Monogamy when there is potential for polygyny: tests of multiple hypotheses in a group-living fish

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Monogamy within social groups where there exists a high potential for polygyny poses a challenge to our understanding of mating system evolution. Specifically, the traditional explanation that monogamy evolves due to wide female dispersion, affording males little opportunity to defend multiple females, cannot apply. Instead, monogamy in groups potentially arises because females compete for breeding resources such as breeding sites, food, and paternal care. We conducted manipulative experiments to determine whether females compete over limiting resources within groups of the obligate coral-dwelling goby, *Paragobiodon xanthosomus* (Gobiidae). Breeding females behaved aggressively toward individuals of their own sex and evicted subordinate females that were large and mature from the group. Experimental removal of nest sites caused breeding partners to breed in alternative nest sites, demonstrating that nest site limitation was not the cause of female competition. Supplemental feeding resulted in an increase in the fecundity of breeding females but no maturation of subordinate females, demonstrating that food-limited female fecundity was a likely cause of female competition. Finally, supplemental feeding of breeding pairs demonstrated that the difference in eggs hatched by fed versus unfed males was less than the difference in eggs laid by fed versus unfed females, suggesting that paternal care limitation might also drive female competition. These results suggest that competition over food and possibly paternal care selects for dominant, breeding females to suppress the maturation of subordinate females to minimize competition. Monogamy in association with group living is therefore likely to have evolved because female competition prevents males from utilizing the potential for polygyny. *Key words:* female competition, food limitation, monogamy, paternal care, reproductive suppression, social group. *[Behav Ecol 19:353–361 (2008)]*

Monogamous mating systems, in which 1 male and female limit the majority of their reproduction with one another, are widespread across a diverse range of animal taxa (Kleiman 1977; Wittenberger and Tilson 1980; Rutberg 1983; Bull 2000; Rahman et al. 2002; Whiteman and Côté 2004b). The occurrence of exclusive relationships involving breeding pairs poses a challenge to our understanding of mating system evolution because 1 sex (usually the male) generally has a higher potential reproductive rate than the other (usually the female) and, hence, should be selected to mate with multiple partners (Clutton-Brock and Vincent 1991; Clutton-Brock and Parker 1992). One of the key hypotheses for monogamy invokes the role of female dispersion and male competition in determining the evolution of mating systems (Emlen and Oring 1977). Specifically, monogamy is expected to occur whenever females are widely distributed such that males are unable to defend multiple females from other males (i.e., when the environmental potential for polygyny [EPP] is low). Conversely, polygynous mating systems are expected to occur whenever females are spatially clumped allowing males to defend multiple females from other males (i.e., when the EPP is high) (Emlen and Oring 1977; Kleimann 1977; Clutton-Brock 1989).

In some cases, however, monogamy occurs despite the availability of multiple unrelated females within the same territory (e.g., Lillandt et al. 2003; Stiver et al. 2005). A possible alternative hypothesis that could explain monogamy in such groups invokes the role of female competition over limiting resources (Wasser and Barash 1983; Warner 1990; Ahnesjö et al. 1993; Berglund et al. 1993; Henson and Warner 1997). Within groups, females are typically organized into hierarchies in which dominant females gain a larger share of available resources than their subordinates (e.g., Frank 1986; Forrester 1991; Webster and Hixon 2000; Wittig and Boesch 2003; Whiteman and Côté 2004b). If resources critical for female reproduction are limited, dominant females are likely to benefit by preventing subordinates from reproducing because this would ensure they maintain sole access to breeding resources and thereby maximize their reproductive success (Wasser and Barash 1983). Because the reproduction of all female group members besides the most dominant female would be suppressed, males would be constrained to monogamy despite the presence of additional females within the group and thus a high EPP.

Monogamy could arise in response to female competition over 3 potentially limiting resources for breeding. First, the reproductive success of females may be limited by a shortage of suitable breeding sites with which to successfully rear offspring (e.g., Leffelaar and Robertson 1985; Newton 1994; Borg et al. 2002; Kokko et al. 2004). Second, the reproductive success of females may be limited by the availability of food resources necessary to produce or feed offspring (Wasser and Barash 1983; Berglund et al. 1993; Clutton-Brock et al. 1998; Ali and Wootton 1999). Third, if paternal care is limiting such that there are constraints on the number of offspring a male can care for simultaneously, and a single female can produce all the

offspring that a male can care for at a given time, females may compete over male care of offspring (Kuwamura et al. 1993). If any of these resources are limiting, dominant females are likely to benefit from suppressing the reproduction of their subordinates because this would minimize competition over resources and maximize their reproductive success (Wasser and Barash 1983; Clutton-Brock and Albon 1985; Woodroffe and MacDonald 1995). Despite the potential for each factor to limit female reproduction, there has yet to be an experimental verification of their relative contributions to the occurrence of female competition in group-living, monogamous animals.

Monogamy is particularly widespread in coral reef fishes that reside solely within small patches of coral or reef habitat (*Amphiprion* spp., e.g., Fricke and Fricke 1977; Buston 2003; *Caracanthus* spp., Wong et al. 2005; *Cirrhites* spp., Donaldson 1989; *Dascyllus* spp., Fricke 1980; *Gobiodon* spp., Cole and Hoese 2001; Thompson et al. 2007; *Paragobiodon* spp., Lassig 1976; Kuwamura et al. 1993). Such habitat-specialist reef fish are characterized by small body size, extreme site attachment to discrete habitat patches that provide access to food and breeding sites, and, in most cases, a demersal spawning mode where eggs are laid onto nests within the habitat patch and are cared for by the breeding male (Munday and Jones 1998). In some of these species, monogamy conforms to the EPP model because the social and mating system shifts from pairs and monogamy in small habitat patches to groups and polygyny in large patches (Fricke 1980; Donaldson 1989; Whiteman and Côté 2004b; Wong et al. 2005). In other species, however, monogamy is the rule even when groups are large and the EPP high (*Gobiodon* spp., Thompson et al. 2007; *Paragobiodon* spp., Lassig 1976, 1977; Kuwamura et al. 1993). It is possible that monogamy in these species could instead have arisen and be maintained due to female competition over limiting resources for breeding.

Here we investigate the occurrence and causes of female competition in the coral goby, *Paragobiodon xanthosomus* (Gobiidae) (see online Supplementary Material). This small (<40 mm standard length [SL]), site-attached goby resides specifically in 1 species of host coral, *Seriatopora hystrix* (Pocilloporidae). Social groups always consist of 1 large male and female (dominant breeders) that breed monogamously with each other (Wong et al. 2007). All other group members are smaller, nonbreeding females (subordinate nonbreeders) that are organized into a size-based dominance hierarchy (Wong et al. 2007). Although *P. xanthosomus* never exhibits polygyny (i.e., it is obligately monogamous), it has the potential to exhibit to polygyny because 1) females are spatially clustered within coral colonies, 2) subordinate females, particularly the high-ranking ones, are of reproductive size and thus capable of reproducing (Wong MYL, in preparation), and 3) the top-ranked subordinate female matures rapidly on removal of the breeding female, suggesting that the reproductive status of subordinates is not ontogenetically but socially constrained (Wong MYL 2007). *Paragobiodon xanthosomus* is also a protogynous hermaphrodite—if the male of a group dies, the breeding female changes sex to become the breeding male and the top-ranked subordinate female becomes the dominant, breeding female (Lassig 1977). Individuals do not forage outside the confines of their coral colony (Lassig 1976) and have only been observed to consume food items that drift through the coral (Wong MYL, personal observation). *Paragobiodon xanthosomus* spawns demersal eggs within the coral onto a nest site with the breeding male providing the vast majority of parental care (Lassig 1977). As a result, females could potentially be subject to limiting sources of breeding sites, food, and paternal egg care.

To determine whether females compete over limiting resources for breeding, we began by assessing the aggressive responses of breeding partners to intruders of different sex, size, and reproductive status to determine whether females compete with other females. If females compete mostly with other females, breeding females were predicted to exhibit agonistic behavior more frequently toward other females compared with males. Additionally, we hypothesized that breeding females employ an eviction strategy whereby they evict subordinate females that represent a threat as resource competitors and tolerate those that pose no threat. If so, we predicted that breeding females would evict subordinate females that are large and mature more frequently than subordinates that are small and immature because the former pose of a greater threat as resource competitors.

We then conducted experimental manipulations of the resources potentially limiting the reproduction of females. Specifically, we tested the hypotheses that 1) nest site limitation, 2) food limitation, and 3) paternal care limitation were responsible for female competition within groups of *P. xanthosomus*. If nest sites are limiting, nest site removal was predicted to result in the complete cessation of reproductive activity within the group. If nest sites are not limiting, pairs were predicted to commence breeding on a new nest site elsewhere in the coral colony. If food limits female fecundity and, hence, promotes female competition, supplemental feeding of dominant, breeding females was predicted to result in an increase in the number of eggs they lay. Additionally, we considered an alternative mechanism whereby subordinates are simply unable to mature because they are out-competed over food by the dominant female. If so, then feeding subordinates an excess amount of food should result in their maturation. Finally, if male care is limiting, supplemental feeding should result in a significant increase in the clutch sizes laid by fed versus unfed females (assuming that fecundity is food limited) but no significant increase in the clutch sizes hatched by fed versus unfed males. This would suggest that males are unable to care for the additional eggs expected to be laid by well-fed females. This study thereby addresses the factors promoting female competition within groups to provide an insight into the occurrence of monogamy in *P. xanthosomus*.

MATERIALS AND METHODS

General methods

The study was conducted at Lizard Island (14°40′S, 145°28′E) on the northern Great Barrier Reef, Australia, between March 2004 and November 2005. All field activities were conducted in the Lizard Island lagoon and laboratory experiments conducted using the aquarium facilities at the Lizard Island Research Station. Corals and their resident gobies were collected from the reef by picking them up from the substrate on snorkel and transferring them back to the boat. Colonies of *S. hystrix* are attached to loose rubble allowing easy collection. Gobies never departed from corals during collection, preferring to hide within the depths of the coral during transportation (Wong MYL, personal observation). Corals were transported to the laboratory and each placed into separate aquaria (39 × 30 × 29 cm) filled with continuously running fresh seawater. All aquaria were situated outside under a Perspex roof ensuring a natural light/dark regime, with a temperature of between 26 and 29 °C depending on the ambient ocean temperature. Gobies were caught by removing their coral from the aquarium and inverting it to allow gobies to dropout into the aquarium. Gobies were collected using a hand net and the coral placed back into its aquarium. There were no adverse transport- or aquarium-related effects on corals or gobies (Wong MYL, personal observation), and all corals and gobies were returned to their original collection site on completion of experiments. All field observations and experiments were conducted using self-contained underwater

breathing apparatus (SCUBA). Individual fish were never reused for separate experiments.

Intrasexual aggression

In the first experiment, breeding partners were presented with conspecifics of the same and opposite sex to determine whether breeding females exhibit more aggression toward individuals of the same rather than opposite sex. Five coral colonies each containing a pair of gobies (i.e., a breeding male and female only) were collected and each placed into a separate aquarium. Gobies were anesthetized by placing them into a small beaker containing a clove oil solution (Munday and Wilson 1997). Each individual was measured (SL $\pm$ 0.1 mm) using calipers and sexed under a dissecting microscope by the shape of their genital papilla—males have a long, conical papilla and females have a short, blunt papilla (Lassig 1977). Individuals were tagged by injecting a small drop of fluorescent elastomer (Northwest Technologies Inc., Shaw Island, WA) into the dorsal musculature. These tags have no adverse effects on growth or survival (Malone et al. 1999). Different colored tags were used for males and females so they could be visually distinguished. Breeding pairs were then placed back onto their original corals and were left to acclimatize in aquaria overnight. The following day, 5 additional gobies were collected from the reef and returned to the laboratory where they were sexed and tagged. At the start of an aggression trial, 1 goby (intruder) was randomly selected, sexed, and placed into a transparent plastic tube (5 $\times$ 3 cm) covered at both ends with cloth gauze. The gauze allowed for the circulation of any chemical cues that may be used by individuals to determine sex. The tube was then placed directly on top of 1 of the experimental coral colonies such that it was at an equal distance between the breeding male and female. Trials commenced as soon as 1 resident partner approached the intruder and each trial lasted for 10 min. During a trial, the frequency of aggressive displays by both partners toward the intruder was recorded. Aggressive displays consist of a direct approach by 1 individual to another while maintaining a head-on or side-on profile and erected fins (Lassig 1976). On completion of a trial, the tube was removed from the coral and the intruder released back onto the reef. Intruders were never used for more than 1 trial. The remaining 4 intruders were randomly presented to the remaining 4 breeding pairs using the same method. The next day, 5 new intruders were collected from the reef and the entire process was repeated until each breeding pair had been tested against a male and female intruder. Therefore, only 1 trial was conducted per pair per day. Additional intruders were collected for testing if there were insufficient intruders of a particular sex to enable testing of all 5 breeding pairs against both an intruder male and female.

In the second experiment, we assessed whether breeding females evicted subordinate females that were large and mature from groups. Thirteen coral colonies each containing 5 group members (i.e., a breeding pair and 3 subordinate females) were collected, and each was placed into a separate aquarium. The rank 3 female (largest subordinate female) was experimentally removed from these groups and was replaced with another female that was 1) immature and the same size as the previous rank 3, 2) immature and larger than the previous rank 3 (but smaller than the breeding female), 3) mature and the same size as the previous rank 3, or 4) mature and larger than the previous rank 3 (but smaller than the breeding female). The order in which the 4 different classes of intruder were presented was random for each group. The responses of the breeding female toward the new rank 3 were observed for 15 min immediately after the new fish was introduced, during which time the new rank 3 was either evicted or tolerated in the group. Evictions were scored when the new

rank 3 was chased out of the coral and entered the dead coral base or the side or bottom of the aquaria (Wong et al. 2007). Groups were left overnight, and the outcome was rescored the following day to ensure the stability of the result (namely eviction vs. coexistence within the group). A previous pilot study indicated that the occurrence of eviction versus coexistence under aquarium conditions is stable after a 24-h period, that is, after this period, an evicted subordinate is unlikely to reenter the group and, conversely, a subordinate that is not evicted is unlikely to be subsequently evicted from the group (Wong MYL, unpublished data). The rescored outcome was used as the outcome for statistical analysis.

Nest site limitation

To determine if nest sites within coral colonies are limiting, 7 coral colonies each containing between 3 and 11 gobies were randomly located on the reef. Each coral colony was observed for 5 min to determine the position of the established nest site and confirm that only 1 nest site was present. Nest sites are characterized by a small patch of algae at the base of a coral branch on which eggs are laid (Lassig 1977). The coral branch on which the nest was located was removed by positioning a screwdriver at the base of the branch and gently tapping the screwdriver with a small hammer. This resulted in a clean break of the particular branch and minimal damage to the rest of the coral. The broken branch with attached egg clutch was removed from the coral and preserved in 70% ethanol. After 2 weeks, each group from which the nest site had been removed was surveyed, and the occurrence of reproductive behavior and the presence of any new nest sites were recorded.

Food limitation

A supplemental feeding experiment was used to test whether the fecundity of the breeding female in groups was food limited. Sixteen coral colonies each containing a pair of gobies (i.e., the breeding male and female only) were collected and placed in a row approximately 2 m from the edge of the reef at 3-m intervals from each other. Each coral colony was uniquely tagged by affixing a numbered cable tie around its base. Pairs were removed from each coral, anesthetized, measured, sexed, and tagged as previously described. Gobies were returned to their original corals on the reef and left undisturbed for 2 days.

Eight of the 16 pairs were randomly assigned to the control treatment ("unfed" pairs) and the remaining 8 pairs to the supplemental feeding treatment ("fed" pairs) (Figure 1—treatments A and B, respectively). Pairs in the supplemental feeding treatment were fed high nutrient commercial fish pellets twice daily (INVE NRD pellets, size 5/8). Food pellets were discharged into each coral by expelling them from a 60-ml syringe, ensuring an excess of pellets. Pellets were trapped in the coral by the coral polyps that ensured that they were retained in the coral. Observations of feeding behavior for each pair were made following feeding to confirm that they were consuming the pellets. Pairs were fed in this way for 3 weeks.

To compare female fecundity in the unfed and fed pairs, the first new egg clutch laid by each pair was collected within 24 h of the eggs being laid at the end of the feeding period. Eggs are white (day 1), turning gray (days 2–3), black (days 3–4), and finally black and silver (days 4–5) whereon hatching occurs (Wong MYL, personal observation). This developmental progression enabled us to determine with accuracy whether egg clutches had just been laid. Egg clutches were collected as described in the Nest site limitation. All gobies were also collected, their body size remeasured, and then released back onto their corals. Egg clutches were placed in vials filled with 70% ethanol and photographed using a digital
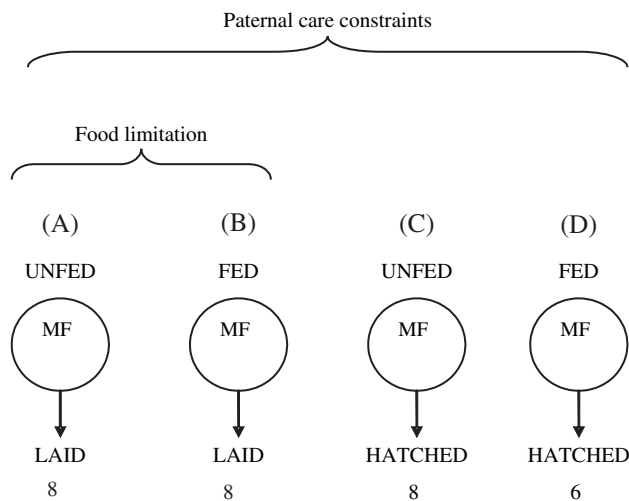
Figure 1
Experimental setup for the food limitation and paternal care constraints experiments. Treatments A and B were used to test whether the fecundity of the breeding female was food limited. Treatments C and D were used to test whether males were capable of caring for an enlarged clutch. Round circles represent coral colonies. M, breeding male; F, breeding female. Numbers under each treatment represent the sample size of pairs per treatment.

camera from which clutch size was determined by counting the number of eggs on the digital image.

In a second feeding experiment, we tested whether supplemental feeding would result in the maturation and breeding of subordinate females. Ten coral colonies each containing 5 group members (i.e., breeding pair plus 3 subordinate females) were collected from the reef and each placed into a separate aquarium. Gobies from each group were removed, anesthetized, measured, sexed, and tagged as previously described and placed back into their original coral colony. Five groups were randomly assigned to the supplemental feeding treatment. These groups were fed twice daily with pellets for 3 weeks. During each feeding bout, food pellets were dispensed over the entire coral such that there was an excess of food available. All group members were observed for at least 5 min to ensure that subordinates were feeding. The remaining 5 groups did not receive supplemental food. These control groups only had access to natural planktonic food arriving in the flow of seawater to their aquaria.

On completion of the experiment, all group members were collected, remeasured, and euthanased with an overdose of clove oil. To assess maturation status, gonads were dissected from the body of each fish and fixed in vials containing FAACC (4% formaldehyde, 5% acetic acid, and 1.3% calcium chloride) for 7 days and then transferred and stored in 70% ethanol. Whole gonads were embedded in paraffin wax, transverse sections made at 5 μm using a rotary microtome, mounted onto glass slides, and stained with Mayer's alum hemotoxylin and Young's eosin–erythrosin. Sections were viewed by light microscopy. In females, germ cells were categorized into the following 5 stages based on descriptions by West (1990): 1) chromatin nucleolar, 2) perinucleolar, 3) cortical alveolar, 4) vitellogenic, and 5) ripe. Females with previtellogenic oocytes, that is, stages 1 and 2, were classed as immature and those with developing and vitellogenic oocytes, that is, stages 3, 4, and 5 classed as mature (West 1990).

Paternal care constraints

To determine whether paternal care was limiting, 2 additional experimental treatments were added to the "Food limitation experiment described in the previous section. Fourteen more coral colonies each containing just a breeding pair were collected and placed approximately 2 m from the edge of the reef. Eight of these pairs were randomly assigned to an unfed treatment and the other 6 to a supplemental fed treatment (Figure 1—treatments C and D, respectively). In both these treatments, egg clutches were collected just prior to hatching (days 4–5) instead of on the day after laying as in the other treatments. This enabled us to compare the sizes of clutches laid by females and hatched by males in response to supplemental feeding.
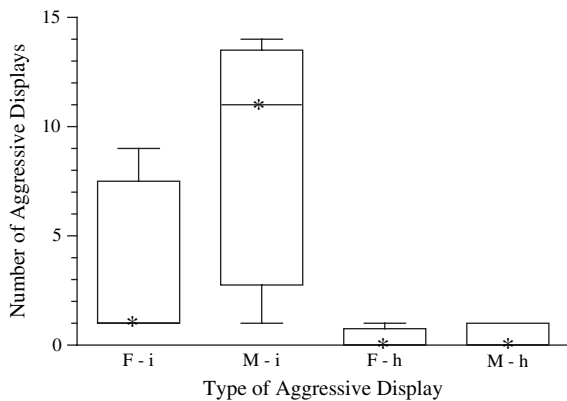
Statistical procedures

We tested whether the distribution of all data was normal using Kolmogorov–Smirnov tests (P values > 0.05) and whether variances were homogeneous using plots of residuals and Levene's tests (P values > 0.05). Nonparametric tests were used in cases where the data violated assumptions of normality and homogeneous variances. The frequency of intrasexual versus heterosexual displays made by males and females was compared using Mann–Whitney U tests. To assess the relative effects of maturity and size on the occurrence of eviction, we conducted a log-linear analysis. A series of models was constructed to test whether the occurrence of eviction was 1) dependent on an interaction between maturity and size, 2) dependent on maturity alone, 3) dependent on size alone, and 4) dependent on maturity and size but not on an interaction between these factors. The method of model constructions follows Munday et al. (2001) where the factors manipulated in the experiment are included in every model, and it is the interaction between these factors and the response variable that is sequentially tested. Models were tested by fitting them in decreasing order of complexity until there was no further significant reduction in the goodness-of-fit statistic (chi-squared value) from one model to the next. By doing so, the simplest model to explain the observed data was found.

A chi-squared test was used to determine whether there were any differences in the number of fed versus unfed subordinate females that had mature oocytes in their gonads. We used a t-test to compare the differences in weight gained by subordinates in fed versus unfed treatments to demonstrate that subordinates in fed treatments actually ate food. To assess whether female fecundity was food limited, we used a general linear model (GLM) with backward stepwise elimination to test the effects of female body size (continuous predictor), feeding (categorical predictor), and an interaction between feeding and body size on the clutch sizes laid by females (response). The predictor variable with the lowest F value and highest nonsignificant P value was removed first from the model. This analysis was conducted because body size is known to influence fecundity in many fish (Bagenal 1967). Similarly, to determine whether male care was limited, we conducted the same analysis but testing the effects of male body size (continuous predictor), feeding (categorical predictor), and an interaction between feeding and body size on clutch sizes hatched by males (response). This analysis was conducted because paternal care ability has often been linked with male size (Kuwamura et al. 1993; Sunobe and Nakazono 1999). Nonsignificant results were analyzed with a power analysis. All statistical analyses were done with STATISTICA v7.

RESULTS

Intrasexual aggression

In the first experiment, breeding females exhibited nearly all their aggressive displays toward intruders of the same sex and rarely displayed to intruders of the opposite sex (Mann–Whitney

Figure 2
Box plot showing number of agonistic displays made by female and male residents toward conspecific intruders of the same (intrasexual) and opposite (heterosexual) sex. F-i, intrasexual aggression by breeding female; M-i = intrasexual aggression by breeding male; F-h, heterosexual aggression by breeding female; M-h, heterosexual aggression by breeding male. Median (asterisk), interquartile range (box) and minimum and maximum values (whiskers) are illustrated.

Figure 3
Percentage frequency of trials in which female intruders were evicted by dominant, breeding females in relation to the reproductive status and size of the female intruders. I, immature female intruder; M, mature female intruder; S, immature female intruder the same size as the previous rank 3 female; L, immature female intruder larger than the previous rank 3 female. Numbers above bars are the total number of trials carried out for each type of subordinate female intruder.

U test: $U = 1.5$, $P = 0.02$; Figure 2). Breeding males also exhibited significantly more aggression toward intruder males compared with intruder females (Mann–Whitney U test: $U = 1.0$, $P = 0.02$; Figure 2).

In the second experiment, all evictions of new subordinates females were carried out by the dominant, breeding female ($n = 24$). Breeding males were never observed to evict intruder females. Both maturity and size significantly affected the frequency with which a rank 3 intruder was evicted (Figure 3). Although eviction was dependent on both maturity and size (Table 1, model 2 provides best and simplest fit to the observed data), removal of maturity resulted in much poorer fit of the model (i.e., a larger differential χ^2 value) than did the removal of size (comparison of models 4 vs. 5: $\chi^2 = 5.53$, degrees of freedom [df] $= 1$, $P < 0.05$). Therefore, the size and especially the reproductive status of subordinate females affect their likelihood of being evicted (Figure 3).
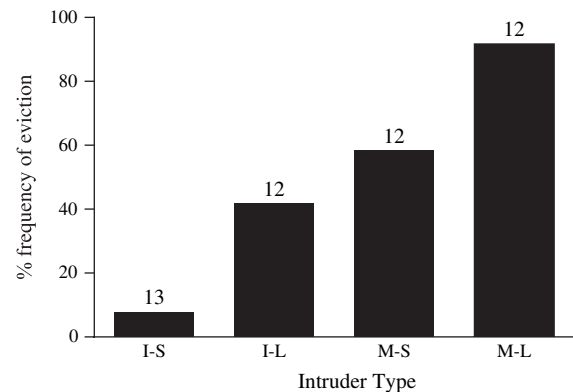
Nest site limitation

In all cases where an existing nest site was removed, a new nest site was established by the breeding male and female within a period of 2 weeks, and eggs were observed on each new nest site.

Food limitation

Clutches laid by females in the fed treatment (mean ± standard error [SE] $= 301.9 \pm 29.4$ eggs) were 48% larger than those in the unfed treatment (mean ± SE $= 204 \pm 22.2$ eggs) (Figure 4). A GLM with backward stepwise elimination revealed that clutch sizes laid by females was significantly affected by feeding ($F = 7.1$, df $= 1,14$, $P = 0.02$) but not female SL ($F = 1.46$, df $= 1,13$, $P = 0.25$). The interaction between feeding and female body size was removed first in the backward elimination process, and before testing each of the main effects separately, because the significance level of the interaction term was highly unstable and found to be driven solely by 1 extreme data point. Removal of this 1 data point in a sensitivity analysis resulted in the interaction term having a lower significance level ($F = 1.3$, df $= 1,12$, $P = 0.27$) than either of the main effects.

Histological examination of subordinate gonads revealed that only 2 of 15 fed and 2 of 15 unfed subordinate females contained any (1–3) maturing oocytes in their gonads. There was no significant difference between the treatments (Chi-squared test: $\chi^2 = 0$, df $= 1$, $P = 1$). Subordinates in fed treatments actually consumed food because the difference in weight gain by subordinates in fed treatments was significantly greater than in unfed treatments (t-test: $t = 6.55$, df $= 28$, $P < 0.001$). There was no breeding or courtship behavior observed between subordinate females and the male during the experimental period. These results suggest that the maturation and breeding of subordinate females is not directly dependent on the availability of food.

Paternal care constraints

Clutches hatched by males in the fed treatment (treatment D) (mean ± SE $= 157.2 \pm 67$ eggs) were 24% larger than males in the unfed treatment (treatment C) (126.1 ± 25.1 eggs) (Figure 4). However, this is only half the magnitude of the increase in clutch sizes laid by females in the fed (treatment B) compared with unfed (treatment A) treatments (i.e., 48%; Figure 4). Backward stepwise elimination revealed no relationship between feeding on clutch sizes hatched ($F = 1.4$, df $= 1,10$, $P = 0.26$), and there was also no interaction between feeding and male body size on clutch sizes hatched ($F = 0.16$, df $= 1,11$, $P = 0.70$). There was, however, a nonsignificant trend toward larger clutch sizes hatched by larger males ($F = 4.3$, df $= 1,12$, $P = 0.06$). These results indicate that fed males did not hatch significantly larger clutches than unfed males even though fed females laid significantly larger clutches than unfed females (Figure 4). However, power to detect a 50% increase in clutch sizes hatched (i.e., the approximate magnitude of the increase in clutch sizes laid by females in fed compared with unfed treatments) was low (post hoc power calculation with $\alpha = 0.05$, $n_{(unfed)} = 8$, $n_{(fed)} = 6$; power $= 0.24$) probably owing to the low sample size of males in the fed treatment (treatment D). This result therefore provides tentative and preliminary support that males are constrained in caring for eggs over and above what a similarly sized female partner would usually lay.

DISCUSSION

Monogamous mating systems in animals are usually thought to occur whenever males are unable to defend more than

Table 1

Log-linear analysis of relationships between intruder maturity and size on the probability of intruder eviction and results of stepwise model testing

Model	Eviction is	χ^2	df	Difference between models	df
1) M × S × E	Dependent on an interaction between M and S	0.00NS		1 and 2; 0.003NS	1
2) M × S + M × E + S × E	Dependent on both M and S	0.003NS	1	2 and 3; 6.926**	1
3) M × S + M × E	Dependent on M alone	6.93*	2	3 and 5; 12.26***	1
4) M × S + S × E	Dependent on S alone	13.66***	2	4 and 5; 5.53*	1
5) M × S + E	Independent of M and S	19.19***	3		

M, maturity (immature or mature); S, size (smaller or larger than original rank 3); E, eviction (evicted or not evicted); NS, nonsignificant.
The best fitting model is underlined.
*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

1 female from other males due to a low EPP (Emlen and Oring 1977). However, an alternative explanation is required for species such as *P. xanthosomus* where monogamy occurs despite the presence of multiple females within groups. Patterns of intrasexual aggression found in this study suggest that females compete with other females within social groups for limiting resources. In general, females are expected to compete with each other due to a limitation of essential resources for breeding (Wasser and Barash 1983). However, the particular resources responsible for limiting the reproductive success of females and thus promoting female competition within groups have often proved difficult to distinguish (e.g., Leffelaar and Robertson 1985; Breiehagen and Slagsvold 1988; Martin et al. 1990), and experimental tests are lacking in monogamous animals.

Results from resource manipulations in this study indicate that nest sites were abundant within the coral, and thus, females were unlikely to be competing over them. The availability of alternative, suitable nest sites is consistent with other studies on monogamous marine gobies that have demonstrated an abundance of nest sites (*Elacatinus evelynae*, Whiteman and Côté 2003; *Gobiosoma evelynae*, Harding et al. 2003; *Valenciennea strigata*, Reavis and Barlow 1998). The size of individual nests has been found to limit the extent of polygyny in the sand goby, *Pomatoschistus minutus*, because males given large nests were able to mate with and care for the egg clutches of more females than males with small nests (Lindström and Seppä 1996). Although we did not test the effects of nest size, it is unlikely that nest size limitation would apply to *P. xanthosomus* because males create nest sites themselves by removing coral tissue from the base of a branch (Lassig 1976) and do not have

to rely on any preexisting substrate that may potentially constrain nest size. The abundance of nest sites therefore indicates that females are not competing over limiting breeding sites.

The positive effect of feeding on female fecundity suggests that female fecundity is food limited and a source of female competition within groups. Given that subordinates fed an excess amount of food for 3 weeks did not mature and breed in this study and that subordinates have the capacity to mature within 2 weeks on removal of the breeding female (Wong et al. 2007), this result suggests that breeding females are suppressing the reproductive status of subordinates in response to food-limited fecundity, as opposed to subordinate reproductive status being simply a product of limited food availability due to competitive exclusion by dominants. It may be expected that if food-limited female fecundity was responsible for reproductive suppression, then the removal of food-limited fecundity to dominants (through feeding) would cause the removal of behavioral suppression and thus lead to subordinate maturation. However, it is unlikely that such a direct link could be experimentally demonstrated because food limitation is likely to have been a continual constraint on the reproductive output of females, resulting in weak selection on dominant females to modify their propensity to suppress the reproduction of subordinates in response to present-day variation in food availability.

Food-limited reproductive success of dominant females as an underlying cause of subordinate reproductive suppression has also been implicated for other social animals (Wasser and Barash 1983; Clutton-Brock and Albon 1985; Woodroffe and MacDonald 1995; Clutton-Brock et al. 1998). For example, dominant females of the cooperative breeding meerkat (*Suricata suricatta*) are known to suppress the reproduction of subordinate females particularly in years when food abundance is low (Clutton-Brock et al. 2001). In addition, Woodroffe and MacDonald (1995) demonstrated that the average number of breeding females within social groups of the European badger, *Meles meles*, declined as the availability of food declined across Britain. This was attributed to an increasing occurrence of reproductive suppression of subordinates by dominant females in response to increasing food competition.

Supplemental feeding of breeding pairs also suggested that the reproductive output of females may be limited by paternal egg care. Females in fed treatments laid clutches that were 48% larger than in unfed treatments, yet clutches hatched by males in fed treatments were only 24% larger than in unfed treatments, that is, the difference between the clutch size hatched by unfed and fed males was less than the difference in the fecundity between unfed and fed females. Furthermore, the 24% increase in clutch sizes hatched by fed versus unfed males may infact be an overestimation of the ability of
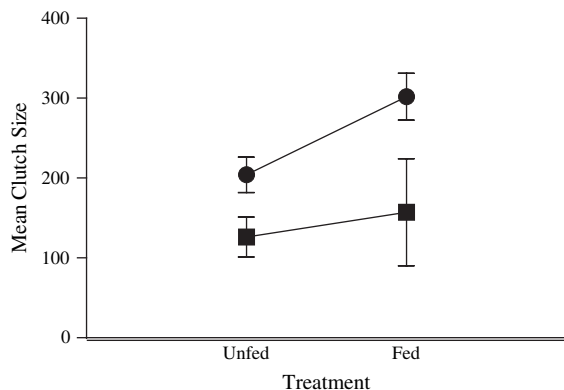

Figure 4
Mean clutch sizes ± SE (number of eggs) laid by females (circles) and hatched by males (squares) in unfed and fed treatments.

males to care for enlarged clutches under natural circumstances because fed males were likely to have had more energy or achieved better physical condition. Given that the feeding experiment was designed to induce similarly sized female partners to lay unnaturally enlarged clutches, this result suggests that males may experience constraints in their ability to care for a clutch of eggs larger than what a similarly sized female partner would usually lay. It also suggests that dominant females are capable of providing males with all the eggs they can successfully care for at a given time. Owing to low power of the experimental effect, this result provides tentative experimental support for the role of limiting paternal care in promoting female competition in *P. xanthosomus*.

Limits on paternal egg care have been invoked in the evolution of monogamy in other marine fishes although the evidence to date is largely indirect and observational. For example, limits on the physical capacity of males to care for multiple clutches has been proposed to explain monogamy in species where males brood eggs in their body (Opistognathidae, Hess 1993; Sygnathidae, Gronell 1984). Although a male's physical dimensions will set an upper limit to the number of eggs they can brood at a given time, it is not yet known whether this upper limit is reached on brooding the clutch of just a single female. Additionally, a positive correlation between male body size and clutch size at hatching in the coral-dwelling goby, *Paragobiodon echinocephalus*, has been interpreted as evidence for paternal care constraints in promoting monogamy (Kuwamura et al. 1993; Whiteman and Côté 2004b). In itself, this result suggests that male care is limited by male size but, without experimental manipulations of clutch size, does not provide direct evidence for the role of paternal care constraints in promoting monogamy. Finally, size-assortative mating and cooperative growth regulation by breeding pairs of another coral-dwelling goby, *Gobiodon histrio*, has been interpreted as evidence for a relationship between size and reproductive success in males as well as females (Munday et al. 2006). Experimental manipulations of the clutch sizes cared for by males in these species are now required to determine how widely paternal care constraints can explain monogamy in animals.

Because we have used an obligately monogamous species, it is not possible to directly determine whether a reduction in resource limitation, and hence female competition, results in a shift from monogamy to polygyny as would be predicted under the female competition hypothesis. What we have demonstrated is that resources critical for female reproduction, namely food and potentially paternal care, are limited and a cause of female competition. This in turn is likely to select for dominant, breeding females to ensure that the reproduction of their subordinates is under some degree of suppression, or else dominant females would not be maximizing their reproductive success. In support of the social suppression of subordinate reproduction by dominants, we have previously shown that subordinate maturation and reproduction is closely tied to the presence or absence of the dominant, breeding female. Specifically, removal of the dominant, breeding female results in the rapid onset of maturation in subordinates, demonstrating that subordinate maturation is under social as opposed to ontogenetic control (Wong et al. 2007). The rapid maturation of subordinates in response to the removal of breeding females, as well as subordinate females being of reproductive size (Wong MYL, in preparation), also emphasizes that these females have the capacity to reproduce despite being nonbreeding subordinates within the group. Combined with the fact that females are spatially clumped within corals, there clearly exists the potential for polygyny to occur within groups. Thus, although we cannot provide evidence for a direct link between resource limitation and female competition all the way through to the resulting mating system, our results do indicate that female competition over limiting resources could play an important role in preventing the utilization of the potential for polygyny in *P. xanthosomus*.

By what mechanisms would breeding females suppress the reproduction of subordinates in *P. xanthosomus*? In this study, breeding females directed almost all their aggression toward intruder females as opposed to males, suggesting that stress-related suppression as a result of direct aggression could be one such mechanism (e.g., Sohn 1977; Borowsky 1978; Faulkes and Bennet 2001; Young et al. 2006). In addition, breeding females evicted intruder females that were, in order of increasing severity, large, mature, and both large and mature. The likely benefit of evicting large and mature subordinates is a reduced likelihood of successful subordinate challenge over limiting resources and social rank (Bernardo 1993; Wong et al. 2007). Given, 1) the absence of subordinates that are mature and/or of similar size to the breeding female in natural groups (Wong et al. 2007), 2) the occurrence of subordinate eviction in direct proportion to the threat posed to breeding females (Wong et al. 2007; current study), and 3) the high costs of being evicted from a group (Lassig 1981; Munday 2002), it is likely that breeding females threaten to evict any subordinate that matures or grows too large (Wong et al. 2007) which is subsequently likely to result in death of the subordinate (Lassig 1981). Consequently, subordinates should respond to the threat of eviction by suppressing their own reproductive status and size (Wong et al. 2007). Further support for this hypothesis comes from studies demonstrating that subordinates can regulate their own reproductive status and size in relation to their social environment (e.g., Heg et al. 2004; Hobbs et al. 2004; Buston and Cant 2006; Wong et al. 2007), as well as demonstrations of the links between the threat of eviction and subordinate growth regulation (Wong et al. 2007). Finally, subordinates have also been shown to reduce their own food intake (Yamagishi et al. 1974; Jobling 1985; Koebele 1985) and by doing so regulate their growth, so they avoid conflict with dominants (Wong MYL, in preparation). Further work is now needed to confirm this mechanism of subordinate reproductive suppression.

To conclude, the dispersion of resources and females and, hence, the ability of males to compete over females does not account for the evolution of monogamy in *P. xanthosomus*—this species is monogamous even though individuals form large social groups in which females are spatially clumped and subordinates have the potential to reproduce. Instead, our results suggest that a limitation of food resources and potentially paternal egg care generates competition between females. This, in turn, is likely to select for the suppression of subordinate reproduction by dominants leading to the occurrence of monogamy within groups. More generally, this study demonstrates that female tolerance of reproductive sharing is not an inevitable consequence of spatial aggregation and group living particularly when there is a strong asymmetry in competitive ability. Mating systems within hierarchical societies may more likely reflect the outcome of conflict and interactions within as opposed to between the sexes.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/.

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