

Social Systems in Habitat-Specialist Reef Fishes: Key Concepts in Evolutionary Ecology

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A major focus in evolutionary ecology lies in explaining the evolution and maintenance of social systems. Although most theoretical formulations of social system evolution were initially inspired by studies of birds, mammals, and insects, incorporating a wider taxonomic perspective is important for testing deeply entrenched theory. Here, we review the contribution of studies of habitat-specialist coral reef fishes to our understanding of the evolutionary ecology of animal social systems. These fishes are ecologically similar but display remarkable variation in mating systems, social organization, and sex allocation strategies. By reviewing recent research, we demonstrate their amenability for experimental testing of key concepts in social evolution and for generating novel insights, including the ultimate reasons for female reproductive suppression, group living, and bidirectional sex change. Habitat-specialist reef fishes are a tried and tested group of model organisms for advancing our understanding of the evolution and ecology of social systems in animals.

Keywords: breeding system, social system, coral reef fish, sex change, cooperative breeding

Ever since Darwin proposed his revolutionary concept of evolution by natural selection, researchers have strived to understand the ecology and evolution of phenotypic traits, including individual behavior. Following Tinbergen (1963), investigations pertaining to behavioral evolution have been centered on addressing the ontogeny, mechanisms, maintenance, and origins of behavior. Among the many behaviors to inspire such investigations, the occurrence and diversity of animal social systems have caught the attention of many researchers. *Social systems*, here defined as encompassing the type of mating system, social organization, and sex allocation patterns observed in a given species, have stirred the imagination, because an understanding of why and how animals breed and interact with each other directly translates into individual fitness. Not only that, but the fundamental importance of reproduction for individuals means that the type of social system often influences other attributes, such as population persistence and extinction risks (Plesnar-Bielak et al. 2012). Social system research thereby enables us to determine how and why an individual reproduces in a certain way and sheds light on the functioning of groups and populations as a whole.

At least three key theoretical constructs have been developed to explain social system evolution and variation in animals. The first construct, mating system theory, is intended

to explain which individual mates with which and how many partners an individual mates with, under the assumption that natural selection has shaped the mating patterns of individuals in a way that maximizes their reproductive value. One of the most widely cited and deeply entrenched hypotheses explaining mating system evolution is known as the environmental potential for polygyny model (EPP; Emlen and Oring 1977). The hypothesis is that monogamy will evolve whenever resources and females are widely dispersed. Under these circumstances, males are unable to defend territories that contain multiple females and must therefore make do with monogamy. Conversely, polygyny will evolve whenever resources and females are clumped together. Under these circumstances, males can better defend and mate with multiple females within a territory, leading to polygyny.

The second construct, cooperative breeding theory, has been the linchpin of explanations of why social groups arise in which many group members are nonbreeders, essentially excluded from reproduction (Brown 1974). The conundrum that this theory addresses therefore relates to why nonbreeders tolerate group living rather than dispersing and breeding independently elsewhere. This framework encompasses four main hypotheses for group living by nonbreeders: the nonbreeders remain in groups because of (1) ecological constraints on dispersal (Emlen 1982),

(2) the benefits of remaining in their current group (Stacey and Ligon 1987), (3) kin-selected benefits of remaining in their current group and helping kin (Hamilton 1963), and (4) future direct benefits of remaining in their current group and inheriting the breeding status (Woollfenden and Fitzpatrick 1978). Therefore, cooperative breeding theory incorporates the roles of ecological, genetic, and social factors in compensating subordinates for the costs of missed reproductive opportunities elsewhere.

Finally, the third construct, sex allocation theory, is intended to explain the selective advantages of sex change and when sex change should occur. Without a doubt, the size-advantage hypothesis (SAH), proposed by Ghiselin (1969), has dominated the literature on the evolution of both protogynous (female to male) and protandrous (male to female) sex change. According to this hypothesis, individuals should change sex if reproductive success increases with size more rapidly for one sex than for the other and ultimately links the type of sex change strategy to the mating system (Warner 1988). When the mating system is polygynous, male reproductive success is likely to increase with body size at a steeper rate than female reproductive success does, because larger males can monopolize multiple females. In these situations, a small individual would be better off as a female, and a large individual would be better off as a male, resulting in female to male (protogynous) sex

change (Warner 1988). Conversely, when the mating system is monogamous, female reproductive success increases more rapidly with size than male reproductive success does. Therefore, a small individual would be better off as a male, and a large individual as a female, resulting in male to female (protandrous) sex change (Warner 1988).

In this review, we highlight recent contributions made by one specific group of coral reef fishes—habitat-specialist reef fishes—to testing the robustness of mating system, cooperative breeding, and sex allocation theories. Habitat-specialist reef fish are members of the Pomacentridae (damselfish), Gobiidae (goby), Caracanthidae (coral croucher), and Cirrhitidae (hawkfish) families (figure 1). Individuals of these species are small bodied and well adapted to living within discrete patches of coral, anemones, and sponges. Being habitat specialists, they are highly site attached; have limited mobility; rely on their particular habitat for food, shelter, and breeding sites; and experience high risks of mortality due to predation outside their habitat patch (Lassig 1981, Munday 2002). Mating systems are highly variable both among and within these species, including monogamy (one male mates with one female), harem polygyny (one male mates with several females), and polygynandry (multiple males and females mate with each other) (figure 1). These fishes also exhibit great variability in social organization, including pair and group formation (figure 1),

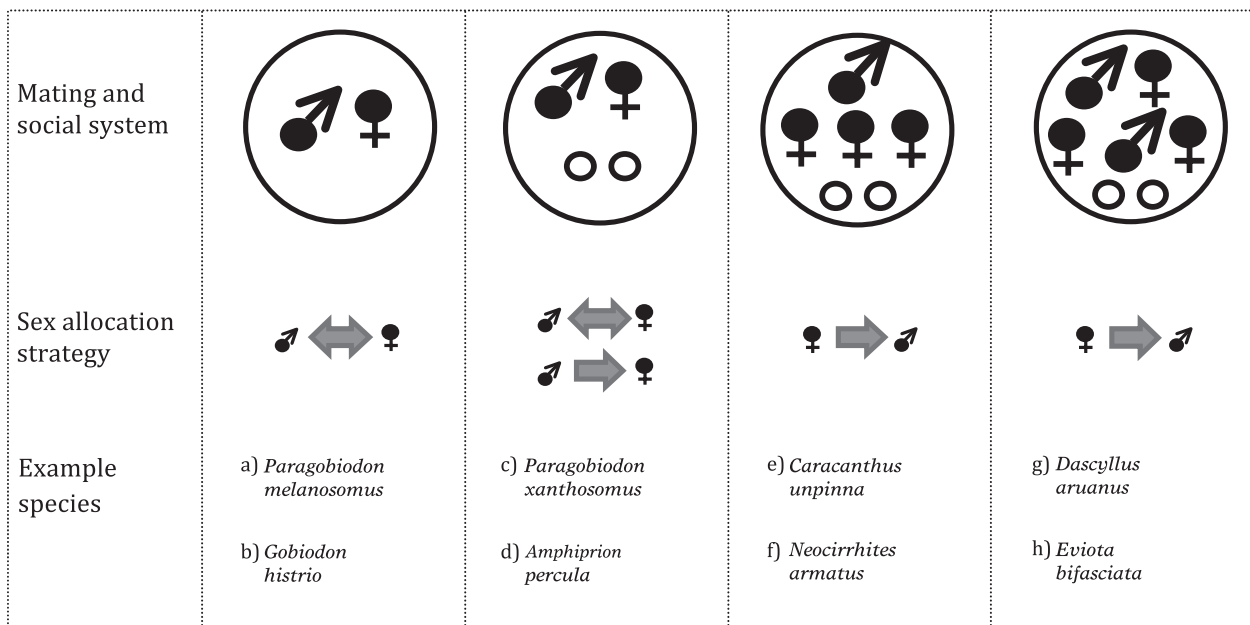


Figure 1. Diversity of mating systems, social organization, and sex allocation strategies in habitat-specialist reef fishes. Some species (a, b) are strictly pair forming and exhibit monogamous mating systems (Lassig 1977, Thompson et al. 2007). Other species (c, d) are group living and exhibit monogamous mating systems (Lassig 1977, Kuwamura et al. 1993, Buston 2003, Mitchell 2003). In other species (e, f), individuals live in groups and exhibit harem polygyny, with one breeder male (♂) mating with multiple breeder females (♀; Donaldson 1989, 1990, Wong et al. 2005). Finally, other species (g) are group living and exhibit multiple monogamous pairs within groups (Thompson et al. 2007) or (h) are group forming but exhibit polygynandry, with multiple breeding males, breeding females, and nonbreeders (the circles; also appearing within other groups) within a group (Cole 2002, Thompson et al. 2007, Wong et al. 2012). See the text for further details.

with group members' being reproductive or nonreproductive depending on the mating system (figure 1). The possible sex allocation strategies are protogyny (female to male), protandry (male to female), and bidirectional sex change

(figure 1). This behavioral variability despite the relative ecological similarity of these species presents a unique opportunity to test the various hypotheses for the evolution of different social systems.

In addition to social system variability, there are at least three logistical reasons why habitat-specialist fishes are particularly tractable for testing theories of social evolution. First, the characteristics of the habitat in which these fishes reside can be easily manipulated. Given that these habitats occur as discrete patches (figure 2a) and that there is considerable natural variation in the size of habitat patches on a reef (Thompson et al. 2007), quantifying the extent of ecological variation in habitat characteristics and how it affects social behavior becomes a straightforward task of measuring the various dimensions and parameters of these habitat patches (e.g., Kuwamura et al. 1994, Munday et al. 2006, Thompson et al. 2007). Furthermore, because these patches are often not firmly attached to the reef pavement, some species can be easily collected and brought back to the laboratory for more detailed behavioral experiments (figure 2b) or collected and repositioned in the field to be included in larger-scale ecological experiments (e.g., Wong 2010).

The second important attribute is the site-attached nature of these species. When habitat patches such as coral colonies are collected and moved, the fish within these habitats will usually hunker down in the coral rather than leaving and swimming to a different shelter. This means that one can manipulate their social characteristics, such as group size, in the field and can expect to return a few weeks or months later to find the same fish that were originally in the habitat (e.g., Kuwamura et al. 1994, Buston 2003, Wong et al. 2007). Individuals can also be identified on the basis of natural color variations or by tagging them with fluorescent elastomer injected just under the skin (Malone et al. 1999), further facilitating the monitoring of individuals within groups and over time, which is important for behavioral and survival measurements. Another

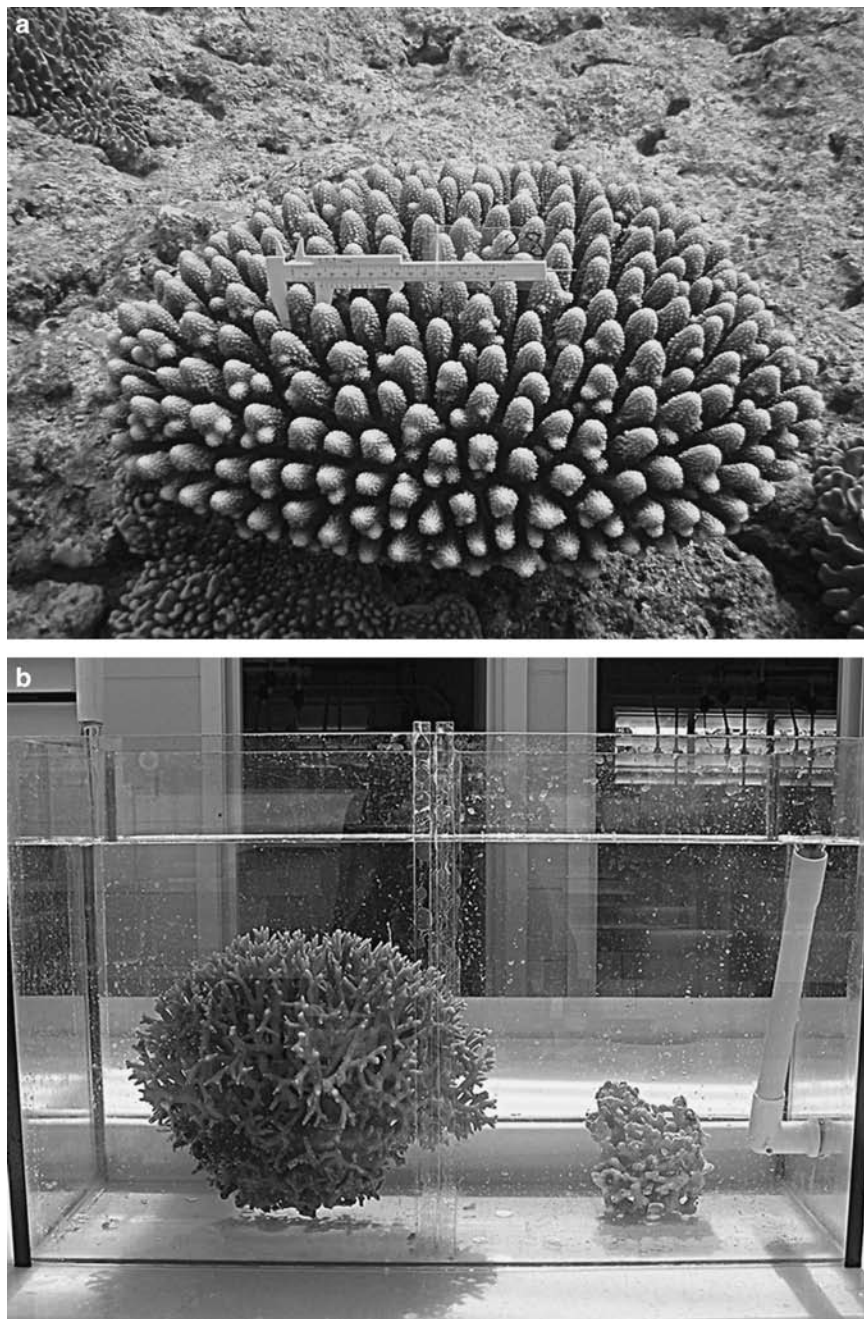


Figure 2. Habitat patches in which habitat-specialist reef fish species reside. (a) A coral colony (Acroporidae) in which *Caracanthus unipinna* (Caracanthidae) resides (Wong et al. 2005). Photograph: Philip L. Munday. Coral colonies represent discrete and spatially isolated clusters of habitat, which facilitates locating, monitoring, and collecting individual fish. (b) A coral colony (Pocilloporidae) in which *Paragobiodon xanthosomus* (Gobiidae) resides (Wong et al. 2007). Coral colonies can be transported and kept in aquariums, allowing more detailed behavioral observations and experiments to be conducted. Photograph: Marian Y. L. Wong.

important feature of individuals is that they can be easily sexed by the shape of their genital papilla, which is helpful for the determination of mating systems, reproductive status, and patterns of sex change (Kuwamura et al. 1994, Nakashima et al. 1996).

The third important attribute is the reproductive or spawning mode of these fishes. Pelagic spawning is observed in some families (Cirrihitidae and Caracanthidae; Donaldson 1990, Cole 2003), whereby eggs are broadcast into the water column. However, demersal spawning is observed in many others (Gobiidae and Pomacentridae; Lassig 1977, Kuwamura et al. 1993, Wong et al. 2008, Buston and Elith 2011), whereby eggs are laid onto a substrate (usually within the confines of the habitat patch or nearby) and cared for by the male until they hatch (e.g., Lassig 1976, Kuwamura et al. 1993, Buston 2004, Wong et al. 2012). For these demersal spawners, eggs are easy to collect, which enables the determination of egg and clutch attributes (Wong et al. 2008, Buston and Elith 2011) and the quantification of reproductive shares and success through parentage analysis (Wong et al. 2012).

Tests of key concepts in evolutionary ecology

Habitat-specialist reef fishes have helped inform our understanding of mating system, cooperative breeding, and sex allocation theory. We now review how studies of these species have contributed to testing the robustness of these three concepts and how they have helped generate new insights.

Mating system theory. Habitat-specialist reef fishes are well suited for testing the key prediction of the EPP model—namely, that as resources (and, therefore, females) become clumped in space, the mating system should shift from monogamy to polygyny (Emlen and Oring 1977). Because the habitat patches provide individuals with essential resources (food, shelter, and breeding sites), one would expect small habitats to support only one female and, therefore, to constrain a male to monogamy, whereas one would expect large habitats to support more than one female and, therefore, to allow males to become polygynous. In other words, there should be a positive correlation between the size of the habitat and group size, combined with shifts in the mating system from pair forming and monogamy in small habitats and to group living and polygyny in large habitats. This correlation has been reported for various habitat-specialist fish species (*Dascyllus marginatus*, Fricke 1980; *Neocirrhites armatus*, Donaldson 1989; *Caracanthus unipinna*, Wong et al. 2005; *Eviota bifasciata*, Thompson et al. 2007), and experimental manipulations of habitat size have provided causal support for this relationship (*D. marginatus*, Fricke 1980).

Although the social systems of some habitat-specialist reef fishes clearly conform to the EPP model, in other species, individuals remain stubbornly monogamous, even in social groups (figure 1; *Paragobiodon xanthosomus* and

Paragobiodon echinocephalus, Lassig 1976, Kuwamura et al. 1993; *Amphiprion percula*, Buston 2003; *Bryaninops yongei*, Munday et al. 2002; *Gobiodon okinawae*, Thompson et al. 2007). The males of these species do not become increasingly polygamous, even though group size—and, therefore, the pool of available mates—increases with habitat patch size. At this point, alternative hypotheses need to be invoked to explain monogamy within social groups.

One of the main alternative hypotheses is that sexual conflict, either between members of the opposite sex (intersexual conflict) or between members of the same sex (intrasexual conflict) determines the mating system (Davies 1989, Arnqvist and Rowe 2005, Chapman 2006). Put simply, when the reproductive interests of individuals collide, the resulting mating system reflects the resolution of this conflict. Much of the early work was focused either on the role of male–female conflict (Davies et al. 1996) or on the role of male–male conflict (Clutton-Brock 1989) in determining the mating system. However, the role of female–female conflict was relatively less well explored, particularly in the context of social groups in which female conflict often manifests itself as the suppression of reproduction in subordinate females (Clarke et al. 2001, Young et al. 2006, Heg 2008). Because females require resources for successful reproduction, it is possible that resource limitation underlies female conflict and reproductive suppression within groups (Berglund et al. 1993, Slagsvold and Lifjeld 1994), although experiments demonstrating whether and which resources limit female reproduction—and, therefore, whether resource limitation underlies reproductive suppression and monogamy in groups—have been distinctly lacking in the literature.

Recent work on the coral-dwelling goby *P. xanthosomus* addressed this deficiency and shed new light on the resources underlying female reproductive suppression (Wong et al. 2008). *Paragobiodon xanthosomus* is an obligate coral-dwelling goby (Gobiidae) that resides in just one type of host coral, *Seriatopora hystrix*. Within groups, only the largest male and female breed monogamously with each other (Lassig 1977), and all other group members are non-breeding subordinate females that are reproductively suppressed (Wong et al. 2008). To determine whether resource limitation was the cause of female reproductive suppression, Wong and colleagues (2008) began by identifying three key resources that could affect female reproductive success. First, the reproductive success of females may be limited by a shortage of suitable breeding sites with which to successfully rear offspring, given that *P. xanthosomus* lays eggs in a nest site within the coral colony itself (Lassig 1976). Second, the reproductive success of females may be limited by the availability of food resources necessary to produce or feed offspring, given that female fecundity in fishes is often limited by the abundance of food (Bagenal 1967). Third, because parental care is only provided by the breeding male (Lassig 1977), the reproductive success of females could be limited by paternal care if the males can

successfully care for the eggs laid by only one female at a time (Whiteman and Côté 2004).

To determine whether nest sites were limiting, Wong and colleagues (2008) experimentally removed the existing nest site used by breeding pairs within the coral. In all cases of removal, the pair simply picked another branch and laid their eggs, which suggests that nest sites were not limiting. To determine whether food was limiting, a field experiment was performed in which both males and females in natural pairs were fed by squirting high-protein marine fish pellets into their coral colony using a syringe. After a 3-week feeding period, egg clutches from each pair were collected as soon as they were laid, and clutch sizes were compared between fed and unfed pairs (figure 3a). As was predicted, the females that were fed laid significantly larger clutches than those that were unfed (figure 3b), which suggests that

food was a limiting factor for female reproduction. In the same experiment, Wong and colleagues (2008) also determined whether paternal care was limiting by collecting egg clutches from fed and unfed pairs just prior to hatching (approximately 4–5 days after laying). Since *P. xanthisomus* males provide sole care of eggs, the size of a clutch at hatching essentially reflects the ability of males to care for their eggs. Therefore, if the males in fed pairs did not hatch significantly larger clutches than did the males in unfed pairs, despite the females in the fed pairs' laying larger clutches than those laid by the unfed pairs, this would suggest that males are unable to care for the eggs laid by more than one female under natural circumstances. Indeed, there was no difference in clutch sizes at hatching between the fed and unfed pairs (figure 3b), which indicates that male parental care is another limiting reproductive resource over which females may compete.

In summary, a refined experimental assessment of the benefits of reproductive suppression and monogamy has demonstrated that resource limitation underlies reproductive suppression and female competition. Therefore, habitat-specialist reef fishes have provided an important new insight into mating system theory. Since these experiments, the role of resource limitation has been reported in a social mammal (Nichols et al. 2012), and those results suggested that resource limitation could serve as a widespread explanation for reproductive suppression and the mating systems of social species in general.

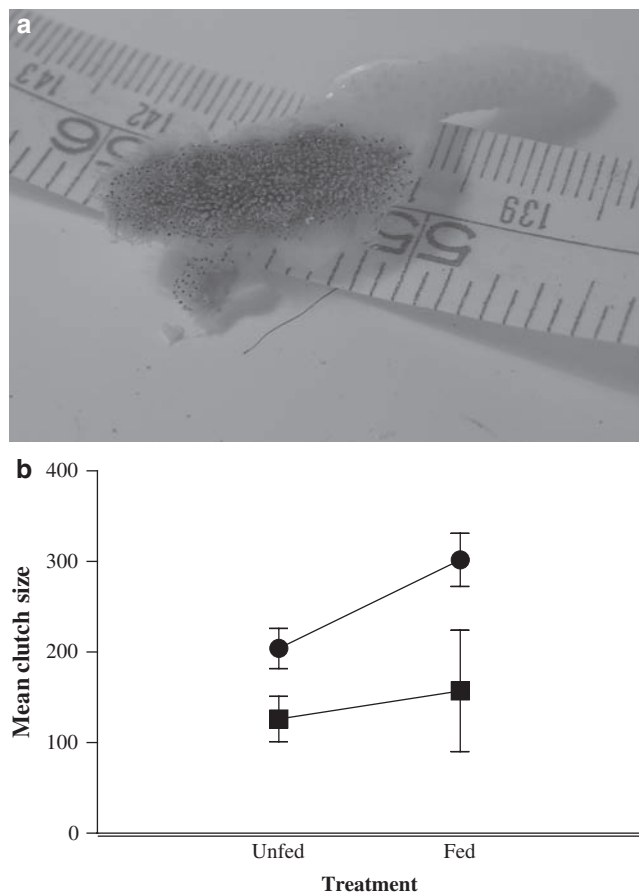


Figure 3. Clutch sizes at laying and hatching of *Paragobiodon xanthisomus* in relation to supplemental feeding. (a) An egg clutch on a coral branch. (b) Average clutch size laid by females (circles) in fed and unfed treatments and the average clutch size hatched by males (squares) in fed and unfed treatments. Both males and females received supplemental food for a period of 3 weeks prior to clutch collection. The error bars represent the standard error. Photograph: Marian Y. L. Wong. Source: Adapted from Wong and colleagues (2008).

Cooperative breeding theory. Habitat-specialist fishes have proven ideal for testing the robustness of cooperative breeding theory, particularly with regard to why subordinates remain in groups as nonbreeders rather than dispersing to breed independently elsewhere. Using the coral-dwelling goby *P. xanthisomus*, Wong (2010) conducted an experiment to test both the ecological constraints and the benefits-of-philopatry hypotheses (Stacey and Ligon 1987, Koenig et al. 1992). The former proposes that habitat saturation and the risks of movement essentially constrain subordinates to living as nonbreeders in groups (Selander 1964, Emlen 1982), whereas the latter proposes that the variation in habitat quality favors subordinates that remain in their current group if the habitat in which they reside is of high quality relative to others in the environment (Woolfenden and Fitzpatrick 1978, Stacey and Ligon 1987).

Wong (2010) set up a cross-factored experimental design, consisting of two levels of habitat saturation (high and low) and two levels of movement risk (short distance and long distance) (figure 4). The corals were left undisturbed for 2 weeks, after which the gobies were collected and the proportion of nonbreeders that had dispersed between corals was quantified for each treatment. As was expected, the subordinates dispersed the most to corals that were of low saturation and did so when the dispersal distance was short (figure 5), which demonstrates that both habitat

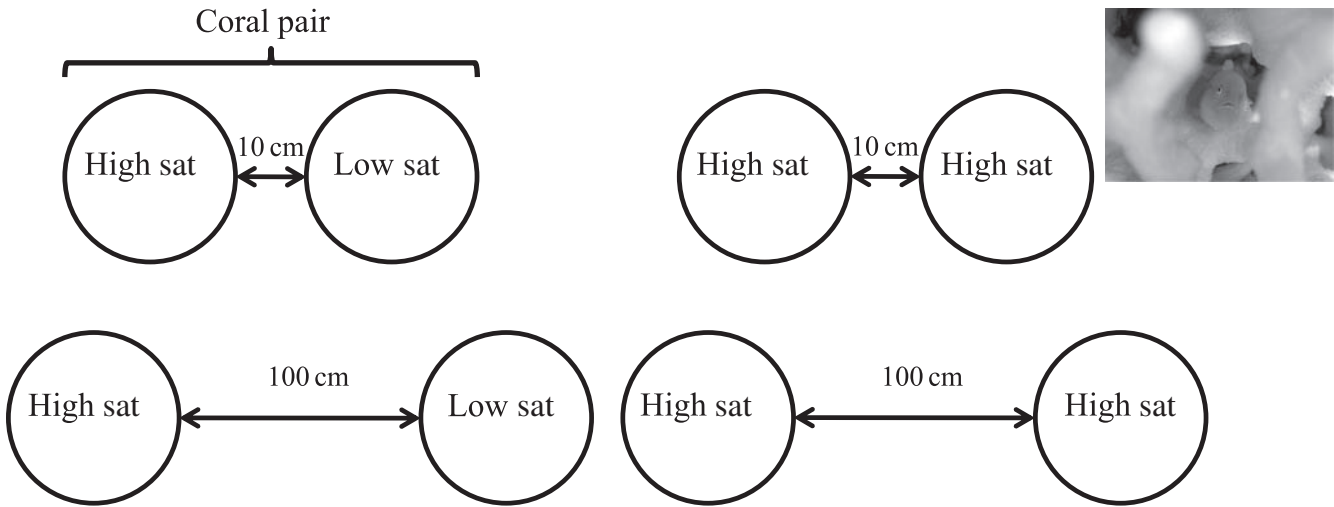


Figure 4. Field experimental test of the role of habitat saturation and the risks of movement on subordinate dispersal. The circles represent coral colonies. The inset shows a goby (*Paragobiodon xanthosomus*), tagged with fluorescent elastomer for individual identification (not visible here). Abbreviations: cm, centimeters; sat, saturation. Photograph: Marian Y. L. Wong. Source: Adapted from Wong (2010).

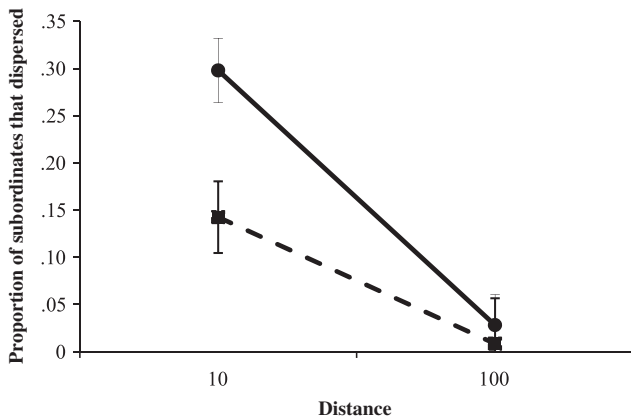


Figure 5. The mean proportions of subordinates that dispersed to another coral that was saturated (squares, dashed line) or unsaturated (circles, solid line), placed 10 or 100 centimeters away from their original coral; the error bars represent the standard error. Source: Adapted from Wong (2010).

saturation and the risks of movement limited subordinate dispersal (Wong 2010).

In a different experiment, Wong (2010) tested the benefits-of-philopatry hypothesis, which states that variation in habitat quality influences subordinate dispersal decisions. Subordinate gobies were therefore given the choice of group living as a nonbreeding subordinate in a large, high-quality coral or becoming a breeder female in a small, low-quality coral (figure 6a). The degree of size difference between the two corals varied, such that the choice of females across a range of coral size ratios (size of the smaller coral divided

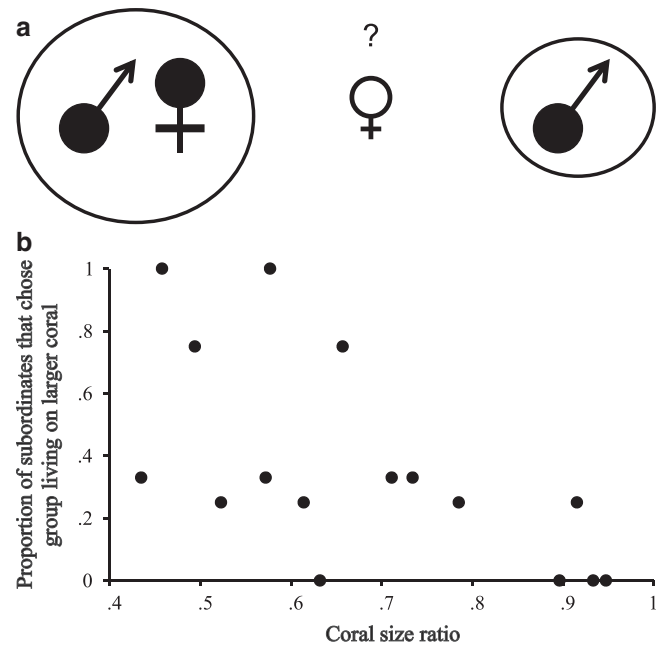


Figure 6. Variation in habitat quality and choice of nonbreeding female. (a) Experimental setup showing a subordinate female (unfilled female symbol) goby (*Paragobiodon xanthosomus*) choosing between nonbreeding status on a large coral (left) and breeding status on a small coral (right). (b) The relationship between the difference in coral size (expressed as the coral size ratio) and the proportion of subordinate females that chose group living as a nonbreeder on the larger of two corals. Source: Adapted from Wong (2010).

by the size of the larger coral) was tested. In support of the benefits-of-philopatry hypothesis, females increasingly settled as nonbreeding group members in the larger coral as the difference in coral sizes increased (figure 6b). In other words, the females avoided the option of immediate reproduction in favor of settling in a larger and therefore higher-quality habitat as a nonbreeder. Therefore, when the quality of available options varies, nonbreeders will trade off breeding for nonbreeding status in a superior habitat.

Besides providing experimental tests of these hypotheses, habitat-specialist fishes have also provided some important new insights into cooperative breeding theory. First, they have helped shift the emphasis away from the indirect benefits of group living (through kin selection) toward the direct benefits of group living. For many years, the role of kin selection in promoting group living and nonbreeding has dominated the literature, mainly because nonbreeding birds, mammals, and especially insects are highly related to their dominant breeding counterparts. For habitat-specialist fishes, however, genetic relatedness is a nonissue, because gametes or larvae are shed into the water column, where they remain for extended periods of time, effectively removing any family cohesion (Buston et al. 2007, 2009). Therefore, habitat-specialist fishes can provide insights into the effects of ecological and social factors on social systems in the absence of any confounding forces of kin selection.

Habitat-specialist reef fishes have also helped shift the emphasis away from the current direct benefits of group living and nonbreeding toward a greater appreciation of the future direct benefits of association. That is, subordinates may opt to remain in groups as nonbreeders because they can eventually inherit the top-ranked breeding position, provided that they survive long enough to do so (Woollfenden and Fitzpatrick 1978, Wiley and Rabenold 1984). Because of the ease with which the social systems of habitat-specialist reef fishes can be manipulated, they are ideal for experimental inductions of rank ascension and breeding-status inheritance (Buston 2004, Wong et al. 2007), through which empiricists can provide rigorous tests of the role of future direct benefits. Although breeding inheritance has been reported in other social animals (e.g., Field et al. 1999, Clarke et al. 2001, East and Hofer 2001), habitat-specialist reef fishes have been unique in demonstrating how this inheritance convention is maintained and, therefore, how groups remain stable over time (Buston 2003, 2004, Buston and Cant 2006, Wong et al. 2007, 2008). Therefore, not only have they enabled us to measure the contribution of one benefit while experimentally or statistically controlling for the effects of others, but they have helped us to advance our understanding of the maintenance of animal societies.

In summary, habitat-specialist reef fishes have been useful models for conducting experimental tests of the key hypotheses of cooperative breeding theory. They have also provided new insights into this theory, demonstrating its potential to explain group living and nonbreeding in species

in which group members are unrelated and in which subordinates can hope to inherit breeding status in the future.

Sex change theory. To make matters more exciting, habitat-specialist fishes have the capacity to change sex over their lifetime, a process otherwise known as *sequential hermaphroditism*. The classic model of sex change, the SAH, predicts that species showing polygyny should exhibit a protogynous sex allocation pattern, whereas those showing monogamy should exhibit a protandrous pattern. Habitat-specialist fishes generally provide support for this model. For example, the coral croucher (*C. unipinna*) exhibits harem polygyny, in which one large male monopolizes multiple smaller females within a coral, and, as was expected, this species shows protogynous sex change (figure 1; Cole 2003, Wong et al. 2005). Similarly, various species of hawkfish (*Cirrhitidae* spp.) show protogynous hermaphroditism in conjunction with a harem mating system (figure 1), although the females may live in separate coral colonies (Sadovy and Donaldson 1995). Conversely, anemonefishes (*Amphiprion* spp.) exhibit monogamous mating systems, in which one large female and a smaller male mate solely with each other and, as was expected, show protandrous sex change (figure 1; Buston 2003).

Besides providing support for the general prediction of the SAH, habitat-specialist fishes have also been useful for verifying the fundamental assumption that there are differences in the rates of increase in reproductive success with size or age between males and females (Warner 1988). Rarely have the exact shapes of the size–fitness curves for males and females been quantified, but this is important for understanding the more intricate aspects of the process of sex change, including the timing of sex change and which individuals within a group change sex (Muñoz and Warner 2004, Kazancıoğlu and Alonzo 2010, Hattori 2012).

To address this issue, size–fitness curves for males and females in the hermaphroditic damselfishes *Dascyllus aruanus* and *A. percula* were recently quantified (figure 1; Buston and Elith 2011, Wong et al. 2012). As was predicted by the SAH, *D. aruanus* is a protogynous hermaphrodite (Cole 2002, Asoh 2003) and exhibits a polygamous mating system (Fricke 1980), whereas *A. percula* is a protandrous hermaphrodite and exhibits a monogamous mating system (Buston 2003). To generate the size–fitness curves of *D. aruanus*, Wong and colleagues (2012) quantified individual reproductive output using a small population of *D. aruanus* located on the reefs surrounding Moorea Island, in French Polynesia. Social groups were monitored during full and new moons, and egg clutches were collected whenever they were laid. After a clutch was collected, each individual group member was captured and measured, and a small fin clip was taken so that parents could later be identified using microsatellite markers. This genetic analysis of parentage enabled the quantification of *reproductive shares* (defined as the proportion of the sampled egg clutch sired or mothered by a particular group member) and *reproductive output*

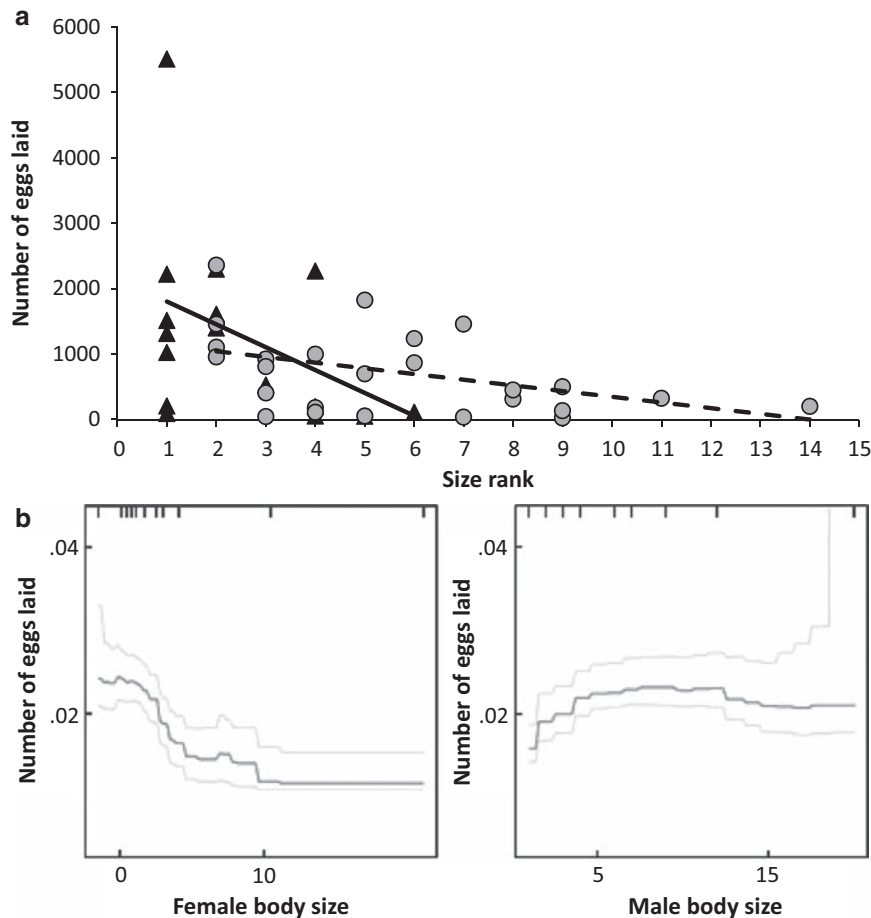


Figure 7. (a) Size–fitness curves for male (triangles, solid line) and female (circles, dashed line) *Dascyllus aruanus*, with size rank based on relative body size. A size rank of 1 represents the largest and most dominant group member, with higher numbers representing declining size and increasing subordination within the group. The number of eggs an individual female contributed to a given clutch, calculated by multiplying the proportional reproductive share of individual females to a given clutch by the total clutch size. Source: Adapted from Wong and colleagues (2012). (b) Size–fitness curve for *Amphiprion percula*. The lefthand graph shows the number of eggs laid as a function of female body size, and the righthand graph shows the number of eggs laid as a function of male body size. The fit lines represent the mean estimate (dark gray) and the 95% confidence intervals (light gray), based on 500 bootstrap replicates. Source: Adapted from Buston and Elith (2011).

(defined as the reproductive share of a particular group member multiplied by the total clutch size) for each breeding group member. As was assumed under the SAH, the size–fitness curve for breeder males was significantly steeper than that for breeder females, regardless of whether fitness was defined as proportional or absolute reproductive output (figure 7a; Wong et al. 2012).

To determine the size–fitness curves for *A. percula*, egg clutches were photographed to determine clutch size, and the body size of all group members was measured (Buston and Elith 2011). Unlike *D. aruanus*, however, a genetic analysis of parentage was not necessary to determine reproductive

shares and output, because *A. percula* is strictly monogamous. As was expected for a protandrous hermaphrodite, a pattern of size–fitness curves opposite that for *D. aruanus* was reported, with the size–fitness curve being steeper for females than for males (figure 7b; Buston and Elith 2011).

Habitat-specialist fishes have therefore proven useful for assessing the predictions and assumptions of the SAH. In addition, the ability to manipulate their social system has proven useful for testing the causes of adaptive variation in the timing of sex change, particularly the role of social context. The SAH, in its basic form, actually predicts one optimal size at sex change at the population level, which is the size at which the fitness curves of males and females intersect (Warner 1988). In reality, the timing of sex change is governed by social conditions at the level of the group, including the relative sizes of group members, the sex ratio of the group, and the local density (for a review, see Munday and colleagues [2006]). For example, protandrous sex change in anemonefishes is triggered by the removal of the large behaviorally dominant female from the group (e.g., Fricke and Fricke 1977) and, therefore, occurs only in response to a change in social context rather than at some invariant size (Munday et al. 2006). Since anemonefishes and other habitat-specialist fishes exhibit strict size hierarchies within groups (Cole 2002, Buston 2003, Wong et al. 2007), although the absolute sizes of fish within these hierarchies vary from group to group (Cole 2002, Asoh 2003, Buston 2003, Hattori 2012), the social control of sex change results in

substantial variation in the timing of sex change and considerable overlap in the size–frequency distributions of males and females in a population (Cole and Hoese 2001, Cole 2002, Wong et al. 2005).

The unique new insight provided by habitat-specialist fishes in relation to sex change is the adaptive significance of bidirectional change. Although bidirectional sex change had been previously reported to occur in invertebrates and other fishes, theoretical explanations were lacking until work was conducted on a distinct set of habitat-specialist reef fishes (Munday et al. 2006). In the 1990s, bidirectional sex change was confirmed in the coral gobies *Gobiodon* spp.

(Nakashima et al. 1996, Munday et al. 1998) and *P. echinocephalus* (Kuwamura et al. 1994). In these species, the mating system is monogamous, and breeders typically reside in pairs within corals (Kuwamura et al. 1994, Nakashima et al. 1996, Munday et al. 1998, Hobbs et al. 2004). Initially, bidirectional sex change was attributed to a growth-rate advantage of females. Because females generally grow faster than males (Kuwamura et al. 1994, Nakashima et al. 1996, Munday 2002), and because it is beneficial for males and females to be of a similar size (Kuwamura et al. 1994, Nakashima et al. 1996, Munday et al. 1998), the smaller individual in a newly formed breeding pair should act as the female, so that it more rapidly catches up to the size of its male mate (Kuwamura et al. 1994, Nakashima et al. 1996). However, not all the predictions of this growth-rate advantage model were borne out under a rigorous experimental assessment of size-related patterns of sex change in the field (Munday 2002). Instead, the fact that gobies have to move between groups following the death of their partner (Kuwamura et al. 1994, Nakashima et al. 1996, Munday et al. 1998) supported an alternative hypothesis—namely, that bidirectional sex change evolved so that individuals could mate with the first partner they encountered, regardless of its sex, and could thereby minimize the need for further risky movement (Munday 2002).

Clearly, the timing of bidirectional sex change is under rigorous social control, because the relative size and sex of a new partner in a monogamous association will determine which individual changes sex and in which direction (Munday 2002, Hobbs et al. 2004). For polygynous habitat-specialist reef fishes, social conditions also influence the occurrence of bidirectional sex change. Recently, the polygynous coral-dwelling hawkfish *Cirrhitichthys falco* (Cirrhitidae) was reported to exhibit protandrous sex change, despite predominant protogyny (Kadota et al. 2012). Protandry occurred when males lost their harem females and a larger neighboring male immigrated into the group, causing the existing male to change sex to become the smaller female. Therefore, bidirectional sex change in these cases is beneficial because it allows males to regain reproductive opportunities as females, despite their having lost the ability to successfully continue competing as a male (Kadota et al. 2012).

Besides the ultimate-cause explanations, habitat-specialist fishes have provided novel insights into the proximate mechanisms underlying bidirectional sex change. By experimentally manipulating levels of estradiol through hormone implantation, Kroon and colleagues (2005) triggered sex change in either direction in the coral goby *Gobiodon erythrospilus*. The important hormonal pathway governing bidirectional sex change turned out to be the aromatase pathway, aromatase being an enzyme that catalyzes the irreversible conversion of testosterone to estradiol. Therefore, when estradiol was implanted, male to female sex change was induced, whereas when an aromatase inhibitor was implanted, female to male sex change was induced (Kroon et al. 2005).

In summary, studies of habitat-specialist fishes have been invaluable for enhancing our understanding of the adaptive significance of sex change and the underlying causes of variation in the timing of sex change. In addition, the discovery of bidirectional sex change in these species has generated important insights into the causes of extreme sexual plasticity, from both ultimate- and proximate-cause perspectives.

Conclusions

Habitat-specialist reef fishes have taught us many things about the evolutionary ecology of mating, social, and sexual systems. Despite their ecological quirkiness, they have been instrumental for testing the generality and robustness of key concepts that are widely applicable to other taxonomic groups. In some cases, they serve as the only examples in which experimental tests of key hypotheses have been performed, owing to the ease with which their habitat and social organization can be manipulated in the lab and in the field. In other cases, these species have provided us with novel insights into the ultimate and proximate causes of social and reproductive behavior. In this way, these species have proven invaluable as model species and should be the focus of future tests of key concepts in evolutionary ecology.

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