Direct selection on mate choice: female redlip blennies pay more for better mates

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Sexual selection may be reduced by costs of mate choice such as predation risk and energetic expense. Despite their theoretical importance, such costs have rarely been quantified or related to the quality of mate obtained. We performed such a study with a wild population of redlip blennies in Barbados. In this coral reef fish, females traveled 0.2–12 m from their feeding territories to the territories of nesting males, where they spawned and left their eggs in the males’ care. Previous studies have shown that larger and older males are better parents and are preferred by females. Here, we found that long-distance trips by females were made primarily toward larger males, and the extra distance traveled beyond the nearest male was correlated with the improvement in size of male obtained. Comparisons with feeding budgets while the females remained on their home territories suggested that costs from lost time and energy were minor, and no predation attempts on females were observed. However, on longer trips the females faced more aggressive attacks from damselfishes, whose territories they crossed. In contrast, no attacks were observed from damselfish when the blennies remained on their own territories. These attacks appeared to be responsible for a greater incidence of scars on females than on males. This difference between the sexes became more pronounced as spawning progressed, and then decreased as females healed during the nonspawning interval. Thus, female blennies endure a cost of interspecific harassment which is correlated with the quality of mate obtained. This cost may restrain sexual selection in this species. 

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with a sharp attack. Once in the nest, females appear to use male age as a second cue for choice (Côté and Hunte, 1995), and may reject a young male by leaving without spawning. These spawning interactions are the only times when males and females associate. Otherwise, both sexes remain on their separate, permanent feeding territories (Nursall, 1977).

We quantified four potential costs paid by female redlip blennies when visiting males: energetic expense, predation risk, risk of territory takeover, and harassment by other fishes (conspecifics and three species of territorial damselfish). By relating these potential costs to the distance traveled, the time taken, and interactions with other species on journeys to and from males of various qualities, we consider whether females pay higher costs for good males, and by implication, whether such costs of choice may limit sexual selection.

METHODS

Breeding Biology

Blennies, ranging from 65 mm to 100 mm, reproduce year-round in two-week cycles starting 10 days before full moon. Before the onset of the spawning period, males remove algae from a cavity within their territories to prepare for nesting. Spawning begins at first light (0600 h during our study) and lasts 5-5.5 h. During this time males are visited repeatedly by females, some of which will spawn a monolayer of benthic eggs in the nest. The clutches are guarded by males until they hatch 4 days later (Marraro and Nursall, 1983). The larvae leave the nest and spend several weeks in the plankton before settling onto a reef. Although males spawn with only a single female at a time, they usually spawn every day of the reproductive period, sometimes with the same female, often with different females. Therefore, clutches at different ages may be found in a male's nest on any given day. Females spawn approximately every other day, with as many as five different males during each two-week period (Côté and Hunte, 1989).

Field Methods

Our study was conducted on a shallow-water fringing reef off the Bellairs Research Institute of McGill University on the west coast of Barbados, West Indies, in December 1992 and January 1993. Our study site consisted of a 200-m coral spur adjacent to the spur studied by Côté and Hunte (1989, 1993), and three nearby patch reefs, yielding a total study area of 250 m². Adult blennies did not move among these sites. We were impressed by the severity of the attacks on females inflicted by the damselfishes, which were generally 2-3 times heavier than blennies, and noticed that many blennies bore wounds ranging from 1-mm-long whitish scratches to 1-cm-diameter patches of torn flesh. To compare the frequency of occurrence of wounds between females and males, we conducted four “scar censuses” at 7-day intervals: one day before spawning, once halfway through the 14-day spawning bout, once at the end of the spawning bout, and once 7 days after the end of spawning. During these censuses we examined all fish closely for the presence of scars and then compared the numbers of males and females bearing at least one scar.

Throughout the study we measured the size of the fish in the field by noting specific substrate features near the head and tip of the tail of resting fish and measuring the distance between these features with a ruler. We usually obtained 3-5 measurements per fish, which were then averaged. This method is accurate to ±2.5 mm (Côté and Hunte, 1989).

When data were available for repeated visits by a given female to the same male, we used the average value of travel times, so each pair contributed one data point to the analyses. These single values were composed of an average of 1.4 (range 1-5) visits per pair. We also used the mean of the time budget activities recorded over successive mornings for each female. Females followed the same routes (within our measurement error of ±10 cm) on the outgoing and return trips, so we report only one-way distances. In 95% of cases females visited only one male per trip. This may be because the fish were familiar with one another as a result of their permanent territory locations (Nursall, 1977; see below). The rare multiple-male trips are excluded from the analyses because we could not relate the potential costs paid to attributes of any one male. Analyses are based on log-transformed data to meet the assumptions of normality and homoscedasticity.
Figure 1
Map of blenny territories and nests (dots) on a typical subsection of the study area. Territories with nests belong to males (stippled), those lacking nests belong to females. Routes taken by five females from their home territories to those of males are indicated with dashed lines.

the assumptions of parametric statistics unless noted otherwise. Means are accompanied by standard deviations.

RESULTS
Travel distance
Figure 1 shows the territory distribution on a subsection of the study site, with examples of routes taken by females to males' territories. There was no evidence of spatial clumping by sex in pairwise comparisons of nearest neighbors. Females traveled 0.2–12.0 m from their home territories to visit males, with an average (one-way) distance of 3.09 ± 2.22 m (SD) (Figure 2). This distance is equivalent to 36 female body lengths or 2.6 territory diameters (mean territory diameter = 1.2 ± 0.2 m (SD), N = 10 territories measured during time budget observations). The average distance traveled was nearly twice as far as the minimum necessary to reach the nearest nesting male (paired t = 6.27, p < .001; Figures 1 and 2).

Note that these are not "sampling trips." Females often swam directly toward males that they could not see at first, and on two occasions we saw females swim directly to territories of males who had disappeared overnight (presumably due to predation). Thus, the females appear to be already familiar with the permanent locations of males, perhaps having learned these over the course of several months of territorial activity and spawning trips.

There was a correlation between the sizes of neighboring (nearest) males and females (N = 74, r = .43, p < .001). Despite the fact that larger females were closer to larger males, they traveled at least as far (or farther than) smaller females (N = 51 females, r = .23, p = .102) and visited larger males (N = 43, r = .43, p = .004; see also Côté and Hunte, 1989).

In some cases, the nearest nesting male was already spawning when visited by a focal female. Because males spawned with only one female at a time, and the mean spawning duration was 16.13 ± 16.49 min (SD; N = 19), females often faced a lengthy wait to gain access to males that were already spawning. Therefore, the nearest male, if already spawning, might not be the nearest "available" male. When such males were excluded from the subset of "nearest" males, the average distance traveled by females still exceeded the minimum distance necessary to find an available mate (paired t = 3.83, p = .001; Figure 2).

A visit to a male's territory represents only the first stage of mate choice, because males then have the option of rejecting females. Females who were rejected had, on average, traveled a shorter distance than those accepted by males (mean distance rejected = 2.43 ± 1.29 m, N = 25; mean accepted = 3.34 ± 2.44 m, N = 43; t = 1.80, p = .076). They were not rejected simply because they were smaller (mean size rejected = 83.5 ± 7.5 mm, N = 25; mean accepted = 86.4 ± 8.2 mm, N = 42; t = 1.40, p = .167). Furthermore, females that spawned after being accepted by the male had traveled farther (mean = 3.81 ± 2.71 m, N = 29) than those that did not spawn (mean = 2.42 ± 1.48, N = 56; t = 2.64, p = .010). Thus, each stage of progress through the two-way mate choice sequence is characterized by increasing travel distances from the females' home territories.

We had predicted that females would travel farther to obtain a higher-quality male, where male quality was correlated with body size (see Côté and Hunte, 1989). This prediction was supported: longer trips were toward larger males (Figure 3A). Note that females whose territories bordered those of
large males were spared long journeys, thus leading to the triangular pattern of data in Figure 3A. A better indication of "choosiness" is the extra time or energy expended to visit a mate beyond the minimum required to reach the nearest potential mate (Reynolds and Gross, 1990). Figure 3B shows that the improvement in size of male obtained is proportional to the extra distance traveled. In 69% of 59 spawning trips where male sizes were known, females traveled beyond the nearest male to their home territory. In 88% of such cases (36/41 trips), females visited males that were larger than the nearest male (Figure 3B). The correlation is stronger for females traveling beyond the nearest "available" male, i.e., excluding males that were close to females but that already had females spawning in their nests (Figure 3C).

Travel time

Time spent by females traveling to and from males' territories was highly variable, primarily because of differences in the amount of time females spent pausing en route, or hiding in crevices. Travel time toward males did not differ significantly from time taken to return to the females' home territories (mean time toward males = 19.6 ± 18.5 s, N = 59; mean time returning from males = 23.9 ± 24.3 s, N = 80; t = 0.84, p = .401). The durations of both parts of the journey were correlated significantly with the distance traveled (time toward male r = .669, N = 59, p < .001; return time r = .738, N = 80, p < .001). However, there were no correlations between travel times and either male or female body size (all four correlation coefficients between -0.15 and 0.15, all p-values >.20, N = 52-51). Thus, unlike travel distances, travel times were not correlated with male quality (body size).

Potential territory loss and predation risk

A potential cost to females of traveling large distances or for long periods of time is takeover of their territories by conspecifics. However, intruders were present in only five of 75 instances where we followed females back to their territories, and all five were evicted readily by the resident females. Thus, loss of food and risk of territory takeover appear to be minimal costs of choice.

Predation risk is more difficult to assess. The most common potential predators were trumpetfish Aulostomus maculatus, sand divers Synodus intermedius, spotted scorpionfish Scorpaena plumieri, and three species of moray (Gymnomuraena funebris, G. moringa, and Murana miliaris). Only one attack was observed, by a sand diver which caught a nesting male.

Attacks from territorial fish

The three species of damselfish had subdivided the entire study area into well-defended territories which overlapped with blenny territories. They were often highly aggressive toward foreign female blennies passing through their territories or waiting for acceptance by spawning males. Some of the attacks were clearly audible underwater when females were beaten into the coral, and females often took shelter in crevices while damselfish swam rapidly back and forth at the entrance. Female blennies crossed an average of 2.4 ± 0.2 damselfish territories and 1.1 ± 0.1 blenny territories when traveling to or from prospective mates. They were attacked, on average, 0.36 ± 0.09 times by damselfishes (N = 87 spawning trips, 90% of attacks by dusky damselfishes) and 0.20 ± 0.04 times by other blennies. Thus, female blennies suffered an average of one attack per round-trip.

There was a close correlation between the combined number of damselfish and blenny territories crossed and the dis-
The magnitude of the costs of choice due to distance traveled, risk of predation, attacks received, and potential feeding costs, can be put into perspective by examining similar activities when females remained on their home territories. While patrolling and foraging, females traveled an average of 9.4 ± 1.8 m during each 10-min observation session, or 0.94 m/min (N = 7 females). Given an average territory perimeter of 3.7 ± 1.2 m, this is equivalent to approximately three rounds of the territory per 10 min. Recall that during spawning visits females traveled an average one-way distance of 5.1 m in 25 s, or 7.42 m/min. Therefore, during every 8 min of activities on their own territories, females traveled the same distance as during an average one-way spawning trip.

Feeding is restricted to home territories, where females took an average of 44.8 ± 10.7 bites from the substrate per 10-min session (N = 10 females), for an average of 4.5 bites per min. Thus, during an average 25-s one-way spawning trip, foraging loss seemed minimal, with an average of two bites lost.

No attacks by predators were observed when females remained on their territories (as with spawning trips). There were also no attacks from damselfish, and the attack rate from neighboring blennies averaged only 0.06 ± 0.12 per 10 min. Because females faced an average of 0.56 attacks per 25-s one-way spawning trip, they were attacked over 200 times more often during spawning trips than when they remained on their territories.

**Scars**

The attacks from conspecifics and damselfishes suffered by female blennies while traveling to mates were probably responsible for whitish scratches and torn skin observed on many individuals. This is suggested by two direct observations of particularly severe attacks leading to new wounds visible afterwards, as well as the much higher attack rate during spawning trips than when females stayed on their own territories (see above) and the lack of observed predation attempts. Weekly censuses showed that at the start of the two-week spawning period there was no difference between the number of males and females showing scars (Figure 4). However, by the middle of the spawning bout, twice as many females as males were scarred, and by the end, four times as many females as males were scarred (Figure 4). The decline in total number of females scarred at the end of the spawning bout coincides with a decrease in spawning activity the preceding week. The scarring rate on males declined throughout the spawning period, probably because males spent increasing amounts of time in their nest-holes guarding the eggs, rather than interacting with neighbors in territorial disputes. During the subsequent two-week nonspawning period the difference between males and females became nonsignificant as females healed and males resumed territorial behavior.

**DISCUSSION**

Female redlip blennies paid higher costs when obtaining high-quality mates. Females that visited large males traveled farther and endured more attacks from other blennies and damselfishes than if they had opted for the closest male. The direct benefits from choosing such males can be substantial. Larger and older males spend more time in the nest, guard the eggs for a longer period in each reproductive bout, and lose a smaller proportion of their egg batches (Côté and Hunt, 1989, 1993). These findings support the prediction that animals should be willing to pay higher costs of mate choice in return for higher benefits (Real, 1990; Reynolds and Gross, 1990). We have focused on direct benefits to the offspring because these are easily measured, but genetic benefits are also possible if there is a heritable component to the longevity of larger and older males. In the barn swallow, *Hirundo rustica*, de Lope and Moller (1993) showed that females whose mates had had their tail feathers elongated experimentally (thus making them more attractive) paid higher costs through increased reproductive effort. This was presumably because of perceived genetic advantages to offspring sired by attractive mates.

In blennies, energetic expense and risk of predation while traveling to mates appear to be minor, compared with the costs of harassment by other species of fish. Obviously, pre-
dation represents a huge potential cost, but its true risk is difficult to assess. No predation attempts were observed on females either during spawning trips or while the females remained on their own territories in a total of 380 h of observations (including Côté and Hunte, 1989, 1993). We do not know how our presence affected predators, but we had the impression that morays, sand divers, and scorpionfish were opportunistic and undeterred by us, with the first two species capturing a herring and a male blenny, respectively, by darting out from 1–2 m below us.

Time budget data showed that every 16 min, females typically traveled as far within their territories while foraging and patrolling as during two-way spawning trips. Foraging time lost during spawning trips could be recouped by taking four extra bites from the algae on their territories. In the only other study documenting the costs of choice in the wild, Gibson and Bachman (1992) reached similar conclusions for energetic costs and predation risk in sage grouse. The risk of territory takeover while female bennies were away on spawning trips is also negligible. Our data showed that intrusions by other bennies were rare, and experiments by Nursall (1977) showed that fish in this population can readily regain their territories even after an absence lasting several hours.

A more important cost was probably imposed on female bennies by the attacks of territorial male damselfishes. Females were virtually never attacked while on their home territories, but they received an average of one attack per round-trip when visiting males. The quest for larger males, which took females farther from home, led to more attacks. Anecdotal observations showed that these attacks cause wounds, and the attack rates we recorded during opportunistic observations of spawning trips were marginally correlated with the number of wounds individuals bore during censuses. These attacks also appeared to be responsible for the increase in the proportion of females bearing scratches and wounds as the spawning period progressed.

Sexual selection in redlip bennies may be restrained by costs resulting from the severe attacks by damselfishes. In another study of interspecific competition, Thornhill (1987) showed that females of one species of scorpionfish (Panopha latipennis) relaxed their standards of choice when the quality of resources offered by males was restricted by another species (P. mirobiata). Similarly, female soldier beetles (Chauliognathus pennsylvanicus) were less choosy about their mates in the presence of aggressive wasps (Mclain, 1981). Most studies of interspecific interactions in sexual selection have involved predator–prey relationships (e.g., Berglund, 1993; Forsgren, 1992; Hedrick and Dill, 1995; Houde and Endler, 1990; Mbanghagen, 1991; Magurran and Nowak, 1991), and host–parasite systems (e.g., Hamilton and Zuk, 1982). The findings reported here support Thornhill's (1987) emphasis on the potential role of interspecific competition in sexual selection.

Other potential limitations on sexual selection in redlip bennies include competition with other females and male mate choice. Males typically care for the eggs of more than one female at a time (Côté and Hunte, 1989). However, their acceptance of only one spawning female at once occasionally results in queues of females waiting at the edge of males’ territories. Some females eventually give up and return to their own territories without having spawned. Thus, a male’s attractiveness to a given female may be limited by his popularity with other females. Male choice may also limit the number of females spawning per male because males are more likely to reject small females, thereby promoting assortative mating (Côté and Hunte, 1989).

Redlip bennies may balance costs of choice, particularly due to interspecific harassment, against benefits through male parental care. This study shows the potential importance of natural selection in the evolution of mate choice (Crowley et al., 1991; Kirkpatrick, 1987; Kirkpatrick and Ryan, 1991; Real, 1990; Reynolds and Gross, 1990). Direct benefits may be important even in species where males provide little to the female and offspring (Reynolds and Gross, 1990). For example, female Uganda kob (Kobus kob thomasi) prefer lek territories in areas that are safe from predators (Deutsch and Weeks, 1992), and female hybrid frogs (Ololygon rubra) prefer males whose size matches their own at a ratio that maximizes fertilization of their eggs (Bourne, 1993). These direct benefits, combined with genetic benefits, may be sufficient to “explain” mate choice if they offset the costs (Kirkpatrick and Ryan, 1991; Reynolds and Gross, 1990, 1992). The advantage of species such as bennies for understanding natural selection on mate choice is that the benefit to females—parental care—is large enough for comparisons of the magnitudes of costs and benefits. More precise tests of this framework should be possible in species where costs and benefits can be measured in the same currencies.

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