



Female mate choice copying affects sexual selection in wild populations of the ocellated wrasse

SUZANNE H. ALONZO

Department of Ecology and Evolutionary Biology, Yale University

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Explaining the factors that determine the distribution of mating success among males is essential to our understanding of sexual selection. Classic theory has focused on how competition among males and female choice for traits of the male or his territory drive sexual selection. Recent theory has also shown that female mate choice copying can alter the strength and direction of selection on male traits. Yet, we know very little about the prevalence and importance of nonindependent female choice in wild populations. In a species with male territoriality and paternal care (the ocellated wrasse, *Symphodus ocellatus*), I first show that females express nonindependent mate choice, responding both to the recent mating success of the male and to the presence of other spawning females rather than to variation in male courtship or defence of the nest. Females were significantly more likely to spawn with the same male when another spawning female was present than when they were alone at the nest, providing some of the first direct evidence of female mate choice copying under natural conditions in the wild. I further show that a short-term experimental increase in a territorial male's mating success attracts more females in the future and increases male paternal care. These observed patterns of female choice and male care are consistent with female choice for the direct benefits of male care where the best indicator trait of male parental effort is the mating behaviour of other females rather than male courtship behaviour or physical traits.

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Determining what causes variation among males in mating and fertilization success is essential to our understanding of sexual selection. Classic theory has focused on how intrasexual competition and intersexual mate choice affect the potential for sexual selection. Empirical and theoretical studies of mate choice have mainly focused on female preferences for male traits and asked whether these preferences are arbitrary or associated with indirect or direct benefits to females (Andersson 1994; Andersson & Simmons 2006; Kokko et al. 2006). One observation not explained by this classic theory is the finding that females in a variety of species express nonindependent mate choice (i.e. the mating behaviour

of one female depends on the mating behaviour of other females; Gibson & Hoglund 1992; Pruett-Jones 1992; Westneat et al. 2000). While evidence of nonindependent female mate choice exists, we know very little about its effect on the evolution of male traits and its importance under natural conditions in the wild.

For example, female mate choice copying has been documented in the laboratory for a number of species (where female mate choice copying is generally defined as a female being more likely to mate with a male after observing another female mating with that male; reviewed in Westneat et al. 2000). Captive studies of both guppies and mollies indicate that female preferences for males can be influenced and even reversed by observing the mating behaviour of other females (e.g. Dugatkin 1992; Witte & Ryan 2002; Amlacher & Dugatkin 2005; Godin et al. 2005; Hill & Ryan 2006; but see Lafleur

Correspondence: S. H. Alonzo, Department of Ecology and Evolutionary Biology, Yale University, P.O. Box 208106, New Haven, CT 06520, U.S.A. (email: suzanne.alonzo@yale.edu).

et al. 1997; Brooks 1999). Female mate choice copying has also been suggested to occur in a variety of other taxa including lekking birds and even humans (e.g. Shuster & Wade 1991; McComb & Clutton-Brock 1994; Marks et al. 1994; Hoglund et al. 1995; Stillman et al. 1996; Jennions & Petrie 1997; Galef & White 1998; Jones et al. 2007). However, under natural conditions it is difficult to differentiate between shared mating preferences and female mate choice copying. As a result, existing evidence for female mate choice copying has either been under artificial conditions or been unable to rule out the possibility that aspects of the male or reproductive site explain the shared mate choice of females. The two most common explanations for female mate choice copying are the avoidance of assessment costs and the reduction of assessment errors by inexperienced females that copy the choice of others (e.g. Losey et al. 1986; Wade & Pruett-Jones 1990; Dugatkin 1992; Pruett-Jones 1992; Kirkpatrick & Dugatkin 1994; Westneat et al. 2000). Hence, females are argued to copy to mate with males that express preferred traits.

Another form of nonindependent female mate choice is found in some fishes with exclusive male parental care where both observational studies and experimental manipulations indicate that females often prefer males with eggs (e.g. Rohwer 1978; Ridley & Rechten 1981; Marconato & Bisazza 1986; Unger & Sargent 1988; Jamieson 1995; Forsgren et al. 1996; Afonso & Santos 2005). This preference for eggs, like female mate choice copying, could arise to avoid assessment costs and errors. However, an additional explanation is that females may prefer males with eggs if individual offspring survival is generally higher on territories with eggs. This can occur because nests with many eggs have a lower per egg risk of predation or filial cannibalism (e.g. Sikkel 1994; Forsgren et al. 1996). In addition, the presence of healthy eggs could indicate the quality of male parental care, or successful males may show increased parental effort (e.g. Sargent 1988). In this case, females are argued to use the presence of healthy eggs or other cues of recent mating success as indicators of higher expected offspring survival.

Despite increasing evidence for nonindependent female mate choice, we still understand little about its evolutionary implications and few studies have explored nonindependent female mate choice under natural conditions. Existing theory predicts that female mate choice copying and other forms of nonindependent female mate choice can alter the strength and even the direction of sexual selection on male traits (Wade & Pruett-Jones 1990; Dugatkin 1992; Pruett-Jones 1992; Marks et al. 1994; Agrawal 2001; Dugatkin 2005) while no empirical work has examined the predictions of this theory. Instead, most empirical research has focused on documenting nonindependent female mate choice and determining the cues used by females to select males (e.g. Dugatkin & Godin 1993; Forsgren et al. 1996; Goulet & Goulet 2006). In addition, we know little about the effect of independent versus nonindependent female mate choice on female fitness (but see Forsgren et al. 1996).

The effect of nonindependent female mate choice on sexual selection will depend on how females choose mates

in the absence of cues of recent male mating success and to what extent variation in male traits versus male mating success influences female mating behaviour. For example, if the first female chooses among males based on a male trait (such as size or colour pattern) and all subsequent females copy the choice of that female (independent of the cue used), the distribution of mating success among males will be highly skewed and selection on the male trait will be very strong. In contrast, if a female chooses mates at random in the absence of any cues of past mating success but otherwise prefers males chosen by other females, then the distribution of mating success among males will still be skewed but there will be no sexual selection on male traits. While it has been shown experimentally in the laboratory that female mate choice copying can reverse female preferences, in the species where nonindependent female mate choice has been suggested, females are also known to first choose among males based on traits (e.g. Downhower & Brown 1980; Houde 1987; Bisazza & Marconato 1988; Long & Houde 1989; Milinski & Bakker 1990; Bakker & Mundwiler 1994; Ptacek & Travis 1997; Kvarnemo & Forsgren 2000; Borg et al. 2006). Here, I present evidence of female mate choice copying under natural conditions in the wild where mate choice is based on the presence of other females rather than on male traits. I further show that a short-term experimental increase in male mating success leads to a lasting increase in future male mating success and parental care behaviour in previously unsuccessful males.

In the ocellated wrasse, *Symphodus ocellatus*, large males defend territories where they build nests of algae, court females and provide parental care (Lejeune 1985). Smaller males in the population, called sneakers, hover around nests and 'sneak' fertilizations by joining a nesting male and female during spawning (Taborsky et al. 1987). Sneakers and nesting males represent separate life history pathways, although it is not known whether they are genetically or environmentally determined (Alonzo et al. 2000). The distribution of sneakers among nests is skewed and positively correlated with mating rate (Lejeune 1985; Taborsky et al. 1987; Wernerus et al. 1989; Alonzo & Warner 2000; Alonzo 2004). During the breeding season, females spend most of their time foraging and produce a new batch of eggs every few days (Taborsky et al. 1987). Females usually visit multiple territories within an area before spawning but then leave the male and his territory and do not provide any parental care (Lejeune 1985; Taborsky et al. 1987). In this species, the key male trait affecting female fitness is male parental care. Fertilized eggs do not survive without male care (Taborsky et al. 1987). Yet, desertion of nests by males before providing parental care is common (Taborsky et al. 1987) and the presence of sneakers does not explain nest desertion (Alonzo 2004).

At any point in time, the distribution of mating success among nesting males is skewed. Yet, extensive research has failed to find any behavioural or physical trait of the nesting male or his territory that can explain this variation in success (Lejeune 1985; Taborsky et al. 1987; van den Berghe et al. 1989; Alonzo & Warner 1999, 2000; Alonzo

et al. 2000; Alonzo 2004). Instead, the best predictor of current mating rate is the recent mating success at the territory within the same nest cycle (Alonzo 2004). Experiments removing successful nesting males indicated that once mating success is established at a site, female visiting and spawning rates do not change when a new, previously unsuccessful male takes over the territory (Alonzo 2004). Two possible explanations for these patterns exist. First, females may simply prefer some unknown aspect of the nest or territory. Second, nonindependent female mate choice due either to the presence of other females spawning or to the presence of eggs in the nest could explain this pattern of male mating success.

Here, I first show that female ocellated wrasse express nonindependent mate choice under natural conditions by documenting the positive effect of other females and recent mating success on female mating behaviour. In the presence of nonindependent female mate choice, how females select a male initially will determine the distribution of mating success among males and the direction and strength of sexual selection. Thus, to examine how this nonindependent female mate choice affects sexual selection in this species, it is necessary to determine what factors explain how males become successful initially and how variation in initial mating success affects future mating success and male parental care. To force females to choose a new male (without a history of recent mating success), I prevented the successful male in a group of otherwise very low- or no-success nesting males from spawning for a few hours and observed the immediate and long-term changes in the mating success and behaviour of focal (previously unsuccessful) males. The combination of these two studies allowed me to first document the existence of nonindependent female mate choice and then determine what factors influence how females initially choose among males or nests and how it affects future mating success and parental care behaviour.

METHODS

Research Site and Study Species

This research was conducted during the breeding season (May–June) in 1996, 1997 and 2000 in the Baie de Revellata near Calvi, Corsica. At the beginning of each field season, nesting males were caught with small nets, measured and individually marked using a subcutaneous injection of a vital stain, alcian blue (Lejeune 1985). Behavioural observations were made daily above 15 m depth using SCUBA. The entire study area (rocky reef habitat along approximately 200 m of coastline) was surveyed daily to locate new nests and to record the presence and identity of the nesting male, the number of sneakers and the parental care behaviour of the territorial male at all existing nests. Past research has shown that a brief observation of the number of sneakers near the nest can be used as a proxy for mating rate at the nest because the number of sneakers shows high repeatability and is correlated with the rate of spawning and pair spawning

(e.g. just the territorial male spawning with the females; Alonzo 2004).

During the approximately 2-month breeding season, nesting males go through three to five nest cycles each lasting on average 10 days. During each cycle, males first build a nest, then court females and spawn before providing care. Nesting males are easily categorized as being in the building, spawning or parental phase of their nest cycle based on their behaviour (Alonzo & Warner 1999, 2000; Alonzo 2004). Successful nesting males will spawn for 3–5 days before providing parental care for 2–6 days (Lejeune 1985; Lejeune & Michel 1986). The number of eggs in a male's nest can range from a few hundred to over 50 000 and there is no evidence that nesting males are limited in the number of eggs they can defend and aerate (Lejeune 1985). Larvae emerge from the nest at night followed by an approximately 2-month pelagic larval stage (Lejeune 1985; Lejeune & Michel 1986). Although deserted eggs do not survive, some nesting males will desert nests with eggs, presumably because the energetic and time costs of parental care and expected future mating opportunities outweigh caring for a smaller number of eggs (Carlisle 1982; Taborsky et al. 1987; Alonzo 2004). It is unknown, however, whether females avoid males based on cues indicating male parental quality or whether males desert because they are unsuccessful.

As described above, there is no evidence for female mate choice among males based on known characteristics of the male or nest site. Experimental manipulations of the number of sneakers present at a nest show that females prefer to spawn at successful nests with few sneakers (van den Berghe et al. 1989; Alonzo & Warner 1999, 2000). Although some evidence suggests that females may prefer nests with high recent mating success (Alonzo 2004), nothing is known about how females initially choose among nests or males. Females often mate at one territory multiple times on a single day, but they do not usually mate with the same male or at the same territory between clutches (Taborsky et al. 1987) because males become unavailable for spawning once they are parental. Females typically spawn within the same general area (Taborsky et al. 1987; Alonzo & Warner 2000), but little is known about female movement patterns. However, females are highly iteroparous during the breeding season, so there is likely to be a trade-off between searching for mates and foraging.

Behavioural Observations

I made 10 min focal observations of each nest using SCUBA, during which I noted all mating and courtship behaviour. I used an observation period of 10 min because it provides a representative sampling of current mating rate and reproductive behaviour of males and females at the nest in this species (Alonzo & Warner 1999, 2000; Alonzo 2004). I remained approximately 3 m from the nest being observed and remained as still as possible during each observation. Territorial males are large and colourful, whereas sneaker males are drab and small. Females are

easily distinguished from males by their coloration and behaviour.

The nest site and identity of the nesting male were noted for each observation. The number of sneakers within 3 m and oriented towards the nest were counted once each minute and averaged over the 10 min observation. I also recorded the number of females that came within 10 cm of the nest (number of female visits), the number of females spawning, total number of spawns and number of spawns joined by sneaker males. In addition, the courtship behaviour and nest defence of territorial males was noted during each observation. Territorial males chase sneakers, other territorial males and other species of fish away from the nest. The number of chases directed to each group was also counted. In addition, males display a number of courtship behaviours including following the female, courtship nest building and courtship spawning (Taborsky et al. 1987). These courtship behaviours were all noted during each observation and summed to represent a courtship rate by the nesting male. Sneaker males do not court females.

Nonindependent Female Mate Choice

The presence of sneakers at a nest is indicative of high recent mating success at a nest in ocellated wrasse (Alonzo 2004). I therefore observed female behaviour at randomly selected nests that either were in the spawning phase of the nest cycle but had no sneakers present (low recent mating success nests) or had multiple sneakers present at the nest (high recent mating success nests). I conducted behavioural observations at these nests as described above noting female spawning behaviour, male courtship and defence and the presence of sneakers. In addition, for each female that visited a nest, I recorded whether the female visited the nest when another female was present or whether the female was alone at the nest. I examined overall differences between low- and high-success nests using two-sample *t* tests assuming unequal variances, because by definition these nests differ in their spawning rates, causing unequal underlying variances in mating behaviour (Ruxton 2006). However, the results remained the same for tests assuming equal variances, and assuming unequal variances is appropriate and conservative given the expectation of underlying biologically driven differences in the variances between groups (Ruxton 2006). I also used paired comparisons (*t* tests and repeated measures ANOVA) to examine the probability that a female would mate in the presence or absence of other females at a given nest. All tests are two tailed.

Neighbour Male Removal Experiments

Once there has been a lot of spawning in a nest, the mating rate at the nest is likely to remain high during the rest of the spawning phase of the nest cycle (Alonzo 2004). Yet, only a few males with no or low mating success will become one of these very successful males within the same nest cycle (Alonzo 2004). However, it was not known how females initially choose among males or

nests, thus causing some males to become very successful. In addition, it was not known whether male mating success itself explains female choice and male parental care behaviour or whether unknown characteristics of the male or nest site act as indicator cues of paternal care. To determine how males initially attain high success and how male mating success itself affects female choice and parental care behaviour, I conducted a two-phase experiment observing the mating success and behaviour of initially less successful males, first when keeping nearby very successful males from spawning and then when allowing these successful males to mate again.

In the first phase, to determine how females initially choose among nests when a nest with high recent mating success is not available, I selected clusters of nests with one very successful male and multiple low-success and no-success males. In this species, nests tend to occur in clusters of three to five nests, and females usually choose a neighbouring male when the preferred male is not available (Alonzo & Warner 2000). I then covered the nest of the very successful male and observed a randomly selected focal male once before and twice after the removal of the successful neighbour. For this experiment, I chose focal nests that were in the spawning phase of the nest cycle (determined by male courtship towards females) at which there were no sneakers present. I observed each focal nest for 10 min, counting the frequency of females visiting the nest, females spawning, total spawns, male courtship and male defence. To determine whether small initial differences in mating rate (equivalent to one or two females spawning) affected the response to the manipulation, I classified focal males as initially 'low-success' or 'no-success' based on whether they were observed to mate prior to the manipulation. Low- and no-success nests had no sneakers present, whereas high-success nests had multiple sneakers present, which is correlated with high mating rates in this species (Alonzo 2004). The nest of the high-success neighbour was then covered using an aquarium net, which allowed the nesting male to remain on his nest but blocked female and sneaker access to the high-success nest. Second (0.5–1 h later) and third (3–4 h later) observations were made at the focal nest following the removal of the high-success neighbour. Changes in mating rate, female visiting rate and sneaker presence at the focal nest were compared using repeated measures ANOVA with no- and low-success males as separate groups. Within time period comparisons were made between no- and low-success males using ANOVA. The data were square-root transformed to address the tests' assumptions of normality. Controls were conducted by observing focal nests in the same way but by covering the nest of an unsuccessful neighbour instead of the successful neighbour.

During the second phase of the experiment, to determine how a short-term experimental manipulation of nesting male mating success affects future female mate choice and male parental care behaviour, I also observed these males throughout the nest cycle. Following the first phase of the experiment, the nests of the high-success neighbours were uncovered and these males were allowed to resume spawning. All focal nests and previously

covered nests were observed daily for the rest of the nest cycle. These observations were used to examine differences in mating success and parental care between male types (naturally high-success, initially low-success and initially no-success males) following the experiment. For phase 2, nesting male mating success was estimated by the number of sneaker males observed at the nest in a 1 min observation. As described above, past research has found this method to be a more reliable indicator of mating success than a short observation of actual mating (Alonzo 2004). If originally high-success males were more attractive (independent of mating success), then focal experimental males that experience an increase in mating success during the first phase of the experiment should not experience a lasting increase in their mating success. By contrast, both originally high-success males (that were covered) and experimentally induced high-success males should have high future mating success, if it is mating success (or eggs in the nest) itself that attracts females. In addition, if mating success rather than male traits determine male parental care, then males that were initially high success and males that were experimentally high success should be equally likely to provide care compared to males that did not experience an experimental increase in mating success as a result of the experiment.

RESULTS

Nonindependent Female Mate Choice

In general, females were more likely to mate at nests with a history of high recent mating success (proportion of all visiting females that spawned at high- versus low-success nests, two-sample t test assuming unequal variances: $t_{60} = -2.14$, $P = 0.036$). Females also spawned with a higher probability when they arrived at a nest where other females were present (repeated measures ANOVA: proportion spawning with versus without other females: $F_{1,49} = 17.42$, $P = 0.0001$; proportion spawning*success type: $F_{1,49} = 0.72$, $P = 0.40$; Fig. 1). However, in the presence of another female, there was no longer a significant effect of the recent history of mating success (high versus low) on the probability that a female would spawn (two-sample t test assuming unequal variance: $t_{46} = -0.598$, $P = 0.55$). In summary, both recent mating success and the presence of other spawning females increased the probability that a female would spawn with a nesting male (Fig. 1). Sample sizes varied slightly because I excluded from the analysis all observations in which the number of females visiting the nest (total, with other females or alone) was zero.

Low-success males actually had higher courtship rates (all rates are per 10 min; $\bar{X} \pm SE$: low: 13.0 ± 0.93 ; high: 4.14 ± 0.79 ; two-sample t test assuming unequal variances: $t_{75} = 7.28$, $P < 0.0001$) and nest defence rates ($\bar{X} \pm SE$: low: 1.37 ± 0.25 ; high: 0.50 ± 0.20 ; two-sample t test assuming unequal variances: $t_{77} = 2.77$, $P = 0.007$) despite their lower female visiting rate ($\bar{X} \pm SE$: low: 4.78 ± 0.49 ; high: 16.96 ± 1.21 ; two-sample t test assuming unequal variances: $t_{36} = -9.35$, $P < 0.0001$) and total

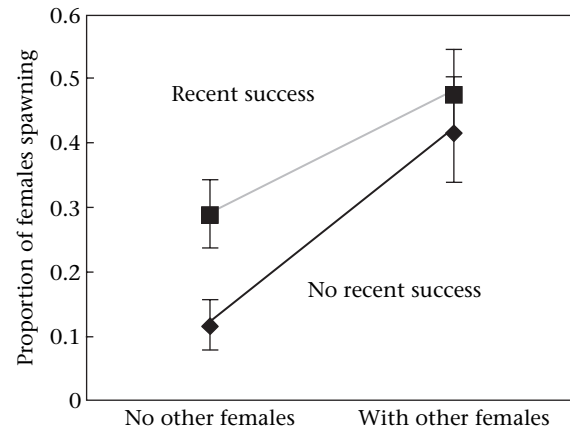


Figure 1. Mean \pm SE proportion of ocellated wrasse females that spawned in the absence (left) and the presence (right) of other females in nests that had no recent history of mating success (◆) and nests that had recently achieved high mating success (■).

spawning rates ($\bar{X} \pm SE$: low: 2.5 ± 0.72 ; high: 10.25 ± 1.85 ; two-sample t test: $t_{35} = -3.9$, $P < 0.0001$).

Neighbour Male Removal Experiments: First Phase

Following the removal of their successful neighbour, focal males experienced an increase in the number of visits by females, number of females spawning, total spawning rate and number of sneakers at the nest (repeated measures ANOVA: visits: $F_{2,78} = 5.10$, $P = 0.008$; females: $F_{2,78} = 3.86$, $P = 0.03$; spawns: $F_{2,78} = 4.65$, $P = 0.01$; sneakers: $F_{2,78} = 16.52$, $P < 0.0001$; Fig. 2). Significant interactions were also found between initial success type and the number of females spawning, the total spawning rate and the presence of sneakers at the nest (repeated measures ANOVA: females*type: $F_{2,78} = 10.17$, $P = 0.0001$; spawns*type: $F_{2,78} = 9.94$, $P = 0.0001$; sneaker*type: $F_{2,78} = 8.61$, $P = 0.004$). Thus, removal of a high-success neighbour increased the presence of females at both nest types (initially no- and low-success). However, the change in mating success was not equal between initially no- and low-success nest types (Fig. 2). Originally low-success males became very successful, attracting many females, followed by an increase in the number of sneakers attracted to their nest (repeated measures ANOVA: $F_{1,39} = 12.76$, $P = 0.001$; Fig. 2). Hence, a very small difference in initial mating success (equivalent to one female spawning) was associated with whether males eventually experienced high mating success. Yet, no significant differences existed between no- and low-success males in their courtship of females or defence of the nest (ANOVA: courtship: $F_{1,29} = 0.13$, $P = 0.72$; defence: $F_{1,29} = 0.17$, $P = 0.69$). For the controls, I found no significant differences between observations for any variable (repeated measures ANOVA: females: $F_{2,18} = 1.27$, $P = 0.30$; spawning rate: $F_{2,18} = 0.86$, $P = 0.44$; sneakers: $F_{2,18} = 0.42$, $P = 0.66$; sneaking rate: $F_{2,18} = 0.78$, $P = 0.47$) except female visiting rate in which there was

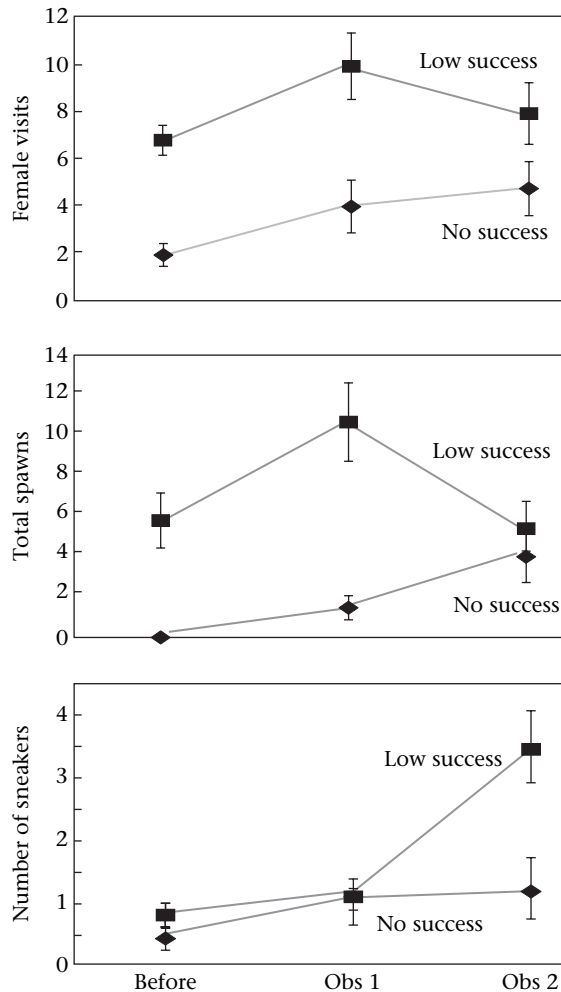


Figure 2. Mean \pm SE number of (a) female visits, (b) total spawns and (c) sneaker males present at focal nests of male ocellated wrasse before and after (Obs 1 = 0.5–1 h; Obs 2 = 3–4 h) removal of their more successful neighbour. Focal males were grouped according to whether they showed low success or no success before removal of their more successful neighbour.

a significant difference between observations (repeated measures ANOVA: $F_{2,18} = 3.52$, $P = 0.051$) driven by a significantly higher female visiting rate in the third observation (repeated measures ANOVA, first versus third observation: $F_{1,9} = 5.21$, $P = 0.048$). For the controls, no differences in courtship (repeated measures ANOVA: $F_{2,18} = 0.56$, $P = 0.54$) or nest defence (repeated measures ANOVA: $F_{2,18} = 1.76$, $P = 0.20$) were observed between observations.

Neighbour Male Removal Experiments: Second Phase

In the second phase of the experiment, the nests of high-success neighbouring males were uncovered and all males were allowed to continue spawning normally. Significant differences in future mating success were found between initially high-, low- and no-mating success males ($F_{2,71} = 4.79$, $N = 74$, $P = 0.01$; Fig. 3). Focal males

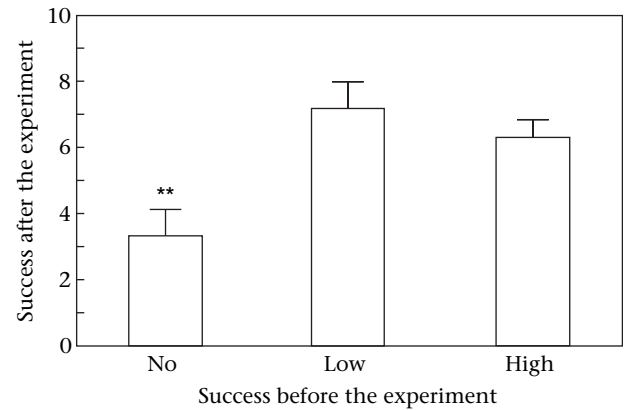


Figure 3. Mean \pm SE daily mating success of initially no-success, low-success and high-success male ocellated wrasse following the experiment. Daily mating success following the experiment was estimated using the number of sneakers present at the nest (see text for details; Alonzo 2004). ** $P < 0.01$.

that were initially low-success had significantly greater success following the experiment than initially no-success males, but there were no significant differences in mating success between the originally high-success neighbours (whose nests were covered during the manipulation) and initially low-success focal males (based on Tukey's post hoc comparison of the means with $\alpha = 0.05$). Males that were initially no-success (and thus did not experience an experimental increase in their mating success; Fig. 2) were also much more likely to desert their nests without providing care (high success (2/36) versus low success (1/19) versus no success (10/19): chi-square tests: $\chi^2_2 = 21.7$, $P < 0.001$; high versus low success: $\chi^2_{1,P} = 0.0007$, $P = 0.98$; high and low success versus no success: $\chi^2_{1,P} = 21.7$, $P < 0.001$; Fig. 4).

DISCUSSION

Female ocellated wrasse expressed nonindependent mate choice in two ways. First, the probability that a female would mate was significantly higher in the presence of another spawning female (Fig. 1). Second, in the absence of other females, individual females were more likely to spawn at nests with a recent history of mating success (Fig. 1). However, the effect of recent mating success disappeared in the presence of other females. Thus both cues of recent mating success (such as eggs in the nest or the presence of sneakers) and the presence of other females directly affected female mate choice. These results are consistent with past observations that a male's current mating success is positively correlated with recent mating success and that mating rates remain high following territorial take-overs (Alonzo 2004). However, these results also demonstrate for the first time that females copy the mating behaviour of other females directly and that female mate choice copying is sufficient to determine the skewed distribution of mating success among nesting males, as females will initially spawn in nests when another female is present. The demonstration that the presence of another female significantly increases the probability of spawning at the

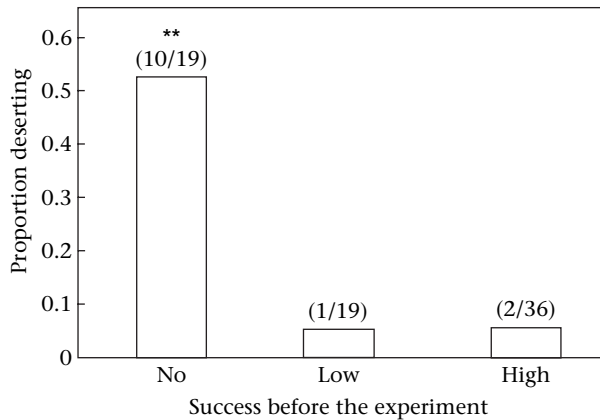


Figure 4. Proportion of initially no-success, low-success and high-success male ocellated wrasse that deserted their nests without providing parental care during phase 2. Values above bars denote the frequency of nests deserted/nests observed. $**P < 0.01$.

same nest is inconsistent with inherent differences between males or nest sites. While a number of studies have shown female mate choice copying under experimental laboratory conditions, no previous study has documented females mating preferentially in the presence of other females under natural conditions. In the whitebelly damselfish, *Amblyglyphidodon leucogaster*, Goulet & Goulet (2006) found that females known to have observed another female spawning with a male were also more likely to be seen spawning with the same male a few days later, but their results do not rule out the possibility that those females were expressing a shared mating preference for unknown traits of the male or nest site. In the ocellated wrasse, females directly copy the mate choice of other females and also express preferences for nests with a recent history of high mating success. Together, these two forms of nonindependent mate choice can explain the skewed distribution of mating success in this species independent of traits of the male or his nest site. The effect of nonindependent female mate choice on the strength and direction of sexual selection depends on how females initially choose among males. In this species, nonindependent mate choice is consistent with no selection on male traits due to female mate choice.

Following the removal of a successful neighbouring male, females preferred males with low previous mating success (Fig. 2). Yet, these males did not show significantly higher rates of courtship or defence and past research has found no evidence of female choice among males based on size, colour pattern or nest site (Wernerus 1988; Wernerus et al. 1989). While this pattern alone could be consistent with differences between focal males or their nest sites in inherent 'attractiveness', the increased mating success of these males persisted even when the initially more successful and thus presumably more 'attractive' neighbours were allowed to resume mating (Fig. 3). Furthermore, the evidence for female mate choice copying described above demonstrates that such small initial differences can be driven by two females arriving at a previously unsuccessful nest simultaneously.

Males that experienced the experimental transfer of mating success due to the manipulation were just as likely to remain with their nest during parental care as were their

initially more successful neighbours (Fig. 4). In contrast, males that did not experience a substantial increase in mating success as a result of the manipulation were much more likely to desert their nests. This pattern is consistent with male parental care behaviour being affected by the males' mating success rather than by intrinsic differences between males a priori. In general, females that choose successful nests were more likely to have a male care for their offspring. This pattern is inconsistent with the classic expectation that females choose among males based on a priori indicator traits of male parental quality. Instead, nonindependent female mate choice generates differences in male mating success, which also determines the expected probability of male parental care and thus probably makes other male traits unreliable indicators of male parental care.

While it is impossible to completely rule out some undetectable variable explaining the initial small variation in mating success among males, the results presented here are consistent with female choice among males based on the presence of other females and recent mating success rather than on the traits or identity of the male. This interpretation is also supported by past research finding no evidence in this species that females choose among males based on their physical traits, courtship behaviour, nest site, nest characteristics or identity despite a highly skewed distribution of mating success among males (Wernerus 1988; Wernerus et al. 1989; Alonzo & Warner 1999, 2000; Alonzo 2004). There is, however, strong evidence that females prefer to spawn in the presence of other females and that recent success at the nests can explain the observed distribution of mating success among males. In turn, more successful males are more likely to provide parental care (Carlisle 1982) regardless of whether their success occurs naturally or results from experimental manipulation (this study; Fig. 4). A likely implication of the observed pattern is that nonindependent female mate choice is favoured in this species because it is strongly associated with obligate male parental care. This preference for the presence of other females may also mediate conflict between the sexes over parental effort (Lindstrom 2000). This has important implications for patterns of sexual selection as a result of nonindependent female mate choice. Despite a strong potential for sexual selection on males (Shuster & Wade 2003), there is no evidence of female selection based on male traits in this species. Nesting males do, however, express secondary sexual characteristics including courtship behaviour, body coloration and large size compared to small and drab females and sneakers. It is likely that these traits are threshold indicators of nesting male status since females will not spawn with sneaker males. Thus, the existence of these sexually dimorphic traits may be explained by female choice between nesting males and sneakers rather than by among-nesting male variation in these traits.

To understand the effect of nonindependent female mate choice on sexual selection, it is essential to know how females choose in the absence of other females or cues indicating the mate choice of other females. Especially in the presence of nonindependent female mate choice, a skewed distribution of mating success among males may not be indicative of strong sexual selection on male traits if

female initial choice is not based on characteristics of the male or his territory. This will be particularly likely for species in which male parental effort increases with mating success as shown here and found in a number of other species (e.g. Sargent 1988). All existing evidence in the ocellated wrasse is consistent with female choice for the presence of other females independent of intrinsic male traits. While most sexual selection theory has focused on female preferences for heritable male traits, it has been argued recently that direct benefits to females may be more important than indirect genetic benefits (Charmantier & Sheldon 2006). One of the most obvious direct benefits of female choice is male parental care. Females are usually argued to choose among males based on indicator traits (Hoelzer 1989; Hill 1991; Buchanan & Catchpole 2000). However, females may also choose directly among males based on male parental care (Pampoulie et al. 2004; Lindstrom et al. 2006). Theory focused on direct benefits has argued that females should choose based on traits expressed by the males that predict a priori the quality of male parental care. Yet, female mate choice can also affect male parental care behaviour (e.g. Davies & Hatchwell 1992; Davies et al. 1992; Forsgren et al. 1996) and male parental effort may be a highly plastic trait dependent on individual experience, interactions within and between the sexes and environmental conditions. As a result, classic theory focused on female choice for fixed male traits will often be insufficient to explain observed patterns of female mate choice and male parental care behaviour in wild populations. Furthermore, we have little understanding of how interactions between females influence female mate choice and male fitness. In the ocellated wrasse it is possible that females choose among males based on the presence of other females because the behaviour of other females is the best indicator trait of male parental care. This evidence for female mate choice copying in the absence of any initial female assessment of male traits has important implications for our understanding of sexual selection as it does not fit within our standard theory of female choice for male traits that indicate male or territory quality, but instead implies that interactions among females may determine the skewed distribution of mating success among males.

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