

Behavioral differences among mutualist species in a shrimp–goby association

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ABSTRACT: Alpheid shrimps and gobiid fishes engage in a mutualism in which shrimp construct burrows that are co-habited with gobies and used as refuge from predators by both. Gobies act as sentinels for shrimp. In the western Atlantic, different goby species have been hypothesized to have a facultative (*Ctenogobius saepepallens*) and obligate (*Nes longus*) association with the shrimp *Alpheus floridanus*. I compared various behaviors among these 2 gobies and another goby that occasionally associates with shrimp (*Coryphopterus glaucofraenum*). The putatively obligate goby had the greatest preference for shrimp burrows versus other shelters, had the greatest partner fidelity, and facilitated more emergence by shrimp by remaining for longer periods at shrimp burrow entrances. These findings provide evidence that in shrimp–goby mutualism, the more specialized and dependent mutualist gobies provide greater services to their shrimp partners.

KEY WORDS: Mutualism · Coevolution · Obligate · Facultative · Shrimp–goby · *Nes longus* · *Ctenogobius saepepallens*

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INTRODUCTION

Among species that engage in mutualism, a range exists from those completely interdependent (obligate) to those that benefit from each other but are not interdependent (facultative; Boucher et al. 1982, Keeler 1985). Additionally, there are commensal species that benefit but provide no benefit in return. The distinction between these 3 strategies is important to the species that use them and the communities they inhabit. For example, obligate and facultative cleaners clean different sets of client species on coral reefs (Francini-Filho & Sazima 2008). Here, I compare 2 behaviors among a putatively obligate and facultative mutualist as well as a third goby species that occasionally associates with the same shrimp partner species.

The first behavior is the demonstration of preference for the service provided by the partner species.

For example, when ‘cleaners’ remove parasites from larger ‘clients’, the service to clients is the cleaning and the service to cleaners is a meal. However, mutualist species may obtain the same service through other means. For example, many cleaners also eat free-living prey items not associated with clients (Côté 2000). Because the survival of obligate mutualists is linked to their partners, it is expected that they should show a greater preference for the service provided by their partners than facultative mutualists or other species that are occasional associates.

The second behavior is the provisioning of a partner species with services, the quality and quantity of which can vary (Noë & Hammerstein 1995). The attractiveness of a mutualist to its partner is dependent on the quality and/or quantity of the service it provides. For example, clients often avoid cleaners from whom they received a poor cleaning (Bshary & Schäffer 2002). Because obligate mutualists have

greater incentive to attract partners than facultative mutualists or rare associates, obligate mutualists should provide their partner species with services in greater quantity and/or of better quality.

I examined these 2 behaviors in the mutualism between alpheid shrimp and gobiid fishes. In this mutualism, 1 or 2 shrimp construct a burrow in the sand that is cohabited with 1 or 2 goby partners (Karplus & Thompson 2011). Both shrimp and gobies use these burrows as refuge from predators. Shrimp-associated gobies are incapable of burrowing and are quickly eaten when shrimp are absent (Thompson 2005). Alpheid shrimp that associate with gobies have poor vision and are thus susceptible to predation while outside the burrow foraging or maintaining the burrow entrance (Jaafar & Zeng 2012). However, shrimp and gobies have a tactile communication system through which the gobies communicate information on the presence of predators (Preston 1978). Before a shrimp emerges from its burrow and while it is outside the burrow, it places its antennae on its goby partner. If a predator is present, the goby rapidly flutters its caudal fin and, when the predator gets very close, the goby retreats head-first into the burrow. Shrimp return to the burrow (or remain inside the burrow) when either of these behaviors is performed. Shrimp without partners rarely emerge from their burrows (Karplus 1992, Lyons 2012).

The present study focused on 3 goby species in the western Atlantic: orangespotted goby *Nes longus*, dash goby *Ctenogobius saepepallens*, and bridled goby *Coryphopterus glaucofraenum*. All 3 use the burrows of the shrimp *Alpheus floridanus*. Researchers have described orangespotted gobies as obligate mutualists and dash gobies as facultative mutualists, but few studies have examined these associations (Karplus 1992, Randall et al. 2005, Kramer et al. 2009, Lyons 2013). Evidence is based on field observations which indicate that orangespotted gobies are always found in association with shrimp (Karplus 1992, Kramer et al. 2009), while dash gobies are often, but not always so (Kramer et al. 2009). Additionally, an aquarium study demonstrated that orangespotted gobies avoid predators more effectively while using shrimp burrows than do dash gobies (Lyons 2013). Bridled gobies are typically found in areas of sand, seagrass, patch coral, and coral rubble (Forrester & Steele 2004), but have not been previously described as shrimp associates (Randall et al. 2005). I have observed bridled gobies using shrimp burrows, but not communicating with shrimp. However, it is possible that bridled gobies provide some other benefit, and do in fact communicate with

shrimp but have not been observed doing so. I refer to them as 'occasional associates'.

In this study, I conducted a set of experiments to examine 2 predictions based on the degree of association with shrimp (obligate, facultative, and occasional) among the 3 goby species: (1) Orangespotted gobies should have the greatest preference for shrimp burrows versus alternative shelters, followed by dash gobies, and then bridled gobies. (2) Orangespotted gobies should provide the greatest service to shrimp (spend the most time guarding shrimp, switch between shrimp least frequently, and be present at burrows where shrimp emerge most frequently), followed by dash gobies, and then bridled gobies.

MATERIALS AND METHODS

Field sites, collection and maintenance

All experiments and observations were conducted at the Perry Institute for Marine Sciences, Lee Stocking Island, Bahamas during 14 June to 20 July 2008, 15 June to 17 August 2009, and 10 June to 20 August 2010. I used 2 shallow (3 to 5 m depth) field sites: Normans (23°45'35.64' N, 76°7'59.64' W) and Woobie (23°49'4.55' N, 76°11'17.43' W). At both sites, the bottom was comprised of sand and contained burrows of the shrimp and other organisms such as stomatopods, lugworms, and jawfishes; Normans additionally contained coral rubble and seagrasses (Lyons 2012). All 3 goby species were present at Normans; bridled gobies were absent at Woobie.

Gobies and shrimp were collected from Normans following the method of Karplus & Vercheson (1978). All collected gobies and shrimp were either in an association with or in close proximity to individuals of the partner species. Gobies and shrimp were maintained in aquaria and fed food flakes ad libitum.

Resource preference by gobies

A laboratory experiment was designed to test whether gobies preferentially use the burrows of shrimp rather than other shelters. Because gobies and shrimp form associations in aquaria in PVC pipes (Karplus et al. 1972, Jaafar & Hou 2012, Zeng & Jaafar 2012, Lyons 2013), pairs of artificial burrows of white PVC pipe (20 cm long and 2.5 cm inner diameter) were placed at opposite ends of 190 l aquaria (119 × 30.5 × 48.5 cm). The diameter of these burrows was similar to the size of actual shrimp burrows, but

the length was shorter due to restrictions imposed by the size of the aquaria (Dworschak & Ott 1993). The PVC pipes were dug into the sand at a 40° angle such that they barely protruded from the sand and were partially filled with sand. A shrimp was placed in one PVC pipe and the other was left empty.

I placed individual gobies midway between the paired burrows and checked their location every 5 min until they were found in one of the 2 PVC pipes. I tested 45 individuals of each goby species that were 35 to 50 mm total length. I analyzed the data using a 3×2 G-test with goby species as the independent variable and choice (shrimp burrow or empty burrow) as the dependent variable. Comparisons of each goby species to the null expectation (shrimp burrow chosen 50% of the time) were conducted using a goodness-of-fit test with the appropriate Bonferroni probability correction (Sokal & Rohlf 1994).

Time budget of gobies

I collected time budget data for the 3 goby species to determine whether gobies spend different amounts of time at different locations around burrows and at different types of shelters following Karplus (1992). I collected time budget information for 20 gobies of each of the 3 species at both sites, except for bridled gobies, which were absent from site Woobie. Gobies were chosen haphazardly for timed observations. I worked in different areas within the 2 sites during different dives to reduce the likelihood of observing the same goby multiple times. After each goby was selected, a 5 min acclimation period (Karplus 1992) preceded a 10 min observation period during which I continually estimated the spatial position of a goby using a reference grid (Fig. 1).

There were 11 dependent variables, i.e. time spent in each of 11 positions (Fig. 1). Because the data did not conform to a multivariate normal distribution, I used a 2-way PERMANOVA with species and site as independent variables and position as the dependent multivariate variable (subroutine 'adonis' R version 2.14.1; Anderson 2001).

Partner fidelity of gobies

I conducted observations to compare partner fidelity among goby species, i.e. the time an individual goby spends with an individual shrimp before switching to another shrimp. For dash and bridled gobies, I did this through direct observation in the

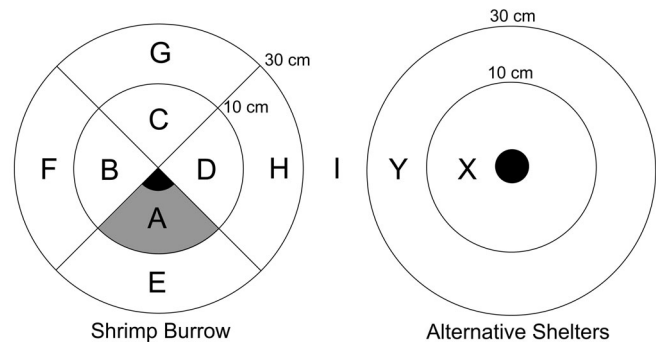


Fig. 1. Positions used to quantify goby location and burrow use in a laboratory study of behavioral differences among mutualist species in a shrimp–goby association. Left: a typical cone-shaped shrimp burrow (Positions A through H); Position A is the area into which shrimp emerge from the burrow. Right: representation of any of various shelters alternative to shrimp burrows (shells, coral rubble, etc.). For both shrimp burrows and alternative shelters, the center (black) is the entrance to the shelter/burrow. Positions on the inner ring (Positions A through D and X), are within 10 cm of the entrance. Positions E through H and Y are between 10 and 30 cm from the entrance. Position I is beyond 30 cm of any entrance. Modified from Karplus (1992)

field during time-budget observations (previous section). However, only 1 orangespotted goby switched burrows during time-budget observations. Videos have revealed that orangespotted gobies rarely switch burrows even with SCUBA divers absent (Lyons 2012). Thus, I tagged 15 orangespotted goby individuals at Normans in July 2009 (8 were located after tagging) and 15 in July 2010 (9 were located). I used visible elastomer tags (Northwest Marine Technologies), which have minimal impact on growth and mortality (Malone et al. 1999). I recorded the burrow entrance in which each individual was located every day for 1 mo.

Shrimp emergence

During the goby time-budget observations described above, I recorded the number of times shrimp exited the burrow while the goby was present at the burrow entrance (Position A, Fig. 1). These data were collected to clarify whether shrimp emerge more often from burrows occupied by one goby species than by others. I standardized shrimp emergence rates to the time the goby was in Position A (emergences per minute spent in Position A). Given that not all gobies entered Position A during the 10 min observations, the sample sizes were unbalanced. There were 20 samples for orangespotted gobies both at Normans and Woobie, 14 and 17 samples for

dash gobies at Normans and Woobie, respectively, and 8 samples for bridled gobies at Normans. Additionally, there were many zeros in the data set (instances in which shrimp never emerged while the goby was in Position A). Thus, I used a 2-way PERMANOVA using goby species and site as independent variables (subroutine 'aovp' R version 2.15.1).

RESULTS

Resource preference of gobies

Preference for the artificial burrow with shrimp versus without shrimp was different among goby species ($G_{\text{adjusted}} = 21.43$, $df = 2$, $p < 0.001$). Orangespotted gobies were found in the burrow with shrimp significantly more often than the 50% null expectation (40 of 45 times; $G_{\text{adjusted}} = 13.13$, $df = 1$, $p < 0.001$), bridled gobies less often than the null expectation (10 of 45 times; $G_{\text{adjusted}} = 0.46$, $df = 1$, $p = 0.022$), and dash gobies were not different from the null expectation (26 of 45 times; $G_{\text{adjusted}} = 0.463$, $df = 1$, $p = 0.496$).

Time budget of gobies

The 3 goby species allocated different amounts of time to different positions in the reference grid (PERMANOVA: $F_{2,99} = 22.29$, $p < 0.001$; Fig. 2). Site did not have a significant effect ($F_{1,99} = 0.525$, $p = 0.728$) and there was no interaction between site and goby species ($F_{1,99} = 1.03$, $p = 0.360$). Orangespotted gobies spent the most time at shrimp burrow entrances (Position A; Figs. 1 & 2). Dash and bridled gobies were often located at non-shrimp burrows, while orangespotted gobies were never so (Positions X and Y; Figs. 1 & 2).

Partner fidelity of gobies

Orangespotted gobies spent more time with shrimp partners before switching to other shrimp (2.52 ± 0.72 d; $n = 17$; mean \pm SE) than did dash (5.48 ± 0.50 min; $n = 20$) or bridled gobies (6.26 ± 0.80 min; $n = 20$).

Shrimp emergence

Shrimp emerged at different rates when the different goby species were present at the burrow en-

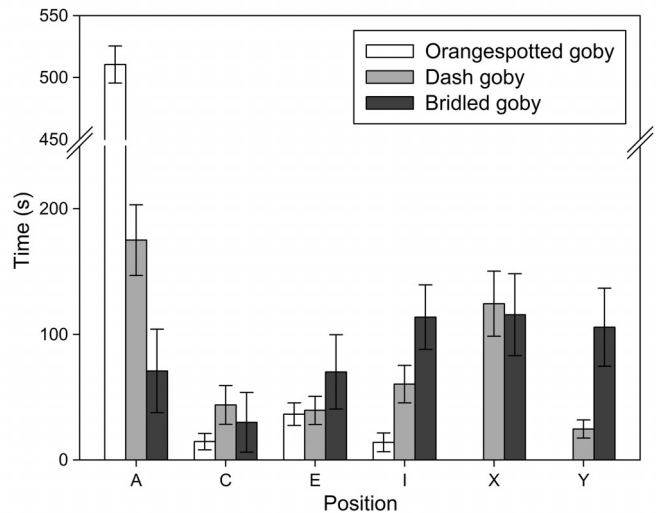


Fig. 2. Duration gobies remained in each position around the burrow (see Fig. 1). Data are mean \pm SE. For orangespotted and dash gobies, data are from both (Normans and Woobie) field sites. For bridled gobies, data are from Normans only. Note the break on the y-axis between 250 and 450 s. Only positions that had major contributions to the total variation are shown

trance (PERMANOVA: $df = 2$, $p < 0.001$). Shrimp emergence did not differ among locations ($df = 1$, $p = 0.784$) and there was no interaction between goby species and location ($df = 1$, $p = 0.706$). Shrimp emerged most often with orangespotted gobies present (2.26 ± 0.21 times min^{-1} in Position A; mean \pm SE), followed by dash (0.51 ± 0.20 times min^{-1} in Position A), and bridled gobies (0 times during 23.6 min spent in Position A). Shrimp were never found emerging without a goby at the burrow entrance.

DISCUSSION

Resource preference by mutualists

The orange spotted goby is more specialized in using the service provided by a mutualist partner than facultative mutualist or occasionally-associated species. A similar result was found for the Indo-Pacific shrimp-goby *Myersina macrostoma*, which is visually attracted to shrimp burrows but not rocks (Jaafar & Hou 2012). Thompson et al. (2013) found that in obligate shrimp-goby networks in the Pacific Ocean, pairings are very specialized in comparison to other mutualism networks; i.e. each mutualist has one or few associates. Thus, specialization for many obligate gobies extends beyond shelter type into specialization on specific partner shrimp species.

Bridled gobies, which have not been previously described as associating with shrimp (Randall et al. 2005), avoided shelters with shrimp in the lab, but occasionally used shrimp burrows in the field. Observations during collection trips suggest that, in nature, bridled gobies do not venture deep into shrimp burrows and may rarely come into contact with resident shrimp. Thus, the bridled goby is perhaps best described as a commensalist species.

It might be expected that shrimp burrows would offer better protection than other shelters, such as rocks or shells, due to their depth (Dworschak & Ott 1993) and, consequently, that all 3 goby species would be specialized in their use. There are several possible explanations for why my results do not support this expectation.

(1) Different goby species do not have equal ability to avoid predators using shrimp burrows. Dash gobies avoid predators with equal effectiveness when they have access to conch shells or shrimp burrows (Lyons 2013). In contrast, orangespotted gobies are better able to avoid predators when they have access to shrimp burrows rather than conch shells (Lyons 2013; this study did not include bridled gobies). Thus, orangespotted gobies benefit from specializing in their use of shrimp burrows, whereas dash gobies would not benefit from specialization. (2) Large orangespotted gobies aggressively exclude smaller conspecific and heterospecific gobies from burrows (Randall et al. 2005, Lyons 2014). Thus, the evolution of a preference for shrimp burrows by dash or bridled gobies may be unlikely given that their access to shrimp is limited by competitive interactions. (3) Shrimp may be able to distinguish between the 3 gobies and aggressively exclude individuals based on species identity (Karplus 1981, 1992, Karplus et al. 1981). Thompson et al. (2013) demonstrated that closely related shrimp species in the Pacific ocean tended to associate with closely related goby species. The 3 gobies studied here are not closely related (Thacker & Cole 2002, Rüber et al. 2003, Thacker 2003, Pezold & Buth 2004) and thus dash and bridled gobies may not substitute for orangespotted gobies.

Services to mutualist partners

Observations by Karplus (1992) and Kramer et al. (2009) indicate that shrimp emerge more often when associated with orange spotted gobies than with dash gobies or notchtongue gobies *Bathygobius curacao*.

My results corroborate these observations and indicate that orangespotted gobies behave in ways that facilitate more frequent emergence by shrimp than do dash or bridled gobies and that shrimp emerge most regularly with orangespotted gobies, followed by dash gobies, and not at all with bridled gobies. Orangespotted gobies spent more time at burrow entrances and remained with individual shrimp for much longer periods than did dash or bridled gobies. Orangespotted gobies warn shrimp with both caudal fin fluttering and head-first dives (Karplus 1992), whereas dash gobies typically use head-first dive warnings and very rarely caudal fin flutter warnings (Randall et al. 2005), and bridled gobies have not been observed providing any warnings. Work on other shrimp–goby networks suggests that shrimp grow at a faster rate when associated with gobies (Thompson 2003), probably because the shrimp forage at least partly outside burrows (Palomar et al. 2004).

Conclusions

Orangespotted gobies have the most incentive to provide the best service to shrimp partners because they are also the most reliant on the use of shrimp burrows as shelter. That more specialized mutualist species provide the greatest service to their partners has been documented in other mutualisms. Damselishes that are more specialized in their use of certain anemone species as shelter provide larger varieties of services to their anemone hosts (Roughgarden 1975); plants that are obligately pollinated by animals provide pollen of greater quality than plants that are additionally wind pollinated (Hanley et al. 2008); and aphids that are obligately protected by ants provide ants with nectar of higher quality and quantity (Völkl et al. 1999, Stadler et al. 2002). This might be a general feature of mutualism.

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