Reproductive control via the threat of eviction in the clown anemonefish

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In social groups, high reproductive skew is predicted to arise when the reproductive output of a group is limited, and dominant individuals can suppress subordinate reproductive efforts. Reproductive suppression is often assumed to occur via overt aggression or the threat of eviction. It is unclear, however, whether the threat of eviction alone is sufficient to induce reproductive restraint by subordinates. Here, we test two assumptions of the restraint model of reproductive skew by investigating whether resource limitation generates reproductive competition and whether the threat of eviction leads to reproductive restraint in the clown anemonefish *Amphiprion percula*. First, we use a feeding experiment to test whether reproduction is resource limited, which would create an incentive for the dominant pair to suppress subordinate reproduction. We show that the number of eggs laid increased in the population over the study period, but the per cent increase in fed groups was more than twice that in unfed groups (205% and 78%, respectively). Second, we use an eviction experiment to test whether the dominant pair evicts mature subordinates, which would create an incentive for the subordinates to forgo reproduction. We show that mature subordinates are seven times more likely to be evicted than immature subordinates of the same size. In summary, we provide experimental support for the assumptions of the restraint model by showing that resource limitation creates reproductive competition and a credible threat of eviction helps explain why subordinates forego reproduction. Transactional models of reproductive skew may apply well to this and other simple systems.

1. Introduction

A central focus of research on social evolution is to understand the causes of variation in reproductive skew [1–3]. Theoretical models often assume that the group's reproductive output is limited, owing to limited availability of critical breeding resources such as nutrition and nest sites, and that individuals compete for reproduction [4–7]. When such reproductive competition exists, dominant individuals may suppress subordinate reproductive efforts by interfering with mating, inducing stress or killing offspring [8–12]. Such interactions have the appearance of being costly and inefficient for both parties, and one might predict that natural selection would favour more efficient solutions if the parties were to have complete information on the outcome [13,14].

Under such conditions of complete information, it may be possible for dominants and subordinates to come to a more efficient, negotiated settlement, whereby the dominant uses the threat of eviction and the subordinate shows reproductive restraint because of this threat [13,15–22]. While the threat of eviction does not seem to be effective in inducing reproductive restraint in mammal groups with multiple subordinates that can respond retroactively to eviction [23], theory suggests that it will be more effective in dyadic relationships or linear

hierarchies where the threat is targeted and eviction is non-reversible [23,24]. Still, it remains unclear whether the threat of eviction is used to induce reproductive restraint in nature.

The clown anemonefish, *Amphiprion percula*, provides a tractable system to investigate these ideas. Groups of *A. percula* are found in close association with sea anemones *Heteractis magnifica* [25–27]. Each group is composed of a dominant breeding pair and a small number of unrelated non-breeders [28–30]. Correlational evidence suggests that the reproductive output of the group is influenced by territory quality [31]. Within each group, there is a size-based dominance hierarchy: the female is largest, the male is second largest, and the non-breeders get progressively smaller [32,33]. Evidence suggests that the size hierarchy emerges because subordinates show growth restraint to avoid eviction by their immediate dominants [27,32].

Here, we test the hypothesis that subordinate *A. percula* will show reproductive restraint because of reproductive competition and the threat of eviction. Specifically, we test two assumptions of the restraint model of reproductive skew. First, reproduction is food limited, leading to reproductive competition within groups and providing an incentive for the breeding pair to evict other mature group members. Food limitation is tested by a food supplementation experiment and comparing the number of eggs laid between fed groups and unfed groups. Second, the breeding pair will evict other mature individuals, but not immature individuals, providing an incentive for some individuals to forgo their own reproduction. This is tested by an eviction experiment and comparing the response of a breeding pair with the introduction of new mature and immature group members.

2. Material and methods

(a) Study population

This study was conducted in May–August 2017 on inshore reefs near Mahonia Na Dari Research and Conservation Centre, in Kimbe Bay, Papua New Guinea. All fieldwork was conducted using SCUBA. From 26 May to 23 June, we identified 52 breeding groups occupying the anemone *H. magnifica* on 10 reefs. Groups consisted of a breeding pair and zero to three non-breeders. Individuals were ranked (1–5) based on their size relative to other individuals within their anemone, with the largest being rank 1. Individuals were also photographed, and the photographs were used to identify individuals and confirm that they survived the entire study and did not move between anemones during the study [26,32,34,35].

We monitored the reproduction of all groups, every 2 days for three lunar months (26 May–21 August). Our monitoring spanned three lunar months rather than calendar months, because *A. percula* breed on a lunar cycle [36]. Breeding was readily detectable. In the days before spawning, the male selected a nest site next to the base of the anemone and cleaned it, and in the days after spawning, the male spent much of his time tending the eggs [37]. The age of the eggs was determined using the colour of the yolk and the presence and developmental stage of the embryos' eyes [30]. The eggs hatched after 7 days. Each clutch was photographed on day 1 or 2 to provide an estimate of the number of eggs laid, and the number of eggs was determined using the Cell Counter plugin for ImageJ.

The study began shortly after a severe mass bleaching event. Many of the anemones studied were visibly affected by unusually high temperatures in Kimbe Bay from March to May 2017. We bore this in mind when it came to designing our two experiments:

(i) a feeding experiment (see below), and (ii) an eviction experiment (see below). For the feeding experiment, the same number of bleached and unbleached anemones was included in both treatment and control groups. For the eviction experiment, bleached anemones were not included in the experiment.

(b) Feeding experiment

To test the hypothesis that food resources for reproduction are limiting, we conducted a feeding experiment with all 52 breeding groups. We collected one lunar month of baseline data (26 May–23 June), then two months of data in which we manipulated (fed) half of the groups ($n = 25$) while keeping the other half ($n = 27$) as controls (24 June–21 August). These groups were randomly stratified to ensure equal amounts of fed/control groups for the reefs closer to shore ($n = 4$ reefs and $n = 32$ anemones) versus the reefs further from shore ($n = 6$ reefs and $n = 20$ anemones) and for bleached anemones ($n = 10$ anemones) versus unbleached anemones ($n = 42$ anemones). See Saenz-Agudelo *et al*. [38], Beldade *et al*. [39] and Chausson *et al*. [40] for the rationale for stratifying by these two factors. Consequently, distance from shore and bleached status were not included as covariates in the analysis.

The treatment groups received one vial (3 ml) of food pellets (New Life Spectrum, marine fish food 1 mm pellets) and one vial (3 ml) of dried brine shrimp (Omega One, freeze dried brine shrimp). The food was kept dry in capped tubes until delivery. Brine shrimp (positively buoyant) were delivered first, by squirting the shrimp onto the anemone with a pipette. The pellets (negatively buoyant) were delivered second by opening the vial and tipping them onto the anemone. Through this method, most food was either immediately consumed by the fish, or it was stuck among anemone tentacles, where the fish could consume it. Some food was consumed by the anemone and other fish species present around the anemone. The control groups were treated in the same manner, by squirting water from an empty vial into the anemone and opening and tipping out another empty vial over the anemone, to control for the possible disturbance caused by feeding.

(c) Eviction experiment

To test the hypothesis that the breeding pair will evict other mature individuals but not immature individuals, we conducted an eviction experiment between 21 and 26 August. Thirteen focal groups, which all consisted of at least three individuals and had bred in the preceding months, were chosen. Only groups consisting of at least three individuals were chosen to ensure that the dominant breeders were predisposed to tolerating a non-breeding subordinate. Only groups that were observed breeding in the preceding months were chosen to ensure the two dominant individuals were indeed breeding adults. All individuals in each group were caught and measured to the nearest 0.1 mm.

At the beginning of the experiment, rank 3 and other smaller individuals (if present) were removed from the focal group, leaving only the two dominant individuals, rank 1 and rank 2 (figure 1). Then, rank 2 (reproductively active male) or rank 3 (non-breeding subordinate) from different groups was introduced, one at a time, on different days, in random order (figure 1). While rank 3 is not reproductively active, they are capable of reproduction [29]. The introduced rank 2 and rank 3 were smaller than the original rank 3, and they were size matched, within 1 mm standard length of each other, so evictions would not be driven by size [32].

Introductions were left overnight and the following day we noted the presence/absence of the introduced individual and 5 min of observations were conducted. Introducees were considered evicted if they had either disappeared overnight or if they spent most of the observed time (≥ 3 min) outside the
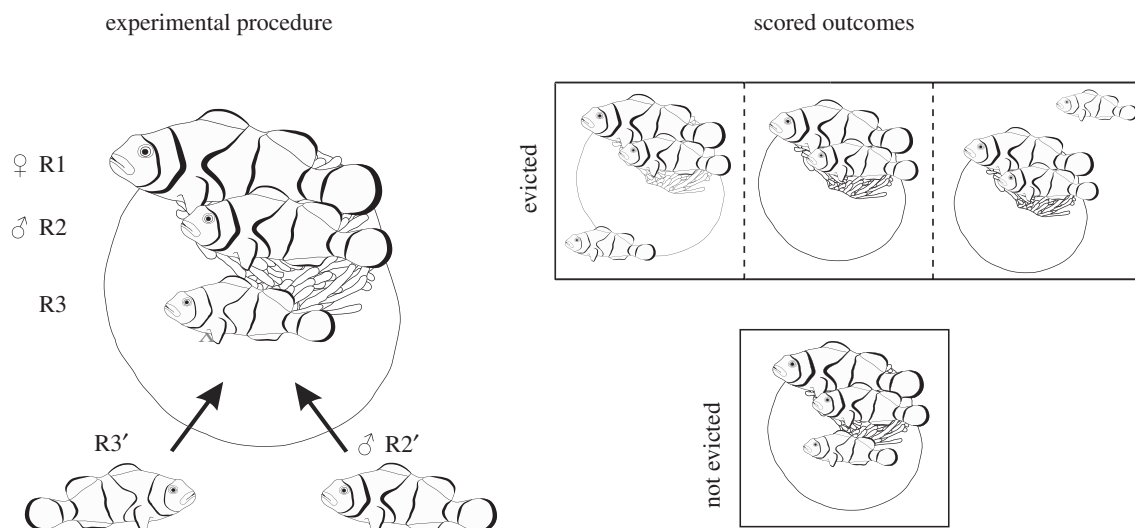
Figure 1. Schematic diagram of the eviction experiment. (a) Focal groups consisted of a breeding pair (R1 and R2) and at least one non-breeding subordinate (R3). The rank 3 individual was removed from the focal group, and a size-matched rank 3 (R3′) and rank 2 (R2′) from other groups were introduced to the focal group one at a time, on separate days and in random order. (b) After 1 day, the introduced individual was scored as either evicted or not evicted. The individual was considered not evicted if it spent the majority of the 5 min observation period among the anemone's tentacles. The individual was considered evicted if it was either not present, or spent the majority of the 5 min observation outside of the anemone's tentacles.

anemone, i.e. with their full body length outside of the range of anemone tentacles (figure 1). If present, the introduced individual was then removed from the focal anemone and returned to its host anemone.

(d) Statistical analysis

All analyses were done in R v. 3.4.2 'Short Summer' [41]. To test the hypothesis that reproduction is resource limited, we fitted a mixed linear model (package 'lme4') using the number of eggs laid per lunar month as the response variable. Month (month 1: baseline; month 2: first treatment month; month 3: second treatment month) and treatment (fed or control) were used as predictor variables. The interaction between month and treatment was included to determine whether the effect of the treatment varied with month. Pair identity (ID) was used as a random factor, to control for the lack of independence between multiple measures of reproduction from the same pair. This was nested in reef ID, which was used as another random factor, to control for the potential lack of independence between multiple measures of reproduction from the same reef. Assumptions of normal distribution and homogeneity were checked using q–q plots and Bartlett's test, respectively [42].

Using the 'MuMIn' package [43,44], marginal R^2, the variance explained by fixed factors, was calculated as follows:

$$R\_GLMM(m)^2 = \frac{\sigma\_f^2}{\sigma\_f^2 + \sum(\sigma\_l^2) + \sigma\_e^2 + \sigma\_d^2}.$$

Conditional R^2, the variance explained by both fixed and random factors, was calculated as follows:

$$R\_GLMM(c)^2 = \frac{\sigma\_f^2 + \sum(\sigma\_l^2)}{\sigma\_f^2 + \sum(\sigma\_l^2) + \sigma\_e^2 + \sigma\_d^2}.$$

Post hoc pairwise comparisons were conducted using least-squares means, implemented in the 'lsmeans' package.

To test the hypothesis that the breeding pair will evict other mature individuals but not immature individuals, we used Fisher's exact tests for contingency tables. Specifically, we tested whether the number of introduced rank 2 that were evicted differed from the number of introduced rank 3 that were evicted. We also used Fisher's exact test to investigate whether there was an effect of being introduced first or introduced second.
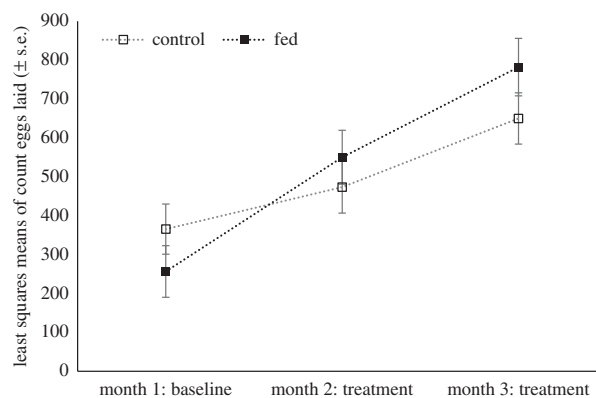

Figure 2. Least-squares means ($\pm$ s.e.) of number of eggs laid per month by control and fed groups of *Amphiprion percula* over three months. Month 1: $n_{control} = 27$, $n_{fed} = 25$; month 2: $n_{control} = 24$, $n_{fed} = 22$; month 3: $n_{control} = 25$, $n_{fed} = 18$.

3. Results

(a) Feeding experiment

The number of eggs laid increased significantly over time and significantly more so in the fed anemones than in the control anemones (figure 2). The mean number of eggs laid was greater in month 3 compared with month 1 in both the fed and control groups (mixed linear model: month, $F_{2,85} = 33.05$, $p < 0.001$; Tukey's honest significant difference (HSD): control, $q_{85} = -284.54$, $p < 0.001$, fed, $q_{85} = -525.421$, $p < 0.001$; figure 2). Treatment alone had no significant effect on the number of eggs laid throughout the experiment (mixed linear model: treatment; $F_{1,41} = 0.01$, $p = 0.482$). However, there was a significant interaction between treatment and month (mixed linear model: treatment $\times$ month; $F_{2,85} = 3.51$, $p = 0.031$; figure 2): the mean number of eggs laid by fed groups increased by 205% between month 1 and month 3, whereas the mean number of eggs laid by the control groups increased by just 78% in the same period (figure 2). The fixed (treatment and month) and random (reef and site) factors together explained 58% of the variance in the data ($R_m^2 = 0.23$, $R_c^2 = 0.58$).
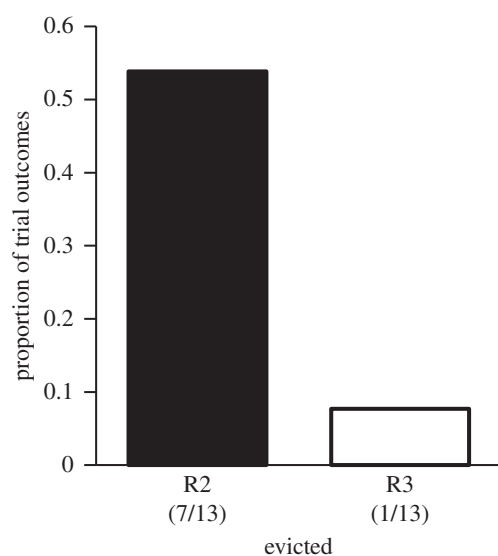
Figure 3. Proportion of rank 2 (R2) and rank 3 (R3) individuals which were evicted by the dominant pair after being introduced to an anemone. $n = 13$ trials per treatment.

(b) Eviction experiment

Both males and females were observed being aggressive towards introduced individuals. The individual introduced first was neither more likely nor less likely to be evicted than the individual introduced second (Fisher's exact test, $p = 1$). Rank 2 individuals (mature males) were significantly more likely to be evicted than rank 3 individuals of the same size (Fisher's exact test, $p = 0.03$), with 54.5% of introduced rank 2 evicted and only 7.7% of introduced rank 3 evicted (figure 3).

4. Discussion

Our experiments using the clown anemonefish, *A. percula*, provide support for two key assumptions of the restraint model of reproductive skew: (i) there is reproductive competition owing to resource limitation, and (ii) dominant individuals readily evict reproductively active subordinates. This helps explain why subordinates exercise reproductive restraint in this system. These results complement similar findings in a similar system—the emerald goby, *Paragobiodon xanthosomus*, which is found in close association with the coral *Seriatopora hystrix*—where reproduction was also food limited and eviction was also dependent on subordinate reproductive state [45]. We consider that there are two reasons for the success of the threat of eviction inducing reproductive restraint in these systems. First, subordinates that are evicted cannot regain access to the group—sea anemones and coral heads are small (less than 1 m across), can be patrolled quickly and easily, and there are few places for subordinates to hide. Second, dominants are able to accurately target specific individuals—not only do subordinates differ markedly in size [32,33,46], but also they have highly variable markings, in visible and ultraviolet spectrum, that have all of the characteristics of individual recognition signals [35,47–49]. These findings suggest that, as predicted by Cant *et al*. [23], in relatively simple, linear hierarchies the threat of eviction by the dominant is sufficient to induce pre-emptive reproductive restraint by subordinates.

It is instructive to compare these findings with others where the threat of eviction does not seem to be sufficient to induce reproductive restraint. In banded mongooses, *Mungos mungo*,

for example, there is evidence of reproductive competition, that dominants can evict subordinates, but no evidence that subordinates exhibit reproductive restraint to avoid eviction [23]. The reasons given for the failure of eviction to induce restraint in that system are that subordinates are able to re-enter the group post-eviction and that dominants cannot perfectly discriminate among subordinates, both of which reduce the incentive to subordinates of cooperating and pre-emptively restraining their own reproduction [23]. Another, less well-known example that supports these ideas is that of the pink anemonefish, *Amphiprion perideraion*, which inhabits the same species of sea anemone as *A. percula*, on the same reefs in Papua New Guinea [26,50]. Compared with *A. percula*, *A. perideraion* have little variation in their markings and are better swimmers, probably making it harder for dominants to target and evict specific individuals. In this system, it seems that subordinates do not show the same level of growth or reproductive restraint, and dominants eventually lose control of their group. Following loss of control, dominant *A. perideraion* leave their anemone for a nearby anemone occupied by *A. percula*, and evict and kill the *A. percula* group *en masse* (P.M. Buston, T.A. Barbasch and T. Rueger 2017, personal observation). This latter example highlights how a small difference in biology can influence the social system that emerges, even in closely related species in the same ecological context.

Our study shows that clown anemonefish subordinates will forgo their own reproduction owing to the threat of eviction, and dominants will embrace subordinates that are not reproductively active. Two outstanding questions remain for this system. First, why do non-breeders then tolerate their situation rather than pursuing alternative options? On the one hand, non-breeders stand to inherit the territory within which they reside, so they gain future genetic benefits [30,46,51]. On the other hand, evidence suggests that non-breeders will neither disperse to breed elsewhere owing to ecological constraints, i.e. habitat saturation and risk of movement [27,29,50,52–54], nor contest for a breeding position owing to social constraints [30,35,46,55]. Second, why do breeders embrace non-breeders rather than evict them? Evidence suggests that breeders do not benefit from the presence of non-breeders in terms of survival, growth, reproduction, rapid mate replacement [30] or by passing on their territory to their offspring [20,28,29]. It is plausible that breeders might benefit from the presence of non-breeders owing to indirect effects mediated by the anemone: non-breeders may enhance anemone growth and reproduction [56–61]; large anemones may enhance fish growth and reproduction [31,62,63].

Our results may also provide a different perspective on the role of monogamy in social evolution. There is a widely recognized association between monogamy and the formation of social groups in which some individuals forgo their own reproduction [64–66]. One hypothesis to explain this association is that monogamy together with delayed dispersal gives rise to groups in which there are high degrees of relatedness among group members, and in such groups, individuals will gain indirect genetic benefits by helping their relatives [67,68]. Under this scenario, monogamy causes high relatedness among group members, which predisposes some individuals to forgo their own reproduction and help others to reproduce. This hypothesis for the association between monogamy and social group formation must be incomplete, however, because there are monogamous social groups composed of non-relatives in many taxa [28,69–71]. Here, we show that, at least for *A. percula*, resource

limitation and the threat of eviction can explain why some individuals forgo reproduction, leading to the formation of monogamous social groups. Under this scenario, reproductive competition and the threat of eviction cause some individuals to forgo their own reproduction, and a social group composed of a monogamous breeding pair and a small number of non-breeders emerge as a result. In other words, monogamy is not the cause of social group formation, rather it is an emergent by-product of the interactions of individuals.

This study can be considered to provide experimental support for the assumptions of the restraint model of reproductive skew [15]. In the clown anemonefish, breeding resources are limited and the threat of eviction leads to subordinates foregoing reproduction. Furthermore, by comparison with other systems, this study provides support for the idea that specific conditions need to be met for the threat of eviction to be effective [22,23,72,73]. In groups with reproductive competition and the threat of eviction, but where it is hard for dominants to target individuals and sustain evictions, subordinates do not seem to pre-emptively restrain their reproduction or growth, as has been observed for the dwarf mongoose [23] and pink anemonefish (P.M. Buston, T.A. Barbasch and T. Rueger 2017, personal observation). In summary, our study suggests that transactional models might be well suited to explain reproductive skew in some, simple systems (e.g. [13]).

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