher, R.E. and Gronell, A.M. 1978. Subcutaneous tagging of small reef fishes. *Copeia*, **1978**: 352–353.

Vehrencamp, S.L. 1983. Optimal degree of skew in reproductive societies. *Am. Zool.*, **23**: 327–335.

Yamagishi, S. and Kohda, M. 1996. Is the cichlid fish *Julidochromis markieri* polyandrous? *Ichthyol. Res.*, **43**: 469–471.

Yanagisawa, Y. and Ochi, H. 1986. Step-fathering in the anemonefish *Amphiprion clarkii*: a removal study. *Anim. Behav.*, **34**: 1769–1780.