

# Nonindependent mating in a coral reef damselfish: evidence of mate choice copying in the wild

Denis Goulet\* and Tamar L. Goulet\*

Department of Biology, University of Mississippi, University, MS 38677, USA

Theoretical and experimental studies have shown that mate choice copying is a viable mating strategy under certain conditions. Copying experiments in fish have been conducted primarily in the laboratory, except for one study conducted in the field under artificial conditions. We investigated whether in a wild population of the coral reef whitebelly damselfish (*Amblyglyphidodon leucogaster*) females copy the choice of other females. Females preferentially spawn with males that have recently mated. To determine if the presence of new eggs in the nest was the reason females chose mates or whether females were mate choice copying, we conducted egg-switching experiments. Eggs from males that recently mated were donated to males that had no eggs. If females are mate choice copying, then donor males with no eggs in the nest should continue to receive additional eggs. If females are using the presence of new eggs as the criterion for mate choice, then foster males with new eggs should receive additional eggs. We found that donor males received new eggs significantly more often than expected. More females mated with donor males than foster males. Furthermore, females preferentially chose to mate with males whom they had seen mating with another female. Females appear to remember the mate choice of other females and choose to mate with those same males even after 1 day. These results suggest that females may be copying the mating decision of other females rather than choosing males based on the presence of new eggs in the nest. *Key words:* copying, damselfish, female mate choice. [*Behav Ecol* 17:998–1003 (2006)]

Females often choose the male with whom they mate. Many models of intersexual selection assume that a female's mate choice is independent (Andersson 1994; Jennions and Petrie 1997). Because females initially invest more energy in offspring than males (Fisher 1958), they may seek a high quality male (Trivers 1972; Parker 1983), thereby increasing the chances of their offspring's survival. Female choice, on the other hand, may be nonindependent and influenced by the social environment (Galef and White 2000; Westneat et al. 2000; Godin et al. 2005). The generality and applicability of nonindependent mate choice are still debated.

One form of nonindependent female mate choice that has received considerable attention is copying, where females copy the choice of other females (Wade and Pruett-Jones 1990; Gibson and Höglund 1992; Pruett-Jones 1992; Dugatkin 1996a, 1996b; Stöhr 1998; Galef and White 2000; Westneat et al. 2000; Sirot 2001). In this paper we define female copying as a nonindependent mate choice in which the probability that a female selects and mates with a given male increases if she observes other females mating with that male (Dugatkin and Godin 1992; Pruett-Jones 1992; Dugatkin 1996a; Witte and Noltemeier 2002). Mate choice copying may increase variance in mating success, thereby influencing the evolution of preferred traits and the opportunity for sexual selection (Wade and Pruett-Jones 1990; Kirkpatrick and Dugatkin 1994; Laland 1994; Agrawal 2001).

Female copying may be advantageous for females unable to differentiate male quality (e.g., younger females) or if it reduces the time and other costs spent on mate searches (Pomiankowski 1987; Slagsvold et al. 1988; Reynolds and Gross 1990; Gibson and Höglund 1992; Pruett-Jones 1992; Dugatkin

and Godin 1993; Nordell and Valone 1998; Stöhr 1998). Reduction in mate search time may increase time available for foraging, which may lead to more egg production and additional mating. Recently, it has been proposed that female mate choice copying may be based on social cues, regardless of male quality (Gibson and Höglund 1992; Dugatkin 1996a, 1996b; Galef and White 2000; Westneat et al. 2000; Godin et al. 2005). For example, in the Trinidad guppy, *Poecilia reticulata*, females that observed other females' mating preferences not only reversed their initial preference and copied the model female but also retained this preference 1 day later (Godin et al. 2005).

Although numerous studies have been performed, female copying is still controversial. Female mate choice copying is difficult to demonstrate because clues of a past female's choice may attest to a male's quality. A female may independently make a mating decision based on this clue. For example, females preferentially mating with males that have eggs in their nest have been viewed by some researchers as copying (Goldschmidt et al. 1993; Knapp et al. 1995; Forsgren et al. 1996; Goulet 1998). Others, however, have argued that there are advantages of mating with males that have eggs. The presence of eggs in the nest may indicate high parental quality (Ridley and Rechten 1981), alter male behavior thereby making the male more attractive to the female (Kraak 1996), and/or increase egg survivorship (Jamieson 1995; Kraak 1996; Brooks 1998). Increased egg survivorship may be in the form of dilution from the risk of predation (Sargent 1988; Sikkell 1994a) or changes in parental care (Sargent and Gross 1993; Sikkell 1994b). Therefore, in order to demonstrate mate choice copying, one must experimentally decouple female mate choice preferences from evidence of past female mate choice.

Attempts to demonstrate mate choice copying are based primarily on research on polygynous species with internal fertilization and no parental care such as quail (Galef and White 1998; White and Galef 1999; White and Galef 2000), grouse

\*Both authors contributed equally to this work.

Address correspondence to D. Goulet. E-mail: dgoulet@olemiss.edu.  
Received 5 October 2005; revised 20 June 2006; accepted 20 July 2006.

(Höglund et al. 1990; Gibson et al. 1991; Höglund et al. 1995), deer (Clutton-Brock and McComb 1993), guppies (Dugatkin 1992; Dugatkin and Godin 1992; Dugatkin and Godin 1993; Briggs et al. 1996; Dugatkin 1996b; Dugatkin and Godin 1998; Dugatkin et al. 2002; Dugatkin et al. 2003; Godin et al. 2005), and sailfin molly (Schlupp and Ryan 1997; Witte and Ryan 1998; Witte and Noltemeier 2002; Witte and Ryan 2002; Witte and Massmann 2003). Studies in fishes have focused primarily on laboratory experiments on sailfin molly, *Poecilia latipinna*, (Schlupp and Ryan 1997; Witte and Ryan 1998; Witte and Ueding 2003) and the Trinidad guppy, *P. reticulata*, (Dugatkin 1992; Dugatkin and Godin 1993; Dugatkin 1996b; Dugatkin 1998; Dugatkin et al. 2002; Dugatkin et al. 2003; Godin et al. 2005). These laboratory studies have demonstrated that mate choice copying can occur. Two feral guppy populations tested in the laboratory, however, did not demonstrate female mate choice copying (Brooks 1996; Lafleur et al. 1997; Brooks 1999).

The sand goby (Forsgren et al. 1996), three-spined stickleback (Patriquin-Meldrum and Godin 1998), and deep-snouted pipefish (Widemo 2006) are the only marine fish species in which mate choice copying has been examined in the laboratory. In the sand goby and three-spined stickleback, female mate choice copying was ruled out. The deep-snouted pipefish laboratory study focused on male mate choice copying (Widemo 2006).

Only one study examined female mate choice copying in the field, although the experiments were conducted in tanks placed in the river (Witte and Ryan 2002). In that study, female sailfin mollies, *P. latipinna*, preferred to associate with males that had an adjacent female partner (Witte and Ryan 2002). The test fish did not have direct access to the stimulus fish nor was mating possible. Our study is the first to test mate choice copying with mating on an unconfined wild population of fish and the first to test female mate choice copying in a coral reef fish.

We used the whitebelly damselfish, *Amblyglyphidodon leucogaster*, as a model species for examining female mate choice copying in the field for several reasons. Being planktivorous, the whitebelly damselfish shows a nonresource based, promiscuous mating system (Goulet 1995; Goulet 1997; Goulet 1998), features associated with organisms that display mate choice copying (Dugatkin 1996a; Brooks 1998; Galef and White 2000; Westneat et al. 2000). Males and females are monochromatic, and there is no sexual dimorphism. Male *A. leucogaster* exhibit variability in reproductive success, suggesting that females are choosing males (Goulet 1998). Female choice is not based on attributes associated with the male such as male body size, courtship behavior, paternal care behavior, or territory size (Goulet 1998). Females do not favor the same male from one breeding season to the next. The reproductive ranking of males changes from year to year, such that males that have high reproductive success 1 year may have low reproductive success the following year. The change in rank from year to year is not due to the nest site, territory size, or location because males retain their nest sites and territories for many years (Goulet 1998).

The presence of eggs in the nest, and the eggs' developmental stage, does influence male reproductive success in *A. leucogaster*. Females preferentially visit and spawn with males that have recently mated. If a male has 2 nests, one with and one without eggs, females will choose to spawn in the nest with eggs (Goulet 1997; Goulet 1998). Egg presence, therefore, is a significant factor in female choice.

Although *A. leucogaster* females preferentially lay eggs contiguously to eggs of similar developmental stage, there is no increased survivorship of eggs based on number of eggs in the nest (Goulet 1997). Male *A. leucogaster* do spend more time tending their nest when they have more eggs in the nest, but time spent tending the nest does not affect hatching success.

Males exhibit the same parental care of their egg batches regardless of the batch's developmental state (Goulet 1998). Therefore, the dilution and parental investment hypotheses do not explain female choice in the whitebelly damselfish and the females' preference to lay eggs in nests that already have eggs. It appears that in *A. leucogaster*, females are not basing their mate choice on variability in male attributes and behaviors, male territory properties, or egg survivorship.

The goal of this study was to determine whether female *A. leucogaster* exhibit mate choice copying in the field. We conducted a series of egg-switching experiments where males that had recently mated had their eggs given to males that had not mated, removing the presence of eggs as a mate choice factor. If females are mate choice copying, then the males that had recently mated should continue to receive more matings even with no eggs in their nest. We also analyzed unpublished data where we followed females as they observed mating events and then noted with which males they subsequently mated.

## METHODS

### Study species

In the coral reef damselfish, *A. leucogaster*, males are permanently territorial. Females traverse the entire reef throughout the day, during which they have many opportunities to observe males, nest sites, and females spawning with males. Mating occurs daily, with peak activity at dawn, from May to September (Goulet 1995). Females lay eggs that are attached to the substrate, that is, demersal eggs. Females are capable of producing a new batch of eggs every 2 days over the breeding season. A female deposits her entire batch of eggs with a single male. All the females in the population mate, and females are promiscuous, mating with as many as 15 males in a given season (Goulet 1997).

A male broods and defends the egg batches that are laid within his nest site. A brood cycle generally lasts from 6–12 days depending on water temperature (Goulet 1995). During the cycle, as the eggs develop, they go through very distinct color phases (Goulet 1997). The eggs can be easily classified as early- (i.e., recently laid), mid-, and late-stage eggs.

In *A. leucogaster*, there is no courtship behavior. Females do exhibit mating preferences. If a male mates on a given day, and possess recently laid eggs within his nest, he is likely to receive more eggs that day and the following day (Goulet 1997; Goulet 1998). Males exhibit differential mating success with some males only receiving 5000 eggs in a reproductive season, whereas other males get as many as 450 000 eggs (Goulet 1998).

### Study site

This study was conducted on a 150-m stretch of fringing coral reef in the Gulf of Eilat, Red Sea (29°30'N, 35°55'E; for a description of the reef see Goulet 1998). Along the forereef, we monitored the population of *A. leucogaster* that consisted of 23 males and 35 females. For the egg-switching experiment, none of the males or females were marked, but males were recognizable as individuals based on their location on the reef where they defended a nest site.

### Artificial nest sites

Males are territorial, and within their territory, they have a specific nest site, an area of dead coral, where females lay their eggs. Previous studies demonstrated that males and females readily adopt artificial nest substrates (Goulet 1995; Goulet 1997; Goulet 1998). In this study, the artificial nest consisted of a 1.5-l plastic bottle that was three-quarters filled with water and one-quarter filled with air. We attached one end

of a 1-m-long, 5-mm-diameter rope to the neck of the bottle and the other end to a standard red brick. When submerged, the bottle floated vertically with the neck downward. This artificial nest site was positioned approximately 50 cm away from a natural nest site. Securing the bottle to a brick allowed us to easily move nests between males. Each bottle was wrapped with a 22 × 28-cm sheet of underwater paper (Nalgene Polypaper) held in place by rubber bands, thereby covering the entire outer vertical surface of the bottle. Females laid their eggs directly onto the underwater paper, choosing the artificial nest site over the natural egg-laying substrate. After the eggs were laid, we traced the surface area of the egg batches onto the underwater paper with minimal disturbance to the nest site (for details see Goulet 1995; Goulet 1997; Goulet 1998). When the eggs hatched, we removed the paper to assess the number of eggs laid. Goulet (1995) previously established that there was a significant correlation between number of eggs laid and the surface area of an egg batch. The bottle standardized the nest site for each male and was large enough such that space was not a limiting factor for egg laying.

### Egg-switching experiment

*Amblyglyphidodon leucogaster* females preferentially lay eggs in nests with early stage eggs (Goulet 1997; Goulet 1998). This choice could be because the eggs signal male success and/or increased egg survivorship or because females copy the choice of other females that have recently spawned. To decouple eggs from male mating success, we conducted a series of egg-switching experiments in July and August 2001. In these experiments, the artificial nest site of a male that had recently mated (donor male) was switched with a male's nest site that had no eggs (foster male). As a result, the donor male now had no eggs in his nest site, and the foster male had newly laid eggs in his nest site. If females are basing their mating decisions on the presence of newly laid eggs in the nest, then it is predicted that the foster male should receive significantly more matings and eggs than the donor male. If females are choosing mates by mate choice copying, then the donor male should receive significantly more matings and eggs than the foster male, even without eggs in the nest.

Prior to an experiment, we monitored the mating activity of the population for 10 days by conducting daily snorkeling surveys from 5:00 AM to 8:00 AM and 6:00 PM to 8:00 PM. We recorded the status of each male's nest site and the number of males that received newly laid eggs. The 10-day hiatus between experiments was used to ensure that egg switching did not alter the spawning behavior of the population. All males had successfully brooded at least one clutch of eggs prior to the switching experiment, and therefore, there were no overt differences between foster and donor males.

For 6 consecutive days, we manipulated 1–3 pairs of nest sites immediately following the dawn mating activity (5:00 AM–8:00 AM). The remainder of the male population was not manipulated, including some males that still had early stage eggs in the nest. We recorded the identity of the donor and foster males and traced the surface area of the eggs laid. This allowed us to identify any new egg batches that were added to the nest site. From donor males, we removed the artificial nest site with the newly laid and fertilized eggs and replaced it with an empty artificial nest site. We gave the nest with the eggs to foster males that did not spawn that day and did not have eggs on their artificial nests. Foster males generally accepted donor eggs and reared them as their own. In cases where foster males ate the donor eggs, these data were not included in the analysis.

After egg switches, we monitored the population for 1 h to ensure that the manipulation had caused no disturbance. Egg

switching had no observable effect on a resident male's behavior or his ability to mate. A second snorkeling survey of the population was conducted from 6:00 PM to 8:00 PM to quantify any mating activity that occurred throughout the day. Because egg batches were distinct, and a female does not lay 2 egg batches in one male's nest in 1 day, we could use the number of egg batches in a male's nest as an indication of the number of females with whom that male mated (Goulet 1997). For each donor–foster manipulation, we recorded for a 48-h period which male received new eggs and the number of females that mated. Three sets of 6-day egg-switching experiments were conducted. Within an experiment, males were manipulated only once, but among experiments, males were used more than once.

### Female mate choice observations

Given that the egg-switching experiments indicated that presence of eggs in the nest is not a cue for mate choice, we analyzed unpublished data that was part of a larger study in which we observed female mating behavior under unmanipulated conditions in the wild (see Goulet 1998 for details). In this study, females were individually marked permitting observers to record data on the mating behavior of each female (see Goulet 1998 for details). With the help of numerous volunteers, the entire population of *A. leucogaster* was surveyed from 5:00 AM to 8:00 PM for three 10-day intervals during July and August in 1990 and 1991. During each survey, 2 observers swam back and forth along the study site. The location of females relative to each male was recorded onto a map of the study site. At each pass of a male's nest site, an observer watched the nest site for activity for 1 min. In the event of mating activity, focal observations were conducted on the nest site. The identity of the spawning females and any females within a 1-m radius were recorded. Females within the 1-m radius were considered to be observing the mating activity at that nest site.

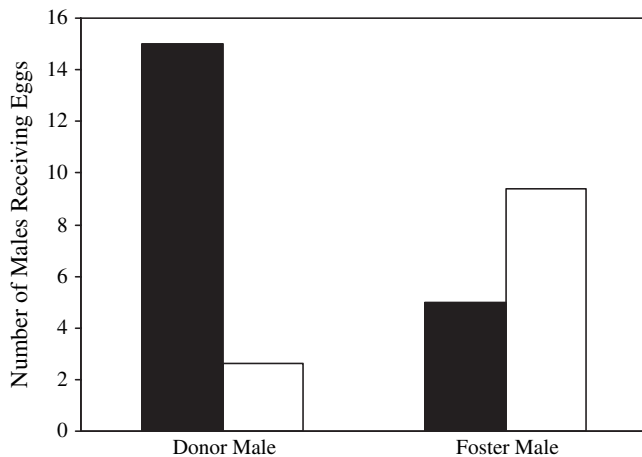
We then looked at the data to determine if females that observed a mating spawned within 48 h of the observation and with which male. The data fell into 3 categories: an observing female mated with the male she observed mating, an observing female mated with a different male, and an observing female did not mate. Because females spawn every other day, females that did not mate were considered not ready to mate and were excluded from the analysis.

## RESULTS

Twenty-six egg switches were performed over the 3 experiments. In 9 cases, the foster male ate the eggs. In 2 cases, neither donor nor foster males received any new eggs during the 48-h observation time, but both donor males did receive eggs a few hours later. These 11 cases were dropped from the analysis, leaving 15 successful manipulations.

Because each experiment was tested against the same null hypothesis, we conducted a heterogeneity chi-square test to determine if the data could be pooled (Zar 1984). This analysis indicated that the experiments were homogeneous ( $\chi^2_{(2)} = 4.59, 0.10 < P < 0.25$ ). The pooled data were analyzed using a chi-square test with Yates correction ( $\chi^2_c$ ) (Zar 1984). Based on previous data (Goulet 1998), we know that males with newly laid eggs in the nest have a 47% chance of receiving more eggs, whereas males with no eggs in the nest have a 13% chance. These values were used to generate our expected values for donor and foster males for the egg-switching experiments.

After the switching of nests, donor males received additional eggs in all 15 manipulations, whereas foster males received eggs in only 5 cases. The number of times donor and/or foster

**Figure 1**

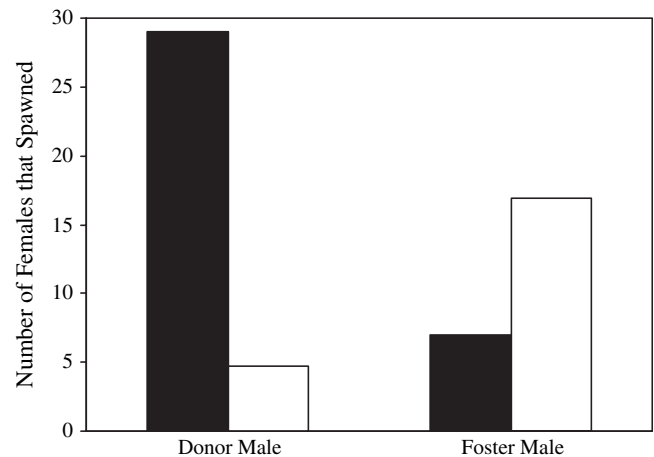
The number of times that donor ( $n = 15$ ) and foster ( $n = 5$ ) males received new eggs after having their artificial nest sites switched. A total of 15 manipulations were conducted in which donor males had their artificial nest site with newly laid eggs switched for a nest site with no eggs. Foster males had their empty nest site replaced with a nest site with eggs from the donor male. Donor males received new eggs significantly more often than expected ( $\chi^2_{c(1)} = 56.08$ ,  $P < 0.001$ ). Dark bars = observed; white bars = expected.

males received new eggs was significantly different from expected ( $\chi^2_{c(1)} = 56.08$ ,  $P < 0.001$ ). Although donor males, by definition, had no eggs immediately following the nest switching, they received more new egg batches than expected, whereas the number of new egg batches received by the foster males did not differ from expected (Figure 1).

To determine if females were laying different number of eggs with donor versus foster males, we compared the average number of eggs males received per mating event. Donor males on average received 8535 eggs per mating (standard deviation [SD] = 6706), whereas foster males received 7474 eggs per mating (SD = 5087). The average number of eggs received per mating by donor males was not significantly different from foster males (unpaired  $t$ -test:  $t_{(30)} = -0.43$ ,  $P = 0.67$ ). This indicates that donor males receive more eggs because they mate with more females and not because they get more eggs per mating.

During the 15 successful manipulations, the males mated 36 times. After the switch of nests, the number of females that mated with donor and foster males was significantly different from expected ( $\chi^2_{c(1)} = 126.48$ ,  $P < 0.001$ ). More females ( $n = 29$ ) mated with the donor males than expected, even though these males had no eggs in the nest, whereas fewer females ( $n = 7$ ) than expected mated with foster males (Figure 2). Given that females can spawn 2 days after laying a batch of eggs (Goulet 1997), it is possible that a female could lay a second batch of eggs with the same male. To count only one mating per female, we focused on the findings obtained within a 24-h period. Twenty-four hours after switching nests, donor males received more new egg batches than expected ( $n_{\text{donor}} = 10$ ,  $n_{\text{foster}} = 2$ ,  $\chi^2_{c(1)} = 53.47$ ,  $P < 0.001$ ) and mated with more females than expected ( $n_{\text{donor}} = 16$ ,  $n_{\text{foster}} = 2$ ,  $\chi^2_{c(1)} = 29.21$ ,  $P < 0.001$ ).

To determine if females that observed mating activity are more likely to mate with the male they watched, we analyzed previously collected data using a chi-square test. Heterogeneity chi-square test (Zar 1984) revealed that data collected from the three 10-day observation periods could be pooled within each year (1990:  $\chi^2_{(2)} = 3.08$ ,  $0.10 < P < 0.25$ ; 1991:  $\chi^2_{(2)} = 5.91$ ,  $0.05 < P < 0.10$ ). Expected values were determined

**Figure 2**

Number of females ( $n = 36$ ) that spawned with donor ( $n = 29$ ) or foster ( $n = 7$ ) males after having their artificial nest sites switched. Donor males had their artificial nest site with newly laid eggs switched for a nest site with no eggs. Foster males had their empty nest site replaced with a nest site with eggs from the donor male. Donor males had significantly more females mate with them than expected, even though they had no eggs in the nest ( $\chi^2_{c(1)} = 126.48$ ,  $P < 0.001$ ). Dark bars = observed; white bars = expected.

assuming a 50:50 probability that a female would mate with the observed male or a different male.

In 1990, there were a total of 122 cases where females observed other females spawning, of which in 103 cases females laid eggs later and in 19 cases females did not mate. Of the 103 occurrences where females spawned later, in 84 cases females laid eggs with the male they had observed other females spawning with and in 19 cases females mated with a different male. In 1991, there were 95 occurrences where females observed other females spawning, of which in 89 occurrences females mated later and in 6 occurrences females did not mate. Of the 89 cases where females spawned later, in 67 of these cases females laid eggs with the male they observed mating with another female, whereas in 22 cases females spawned with a different male. In both years, the number of females that chose to spawn with males they had previously observed mating was significantly higher than expected (1990:  $\chi^2_{c(1)} = 39.77$ ,  $P < 0.001$ ;  $\chi^2_{c(1)} = 21.75$ ,  $P < 0.001$ ).

## DISCUSSION

Female mate choice copying is a reproductive strategy that may be advantageous in nonresource based and promiscuous mating systems (Wade and Pruett-Jones 1990). Female mate choice copying may reduce the cost of selecting a mate among males whose qualities are difficult to ascertain. Demonstration of female mate choice copying, however, is difficult because often there is evidence of past female mate choice. This can be the product of mating (e.g., eggs) or a change in male behavior as a result of mating, both of which may influence female choice not by copying (Jamieson 1995). To demonstrate female mate choice copying, it is necessary to rule out other criteria by which a female may be choosing a male such as variability in territory properties, male attributes and behaviors, and presence of eggs in a nest.

We tested female mate choice copying and mating in a wild population of the planktivorous, promiscuous, tropical damselfish *Amblyglyphidodon leucogaster*. Other studies demonstrating mate choice copying have focused only on mate choice and not on observing the outcome of mate choice, that is, the

mating itself. For example, in a series of mate choice tank experiments conducted in a river, wild female sailfin mollies associated with the male they observed with another female rather than a lone male (Witte and Ryan 2002). In that experimental design, mating was not possible. In laboratory experiments on the deep-snouted pipefish, the position of the focal fish and the ornament display and courtship dance were recorded but not mating (Widemo 2006). Our study not only demonstrates mate choice but also documents increased reproductive success, in the form of more egg batches, received by the chosen males. It is also the first to examine female mate choice copying in a wild population of a coral reef fish.

*Amblyglyphidodon leucogaster* females mate nonindependently (Goulet 1998). Female preference of one male over another could not be explained by a male's territory size, distance from the female feeding site to a male's territory, nor the number of female night sites within a male's territory (Goulet 1998). Male behaviors, such as courtship behavior or parental care, or male attributes, such as male body size, were also not choice parameters (Goulet 1998). Potentially, a parameter that was not measured could be driving female mate choice. This possibility is unlikely given that although males retain the same territories from year to year, male reproductive success changes from year to year. The only consistent indicator of female mate choice was the presence of newly laid eggs in the nest.

The current study provided the possibility of uncoupling egg presence from female mate choice. Our results show that females preferentially mate with males that have recently mated. Females chose to mate with donor males even though the males did not have evidence of the mating (i.e., eggs in their nests). Furthermore, presence of early stage eggs did not make males more attractive to females. Foster males, even with newly laid eggs in their nest, received fewer matings than expected, suggesting that egg presence is not the mate choice criterion. Although it is possible that females are choosing males based on some as yet undetermined attribute, the results of the egg-switching experiments are consistent with female mate choice copying.

In contrast to our study, in the sand goby, females preferentially chose to mate with males with eggs in the nest, and when the eggs were removed, no preference for males was observed (Forsgren et al. 1996). In the sand goby, however, the presence of other eggs reduced the risk of a female's eggs being eaten. Hatching success was related to initial brood size, and males exhibited less filial cannibalism when they possessed large broods (Forsgren et al. 1996). In *A. leucogaster*, females mate with males that have eggs in their nests, but there is no increased survivorship of eggs based on number of eggs in the nest (Goulet 1998). Even when the eggs are removed, as occurred in this study, females still chose the males that had previously mated.

Studies on freshwater poeciliids have demonstrated that a female's mating preference can be influenced by observing the mate choices of other females (Dugatkin et al. 2002; Witte and Ryan 2002; Dugatkin et al. 2003; Godin et al. 2005). Female *A. leucogaster* have many opportunities to observe females spawning with males. During mating events, nonmating females are positioned in the vicinity and observe mating. Females traverse the reef throughout the day and can observe additional matings and evidence of recent matings (i.e., eggs in the nest). Observations of female spawning patterns revealed that female preference for males was nonindependent (Goulet 1998). A female that had observed mating was significantly more likely to mate with the male she had observed mating with other females than with a male she had not observed mating. Furthermore, females prefer to mate with males that had previously mated regardless of whether the males retain the evidence of the mating, that is, the eggs. These results suggest

that females are basing their mate choice decisions on observing other matings, which is consistent with mate choice copying. Female mate choice copying in *A. leucogaster* falls within the category of learned, nonindependent mate choice, based on the association-to-male mechanism as described by Westneat et al. (2000).

Female mate choice copying in *A. leucogaster* may be based on memory. In our experiments, females had an opportunity to observe mating at dawn, after which the egg switching was performed. A female preferentially chose to mate with a male that had mated on the previous day, regardless if that male retained the eggs or not when she mated with him. In laboratory studies of the sailfin molly and Trinidad guppy, copying females remembered which male the model female had chosen even after 1 day (Witte and Massmann 2003; Godin et al. 2005). Such cognitive and learning abilities are common in fishes (Mazeroll and Montgomery 1995; Laland and Reader 1999; Brown and Laland 2003; Reader et al. 2003).

By utilizing female mate choice copying, females could increase their feeding opportunities, which could increase egg production and ultimately increase female reproductive success. Reproductive success in female whitebelly damselfish is correlated with spawning frequency (Goulet 1997). Although it is still unknown how female *A. leucogaster* make an initial selection of a male, after a female mates with a male, other females seem to copy the mating decision of the initial female.

We thank Director A. Baranes, the faculty, staff, and students of the Interuniversity Institute of Eilat, Israel for providing office space and logistical support during our stay. We also thank the Israeli Nature Reserve Authority for granting us permission to conduct this study. A special thanks to A. Berkovitz, C. Bright, D. Camras, L. Karp, D. Forestier, S. Freedman, H. Geer, J. Gerwin, H. Hedaya, C. Johnson, S. Kahn, D. Lindell, A. Marshall, A. Mazeroll, E. Meroz, C. Northey, G. Nudnik, A. Prat, K. Rowe, M. Rozemeijer, K. Smith, M. Tacher, O. Tchelet, N. Udell, A. Weeks and A. Williams, who volunteered for many hours of observation. R. Buchholz, U. A. Liberman, and 2 anonymous reviewers provided valuable comments on the article.

## REFERENCES

- Agrawal AF. 2001. The evolutionary consequences of mate copying on male traits. *Behav Ecol Sociobiol* 51:33–40.
- Andersson M. 1994. *Sexual selection*. Princeton, NJ: Princeton University Press.
- Briggs SE, Godin J-GJ, Dugatkin LA. 1996. Mate-choice copying under predation risk in the Trinidadian guppy (*Poecilia reticulata*). *Behav Ecol* 7:151–7.
- Brooks R. 1996. Copying and the repeatability of mate choice. *Behav Ecol Sociobiol* 39:323–9.
- Brooks R. 1998. The importance of mate copying and cultural inheritance of mating preferences. *Trends Ecol Evol* 13:45–6.
- Brooks R. 1999. Mate choice copying in guppies: females avoid the place where they saw courtship. *Behaviour* 136:411–21.
- Brown C, Laland KN. 2003. Social learning in fishes: a review. *Fish Fisheries* 4:280–8.
- Clutton-Brock TH, McComb K. 1993. Experimental tests of copying and mate choice in fallow deer (*Dama dama*). *Behav Ecol* 4:191–3.
- Dugatkin LA. 1992. Sexual selection and imitation: females copy the mate choice of others. *Am Nat* 139:1384–9.
- Dugatkin LA. 1996a. Copying and mate choice. In: Heyes CM, Galef BG Jr, editors. *Social learning in animals: the roots of culture*. New York: Academic Press. p 85–105.
- Dugatkin LA. 1996b. Interface between culturally based preferences and genetic preferences: female mate choice in *Poecilia reticulata*. *Proc Natl Acad Sci USA* 93:2770–3.
- Dugatkin LA. 1998. Genes, copying, and female mate choice: shifting thresholds. *Behav Ecol* 9:323–7.
- Dugatkin LA, Druen MW, Godin J-GJ. 2003. The disruption hypothesis does not explain mate-choice copying in the guppy (*Poecilia reticulata*). *Ethology* 109:67–76.

- Dugatkin LA, Godin J-GJ. 1992. Reversal of female mate choice by copying in the guppy (*Poecilia reticulata*). *Proc R Soc Lond B* 249:179–84.
- Dugatkin LA, Godin J-GJ. 1993. Female mate copying in the guppy (*Poecilia reticulata*): age-dependent effects. *Behav Ecol* 4:289–92.
- Dugatkin LA, Godin J-GJ. 1998. Effects of hunger on mate-choice copying in the guppy. *Ethology* 104:194–202.
- Dugatkin LA, Lucas JS, Godin J-GJ. 2002. Serial effects of mate-choice copying in the guppy (*Poecilia reticulata*). *Ethol Ecol Evol* 14:45–52.
- Fisher RA. 1958. *The genetical theory of natural selection*. 2nd ed. New York: Dover.
- Forsgren E, Karlsson A, Kvarnemo C. 1996. Female sand gobies gain direct benefits by choosing males with eggs in their nests. *Behav Ecol Sociobiol* 39:91–6.
- Galef BG Jr, White DJ. 1998. Mate-choice copying in Japanese quail, *Coturnix coturnix japonica*. *Anim Behav* 55:545–52.
- Galef BG Jr, White DJ. 2000. Evidence of social effects on mate choice in vertebrates. *Behav Processes* 51:167–75.
- Gibson RM, Bradbury JW, Vehrencamp SL. 1991. Mate choice in lekking sage grouse revisited: the roles of vocal display, female site fidelity, and copying. *Behav Ecol* 2:165–80.
- Gibson RM, Höglund J. 1992. Copying and sexual selection. *Trends Ecol Evol* 7:229–31.
- Godin J-GJ, Herdman EJE, Dugatkin LA. 2005. Social influences on female mate choice in the guppy, *Poecilia reticulata*: generalized and repeatable trait-copying behaviour. *Anim Behav* 69:999–1005.
- Goldschmidt T, Bakker TCM, Feuth-De Bruijn E. 1993. Selective copying in mate choice of female sticklebacks. *Anim Behav* 45:541–7.
- Goulet D. 1995. Temporal patterns of reproduction in the Red Sea damselfish *Amblyglyphidodon leucogaster*. *Bull Mar Sci* 57:582–95.
- Goulet D. 1997. Reproductive behavior and spawning success of female *Amblyglyphidodon leucogaster* (Pisces, Pomacentridae) from the Red Sea. *Environ Biol Fish* 50:49–60.
- Goulet D. 1998. Spawning success in the damselfish *Amblyglyphidodon leucogaster*: the influence of eggs in the nest. *Anim Behav* 55:651–64.
- Höglund J, Alatalo RV, Gibson RM, Lundberg A. 1995. Mate-choice copying in black grouse. *Anim Behav* 49:1627–33.
- Höglund J, Alatalo RV, Lundberg A. 1990. Copying the mate choice of others? Observations on female black grouse. *Behaviour* 114:221–31.
- Jamieson IG. 1995. Do female fish prefer to spawn in nests with eggs for reasons of mate choice copying or egg survival? *Am Nat* 145:824–32.
- Jennions MD, Petrie M. 1997. Variation in mate choice and mating preferences: a review of causes and consequences. *Biol Rev* 72:283–327.
- Kirkpatrick M, Dugatkin LA. 1994. Sexual selection and the evolutionary effects of copying mate choice. *Behav Ecol Sociobiol* 34:443–9.
- Knapp RA, Sikkil PC, Vredenburg VT. 1995. Age of clutches in nests and the within-nest spawning-site preferences of three damselfish species (Pomacentridae). *Copeia* 1995:78–88.
- Kraak SBM. 1996. 'Copying mate choice': which phenomena deserve this term? *Behav Processes* 36:99–102.
- Lafleur DL, Lozano GA, Sclafani M. 1997. Female mate-choice copying in guppies, *Poecilia reticulata*: a re-evaluation. *Anim Behav* 54:579–86.
- Laland KN. 1994. Sexual selection with a culturally transmitted mating preference. *Theor Popul Biol* 45:1–15.
- Laland KN, Reader SM. 1999. Foraging innovation in the guppy. *Anim Behav* 57:331–40.
- Mazeroll AI, Montgomery WL. 1995. Structure and organization of local migrations in brown surgeonfish (*Acanthurus nigrofuscus*). *Ethology* 99:89–106.
- Nordell SE, Valone TJ. 1998. Mate choice copying as public information. *Ecol Lett* 1:74–6.
- Parker GA. 1983. Mate choice and mating decisions. In: Bateson PPG, editor. *Mate choice*. Cambridge, UK: University of Cambridge Press. p 141–66.
- Patriquin-Meldrum KJ, Godin J-GJ. 1998. Do female three-spined sticklebacks copy the mate choice of others? *Am Nat* 151:570–7.
- Pomiankowski A. 1987. Sexual selection: the handicap principle does work—sometimes. *Proc R Soc Lond B* 231:123–45.
- Pruett-Jones S. 1992. Independent versus nonindependent mate choice: do females copy each other? *Am Nat* 140:1000–9.
- Reader SM, Kendal JR, Laland KN. 2003. Social learning of foraging sites and escape routes in wild Trinidadian guppies. *Anim Behav* 66:729–39.
- Reynolds JD, Gross MR. 1990. Costs and benefits of female mate choice: is there a lek paradox? *Am Nat* 136:230–43.
- Ridley M, Rechten C. 1981. Female sticklebacks prefer to spawn with males whose nests contain eggs. *Behaviour* 76:152–61.
- Sargent RC. 1988. Paternal care and egg survival both increase with clutch size in the fathead minnow, *Pimephales promelas*. *Behav Ecol Sociobiol* 23:33–7.
- Sargent RC, Gross MR. 1993. Williams' principle: an explanation of parental care in teleost fishes. In: Pitcher TJ, editor. *The behaviour of teleost fishes*. New York: Chapman & Hall. p 333–61.
- Schlupp I, Ryan MJ. 1997. Male sailfin mollies (*Poecilia latipinna*) copy the mate choice of other males. *Behav Ecol* 8:104–7.
- Sikkil PC. 1994a. Filial cannibalism in a paternal-caring marine fish: the influence of egg developmental stage and position in the nest. *Anim Behav* 47:1149–58.
- Sikkil PC. 1994b. Why female garibaldi prefer males with young: a test of the parental investment hypothesis. *Ethol Ecol Evol* 6:191–211.
- Sirot E. 2001. Mate-choice copying by females: the advantages of a prudent strategy. *J Evol Biol* 14:418–23.
- Slagsvold T, Breieghagen T, Stenmark G, Lifjeld JT. 1988. On the cost of searching for a mate in female pied flycatchers *Ficedula hypoleuca*. *Anim Behav* 36:433–42.
- Stöhr S. 1998. Evolution of mate-choice copying: a dynamic model. *Anim Behav* 55:893–903.
- Trivers RL. 1972. Parental investment and sexual selection. In: Campbell B, editor. *Sexual selection and descent of man*. Chicago, IL: Aldine. p 136–79.
- Wade MJ, Pruett-Jones SG. 1990. Female copying increases the variance in male mating success. *Proc Natl Acad Sci USA* 87:5749–53.
- Westneat DF, Walters A, McCarthy TM, Hatch MI, Hein WK. 2000. Alternative mechanisms of nonindependent mate choice. *Anim Behav* 59:467–76.
- White DJ, Galef BG Jr. 1999. Mate choice copying and conspecific cueing in Japanese quail, *Coturnix coturnix japonica*. *Anim Behav* 57:465–73.
- White DJ, Galef BG Jr. 2000. 'Culture' in quail: social influences on mate choices of female *Coturnix japonica*. *Anim Behav* 59:975–9.
- Widemo MS. 2006. Male but not female pipefish copy mate choice. *Behav Ecol* 17:255–9.
- Witte K, Massmann R. 2003. Female sailfin mollies, *Poecilia latipinna*, remember males and copy the choice of others after 1 day. *Anim Behav* 65:1151–9.
- Witte K, Noltemeier B. 2002. The role of information in mate-choice copying in female sailfin mollies (*Poecilia latipinna*). *Behav Ecol Sociobiol* 52:194–202.
- Witte K, Ryan MJ. 1998. Male body length influences mate-choice copying in the sailfin molly *Poecilia latipinna*. *Behav Ecol* 9:534–9.
- Witte K, Ryan MJ. 2002. Mate choice copying in the sailfin molly, *Poecilia latipinna*, in the wild. *Anim Behav* 63:943–9.
- Witte K, Ueding K. 2003. Sailfin molly females (*Poecilia latipinna*) copy the rejection of a male. *Behav Ecol* 14:389–95.
- Zar JH. 1984. *Biostatistical analysis*. 2nd edition. Englewood Cliffs, NJ: Prentice-Hall.