

A trade-off generated by sexual conflict: Mediterranean wrasse males refuse present mates to increase future success

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A variety of mechanisms, including intrasexual competition, intersexual conflict, and physiological constraints, can explain patterns of reproduction and the adaptive value of specific behaviors. In a Mediterranean wrasse, *Symphodus ocellatus* (Labridae), large, nesting males occasionally refuse to spawn with willing females in the presence of small, sneaker males. We explored the possible adaptive significance of this behavior. Nesting males refuse females despite the fact that it reduces their immediate mating success. This nesting-male behavior also decreases female and sneaker mating success and occurs when sneaker males surround the nest. Experiments that decreased the number of sneakers around nests showed that nesting males respond immediately to mating opportunities when fewer sneakers are present, and thus they are not simply constrained by a lack of energy or lack of sperm. Experiments that increased the number of sneakers at the nest caused nesting males initially to refuse spawning opportunities, followed by a subsequent decrease in sneaker presence and an increase in mating rate. We propose that this behavior is the result of a trade-off between immediate mating success and future reproduction created by competition between males and conflict between the sexes. Males reduce their immediate mating success by reducing spawning at the nest; sneaker males subsequently leave, and this decreases mate competition for the nesting male. Unresponsiveness of nesting males also causes sexual conflict between females and nesting males over mating. We argue that this behavior and the existence of a trade-off can only be understood by examining intersexual conflict and intrasexual competition simultaneously. *Key words*: mating systems, Mediterranean wrasse, reproductive behavior, reproductive trade-off, sexual conflict, *Symphodus ocellatus*. [*Behav Ecol* 10:105–111 (1999)]

The diversity of mating systems and reproductive strategies has long fascinated researchers, and theory has focused on explaining patterns of observed variation and examining the adaptive value of specific behaviors. Many behaviors are believed to be adaptive responses to interactions within or between the sexes (Darwin, 1871; Hammerstein and Parker, 1987; Parker, 1970, 1979, 1983). For example, competition between males for access to mates or resources can drive the evolution of male secondary sexual characteristics. Conflict between the sexes is also recognized as an important factor explaining otherwise counterintuitive observations such as multiple mating and extrapair copulations in monogamous birds (Andersson, 1994; Davies, 1989, 1992; Hammerstein and Parker, 1987). Although female mate choice has been well documented, evidence for male choosiness also exists and is predicted in situations where male fitness is limited by factors other than access to females (Andersson, 1994; Clutton-Brock and Vincent, 1991; Parker, 1970).

Our aim here was to understand the counterintuitive observation that in a Mediterranean wrasse, *Symphodus ocellatus*, males sometimes refuse to mate with willing females. This behavior could be the result of simple energetic depletion. If males have exhausted their energy or sperm reserves, it may be necessary for them to refuse mates until more energy or more sperm is available. However, they might adopt this behavior as an adaptive strategy to select mates or mating opportunities that increase their overall reproductive success. In

S. ocellatus, nesting males do not seem to select mates, but instead go through phases where they simply refuse to mate with visiting females. This extreme form of “choice” does not depend on female identity because females often return and spawn with the same nesting male who refused them earlier (Alonzo and Warner, personal observations). Thus, there are strong indicators that the tactics involved are considerably more complex than simple mate choice.

S. ocellatus is a Mediterranean wrasse found on rocky and eel grass substrates in shallow coastal waters (<15 m deep) (Fiedler, 1964; Voss, 1976). Estimates of adult densities range from 0.34 to 0.94 individual/m² (Lejeune, 1985; Taborsky et al., 1987). There is no evidence for sex change in this species (Bentivegna and Benedetto, 1989; Warner and Lejeune, 1985). The breeding season lasts for approximately 2 months, between May and June (Fiedler, 1964; Lejeune, 1985; Voss, 1976), during which time the sexes are temporarily dichromatic (Lejeune, 1985; Voss 1976). Although the density of nests varies, mating success does not seem to change during the reproductive season. Spawning is demersal and occurs daily from sunrise to sunset (Fiedler, 1964; Lejeune, 1985). Females spawn every few days; successful males may spawn multiple times per minute (Taborsky et al. 1987; Warner and Lejeune, 1985). Individuals live up to 2 or 3 years (Lejeune, 1985; Warner and Lejeune, 1985) and reach a maximum of 8.5 cm standard length.

In *S. ocellatus*, distinct classes of male reproductive behavior exist (Taborsky et al., 1987). The most obvious behavior is that of the nesting male. These males build nests out of algae, court females, and care for the eggs (Gerbe, 1864; Soljan, 1930; Taborsky et al., 1987). undefended eggs have no chance of survival (van den Berghe et al., 1989; Alonzo and Warner, personal observations), and about one-third of all nests are deserted by the nesting male before the end of the nest cycle

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(Taborsky et al., 1987). The success of the nest seems to determine the probability of desertion (Wernerus, 1988; Wernerus et al., 1989).

Other males in the population perform typical sneaking behavior (Taborsky, 1994; Taborsky et al., 1987). These males hover around actively spawning nests and attempt to join the nesting male's spawns (Lejeune, 1985; Taborsky et al., 1987; Wernerus, 1988). They have mature testes and are capable of fertilizing eggs (Alonzo and Warner, personal observations; Warner and Lejeune, 1985). Sneakers move freely between nests, whereas nesting males tend to remain within a 10-m range the entire season (Taborsky et al., 1987; Wernerus et al., 1989). Sneakers are approximately six times more common than nesting males (Warner and Lejeune, 1985), and males do not switch between behavior types during a reproductive season (Taborsky et al., 1987). Sneakers are younger than nesting males, which may explain their difference in frequency; yet sneakers and nesting males appear to be separate life histories (Alonzo, Taborsky, and Wirtz, in preparation).

Although it is not known if sneaker and nesting male sperm compete, both males produce and release sperm that is capable of fertilizing eggs (Alonzo and Warner, unpublished data). Sneakers produce approximately four times more sperm per spawn than nesting males (Alonzo and Warner, unpublished data). Nesting males thus often find themselves in situations of extreme sperm competition. It is possible that nesting males refuse to spawn with females because of this competition with sneakers. In situations of high sperm competition, nesting males could conceivably gain nothing by spawning. However, nesting males do not consistently refuse to spawn in the presence of sneakers.

Multiple studies on female choice in this species have failed to show any relationship between male mating success and any intrinsic male or nest character; nevertheless, nesting-male success varies greatly (van den Berghe et al., 1989; Wernerus, 1985, 1988; Wernerus et al., 1987, 1989). Females visit many nests and will spawn in only a few of those that they visit (Taborsky et al., 1987). Females may visit and spawn in a single nest repeatedly through one day, but they do not remain loyal to a given male between days or nest cycles (Taborsky et al., 1987). Females have been observed traveling up to 100 m between nests (Taborsky et al., 1987). Females, however, do seem to spawn with a greater frequency in nests that have had past mating success (Wernerus, 1988), and they prefer nests without sneaker males (van den Berghe et al., 1989). It has been argued that females of this species do not choose males, but instead choose spawning situations (Wernerus, 1988; Wernerus et al., 1989). Because females return to nests repeatedly, nesting males may be able to delay spawning without losing females.

The cost of sneaker males to nesting males is not only shared paternity through sperm competition, but reduced mating success (van den Berghe et al., 1989). A strong correlation exists between previous mating success and the number of sneaker males at a nest (Lejeune, 1985; Wernerus, 1985, 1988). When sneaker males were experimentally removed, the mating success of the nest increased threefold (van den Berghe et al., 1989). Females obviously prefer nests without sneaker males, as do nesting males. However, sneaker males prefer nests with high spawning rates, as do other females. Similarly, the threat of nesting male desertion influences females to choose nests with high past mating rates. This mating skew correspondingly increases the skew in sneaker distributions and causes females and sneakers to be in conflict. Some nests are very successful, but with this success comes many sneakers. Nesting males that are successful should have behaviors to cope with the presence of sneakers.

Our previous observations indicated that nesting males

sometimes refuse to spawn with willing females. This behavior is only observed, however, in the presence of a large number of sneaker males. In this study, we examined the possible adaptive significance of this behavior as a response to sneaker presence. If this behavior is an adaptive strategy to decrease competition with sneakers, the behavior should respond to changes in sneaker presence at the nest and should increase long-term mating success for nesting males. This behavior could also result simply from complete sperm or energy depletion; the male may be physically unable to court females or to spawn. If this is the case, nesting males should not alter their behavior toward females in response to changes in the number of sneakers at the nest. We first document the circumstances under which mate rejection occurs. We then describe the results of manipulative experiments intended to identify the causes of the behavior.

Research site

Reproductive behavior is easily observed in shallow waters along the coast of Corsica from May through June (Michel et al., 1987). All research was conducted under natural conditions near the University of Liege (Belgium) Marine Laboratory, La Station de Recherches Sous-Marin et Océanographique (STARESO), located near Calvi, Corsica, France. A high density of *S. ocellatus* individuals is found in Revellata bay near the research station. All observations were made on the rocky substrate within 200 m of shore above 15 m depth using scuba equipment. Research was conducted during May and June of 1996 and 1997.

Observations of nesting male unresponsiveness to females

To document the dynamics of the behavior, we first observed nesting males. We wanted to determine how often and under what circumstances nesting males become unresponsive to females. Because this behavior had only been seen in the presence of sneaker males, we focused our observations on nests with many sneakers present.

Methods

We conducted 30-min observations of nests with a minimum of five sneakers within 3 m of the nest. Given this basic criterion, nests were chosen at random. The observer remained between 2 m and 3 m from the nest and as still as possible throughout the observation. One individual conducted all of the observations. Every minute, we noted the number of sneakers within 3 m of the nest. Distances were estimated visually. Females, sneakers, and nesting males can be differentiated by their behavior and morphology. Nesting males have a distinct color pattern and are larger than all other individuals in the population, which easily distinguishes them from sneaker males and from females. Females can be distinguished from sneaker males by the absence of a brightly colored spot on their opercles, by the shape of their abdomen and genital papillae, and by the absence of aggressive behavior from nesting males. We counted the number of females visiting and spawning in the nest. A female visiting the nest was defined as any female coming within 10 cm of the nest. For every female, we noted the nesting male response. Nesting males were defined as responding to the female if they courted the female ("nest showing" and "courtship spawning"; Taborsky et al., 1987) and guided the female into the nest. If nesting males remained away from or tried to block access to the nest, we considered males unresponsive to females. Females can ignore a nesting male's unresponsiveness and begin to lay eggs in the nest. This behavior can induce

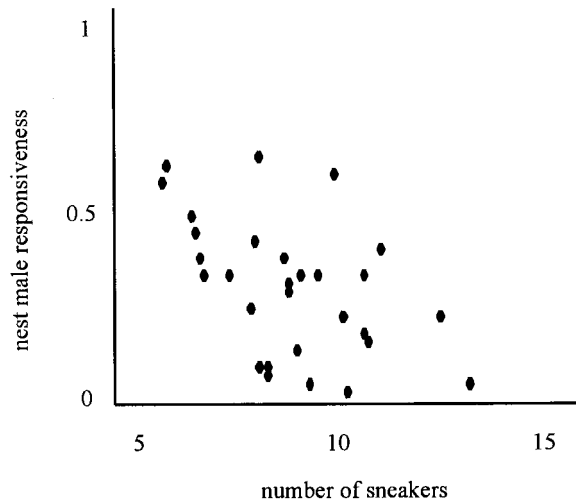


Figure 1
The relationship between nesting male responsiveness and the number of sneakers at the nest is negative. Nesting male responsiveness is represented by the percentage of females visiting the nest to whom the nesting male responds.

the nesting male to spawn as well. For each female, we recorded the nesting male response, the number of times she spawned, and the number of spawns joined by sneakers. A total of 28 nests were observed.

Data analysis

First, we calculated and tested for significance the partial correlation coefficients between the following variables: the number of sneakers at the nest, the percentage of females to whom nesting males responded, and the proportion of spawns sneaked. Second, females visiting a nest were divided into females to whom the nesting male responded and females to whom the nesting male did not respond. The proportion of females visiting that spawned and the proportion of spawns sneaked were compared between these two situations. If possible, we made comparisons using paired *t* tests. If the differences deviated significantly from normality according to a Wilk-Shapiro test (Shapiro and Wilk, 1965; Zar, 1996), we attempted transformations for normality. If this was unsuccessful, a Wilcoxon signed-ranks test was used. All tests were two tailed.

Results

All 28 males were both responsive and unresponsive to females during the 30-min observation. Individual nesting-male responsiveness was negatively correlated with the average number of sneakers present (Figure 1; $r = -.41$, $p < .05$, $n = 28$). All other partial correlations were not significantly different from zero. The proportion of females spawning was higher when nesting male were responsive to females (mean = 0.44) than when they were unresponsive (mean = 0.09, $t = 7.42$, $p < .001$), and 50% of spawns were sneaked when nesting males were responsive compared to 98% when the nesting male was unresponsive ($S = 81$, $p = .0257$).

Conclusions from observations

Nesting males tend to be more unresponsive when sneakers surround the nest and are more responsive when the number of sneakers near the nest is low (Figure 1). There may be a

short-term cost for being unresponsive: the probability a female will spawn is lower and the probability any spawn that does occur will be joined by a sneaker is higher when the nesting male is unresponsive to females. Why then would nesting males actively decrease their mating rate by refusing to spawn with willing females? At this point, the observational data cannot distinguish cause from effect. In particular, we do not know whether nesting male unresponsiveness is causing the change in the number of sneakers present (e.g., nesting male unresponsiveness attracts sneakers) or simply responding to it. To examine this behavior in more detail, it was necessary to conduct experiments.

Experimental manipulations of the number of sneakers at nests

We manipulated the number of sneakers at nests experimentally to examine the effect of sneakers on nesting-male behavior. If nesting males do not respond to experimental changes in sneaker number, then we can conclude that their behavior is not a strategy to decrease competition with sneakers. Males may simply be energy or sperm limited and, although the behavior decreases mating success, avoid spawning out of necessity. That is, they may be unresponsive because they are unable to mate with females regardless of sneaker number. Nesting males could also refuse to spawn in the presence of many sneakers simply because their reproductive gain from spawning is negligible due to sperm competition. Thus, nesting males could be simply waiting for better spawning opportunities. Nesting male unresponsiveness may also be a longer-term adaptive strategy in response to sneakers. We know that past mating success is positively correlated with the number of sneakers at the nest (Lejeune, 1985; Wernerus, 1988) and that increased sneaker presence reduces both the proportion of females spawning in the nest as well as the mating rate (Alonzo and Warner, in preparation; van den Berghe et al., 1989). Therefore, if nesting males can adopt strategies to reduce sneaker presence at the nest, their individual mating success may be increased in the long term. This could occur even if the change is only temporary. If males refuse to mate with females and this leads to lower sneaker presence in the future, male refusal may represent a trade-off between future and present success. If this is so, nesting males are predicted to avoid spawning in response to increased sneaker presence. Subsequently, sneaker presence should decrease and nesting male success should increase (Figure 2). This will be adaptive if the time-averaged mating rate of nesting males is higher than simply spawning in the presence of sneakers continuously.

This behavior has a dynamic component. If the nesting-male behavior is a strategy in response to conflict with sneakers, then nesting males should respond to manipulated increases in sneaker presence by becoming unresponsive and by increasing responsiveness to females if sneaker number is reduced. In contrast, if the behavior results from energy limitation, males should not respond to experimental manipulation of the number of sneakers present at the nest. If this behavior does result from a trade-off between present and future mating success for the nesting male, then it would follow that the nesting male's success should increase after a period of unresponsiveness, and the number of sneakers at the nest should decrease.

Methods

Experiments were conducted during May and June of 1997 at the site described above. During these experiments, each observation lasted 10 min. We performed two sets of experi-

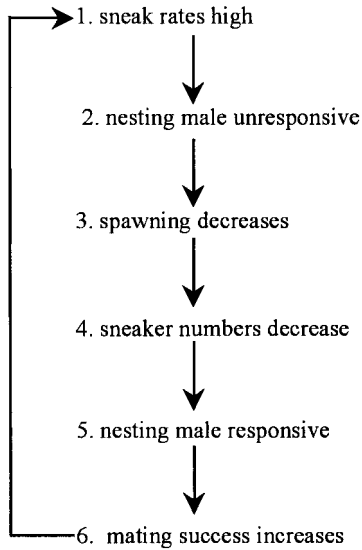


Figure 2

A dynamic strategy dealing with competition. Nesting males may reduce future competition if sneakers leave due to decreased spawning at the nest.

ments: sneaker decreases and sneaker increases. For both experiments, we observed 15 different nesting males, and nests were observed once before and twice after the manipulation. We counted the number of sneakers present at the nest every minute and averaged this over the 10-min period. All other variables are totals per 10 min. During each observation we noted the identity of the males, the number of sneakers present, the number of females visiting and spawning in the nest, the total number of spawns, the total number of sneaked spawns, and the number of chases as described above. Female visits, females spawning, total spawns, and spawns sneaked were divided into situations in which the nesting male responded or did not respond to the female when she visited the nest.

For the sneaker decreases experiment, nests with a minimum of five sneakers were selected at random. Each nest was observed for 10 min. Following this observation, we caught sneakers using small, hand-held nets. These males were held nearby in a small, enclosed container. After the number of sneakers present around the nest had been reduced significantly (by a minimum of three), we left the nest undisturbed for 5 min. The nest was then observed a second time as before. Subsequently, the captive males were released away from the nest. Some of these sneaker males rejoined their original nests, while new sneakers appeared as well. After a 30-min period, we observed the nest in the same way a third time. Controls were conducted by following exactly the same protocol, except the sneakers were released immediately after being caught ($n = 5$).

For the sneaker increases experiment, a nearby nest was covered that had many sneakers present. Most of the sneakers from the covered nest then moved to the focal nest. Therefore, nests were chosen that had sneakers and were in close proximity to another nest (within 5 m) that also had many sneakers present (minimum of five). We observed the focal nest for 10 min. Following this observation, the nearby nest was covered. From pilot observations it was apparent that 20–30 min were necessary for sneakers to leave a nest that had been covered. Therefore, we allowed 30 min to pass after the nest was covered before observing the focal nest again. After a second period of 30 min, the nest was observed for a final

10 min. The nearby nest remained covered for this observation. We conducted controls by following exactly the same protocol, except that we covered an active nest that did not have sneakers present at the nest ($n = 5$).

Data analysis

For all analyses, we represent female mating success by the proportion of females spawning. This is an estimate of the probability a given female will spawn in the nest she is visiting. We use the average number of sneaked spawns per sneaker to represent the success of sneaker males. This is calculated by dividing the total number of sneaked spawns per observation by the average number of sneakers present at the nest. We estimated nesting male success by the number of pair spawns that were not sneaked per observation. This is a conservative measure because it assumes the nesting male does not obtain any fitness from sneaked spawns. Clearly, other possible measures of mating success exist, but the qualitative results did not differ when variations on these measures were used.

We conducted analyses separately for sneaker decreases and sneaker increases. Female, sneaker, and nesting male success were calculated as described above. If the assumptions of the test were met, comparisons between the three observations were made using repeated-measures ANOVAs, and F values are reported. A Friedman's nonparametric, two-way ANOVA was conducted when variables deviated significantly from normality according to a Kolmogorov-Smirnov test (Zar, 1996) or from equal variances according to a Levene-Median test (Snedecor and Cochran, 1989). In these cases, we report the chi-square value. Pairwise comparisons were made using the Student-Newman-Keuls method (Zar, 1996). The proportion of spawns sneaked could not be compared because in too many observations the total number of spawns was zero, rendering this measure undefined.

Results

For the sneaker decreases experiment, the number of sneakers at the nest differed significantly between observations, indicating that the manipulation was successful (see Figure 3). Female visitation rate did not differ significantly between observations, but the number of females spawning, number of spawns sneaked, and the total number of spawns were significantly higher in the second (low sneaker number) observation (Table 1). Chases of sneaker males by nesting males occurred significantly more often with lower sneaker numbers (Table 1). Female, sneaker, and nesting-male success were all significantly higher with lower sneaker numbers in the second observation (Table 1). The proportion of females to whom the nesting male responded was significantly higher in the second observation (Figure 3). Controls indicated that when sneaker number did not increase, all other variables remained unaffected.

For the sneaker increases experiment, the number of sneakers at the nest was significantly higher in the second observation (Figure 4). Female visitation rate was higher in the second (high sneaker number) observation than both the third and first (Table 2). Number of females spawning and total number of spawns were greatest in the first observation (Table 2). The number of spawns sneaked did not differ between observations (Table 2). The number of chases by nesting males was highest in the first observation and lowest in the second observation (Table 2). Nesting males responded to proportionally fewer females in the high sneaker number observation (Figure 4). Female, sneaker, and nesting male success were all higher in the first and final observation period

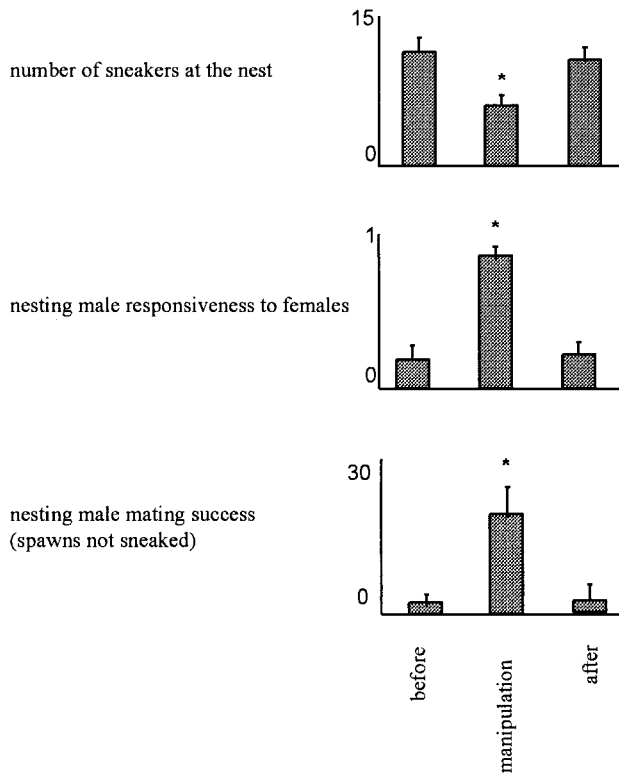


Figure 3
Nesting male behavior experiments: sneaker decreases.

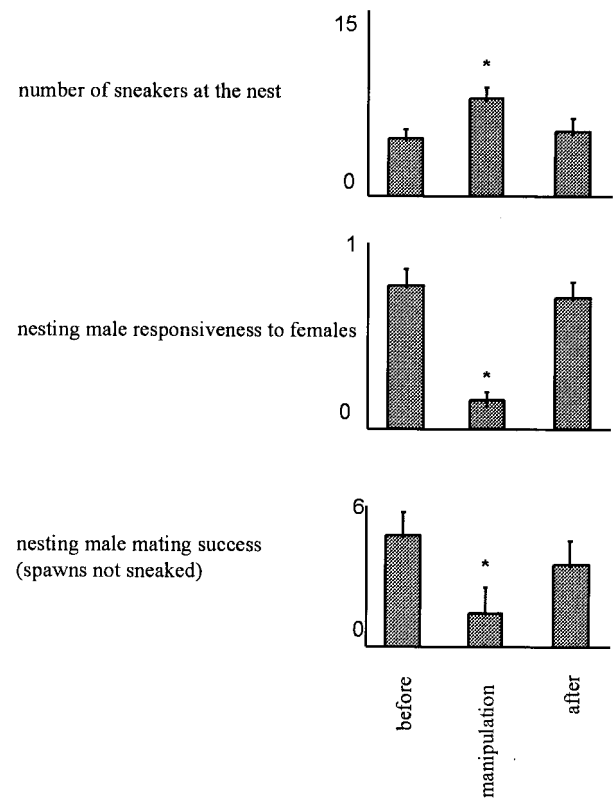


Figure 4
Nesting male behavior experiments: sneaker increases.

than in the second (Figure 4, Table 2). Controls indicated that when sneaker number did not increase, all other variables remained unaffected.

Conclusions from experiments

Males responded to experimental changes in sneaker presence. When sneaker number was decreased, nesting males became more responsive to females immediately, and those same males became unresponsive again when the number of sneakers at the nest increased. This argues against energy or sperm depletion in the sense that males were capable of courtship and spawning as soon as the number of sneakers decreased. Similarly, when sneaker number was increased, males went from being responsive to being unresponsive. Nesting males

may simply avoid high-competition spawning situations. However, a period of unresponsiveness was also followed by decreased sneaker number and increased mating success in later spawning periods. Note that this occurred despite the fact that nothing was done experimentally to decrease sneaker number in the final observation.

Comparing the results of the two experiments, one can see that the mating success of nesting males is not only determined by the number of sneakers at the nest (Tables 1 and 2). Nesting males with experimentally reduced sneaker numbers have much higher mating success than nesting males with the same number of sneakers present naturally. This difference in mating success can be explained by the history of these nests. Past mating success at the nest is positively cor-

Table 1
Results of the experimental decreases of sneakers at the nest

Variable	Observation			Statistic
	Before	During	After	
Sneakers at the nest	<u>10.77 (0.67)</u>	5.68 (1.36)	<u>10.01 (0.46)</u>	$F = 67.5 p < .001$
Nesting-male responsiveness	<u>0.18 (0.04)</u>	0.84 (0.03)	<u>0.21 (0.03)</u>	$F = 191.5 p < .001$
Female visits	<u>19.80 (1.81)</u>	<u>18.67 (2.35)</u>	<u>20.20 (61.5)</u>	$\chi^2 = 2.1 p = .404$
Females spawning	<u>2.53 (0.86)</u>	11.53 (2.06)	<u>2.47 (0.43)</u>	$\chi^2 = 13.2 p = .001$
Total spawns	<u>4.00 (1.36)</u>	27.47 (6.36)	<u>4.53 (1.04)</u>	$\chi^2 = 15.5 p < .001$
Spawns sneaked	<u>2.20 (0.51)</u>	7.80 (1.98)	<u>1.67 (0.64)</u>	$F = 6.916 p = .004$
Pair spawns (nesting male success)	<u>2.33 (0.91)</u>	19.67 (4.52)	<u>2.33 (0.62)</u>	$\chi^2 = 18.6 p < .001$
Sneaks per sneaker (sneaker success)	<u>0.23 (0.05)</u>	1.69 (0.55)	<u>0.18 (0.08)</u>	$\chi^2 = 16.2 p < .001$
Proportion of females spawning (female success)	<u>0.11 (0.03)</u>	0.60 (0.08)	<u>0.13 (0.03)</u>	$\chi^2 = 16.2 p < .001$
Chases	<u>19.4 (3.40)</u>	43.60 (6.99)	<u>16.13 (1.86)</u>	$\chi^2 = 12.2 p = .002$

Means are given with the standard error of the mean in parentheses. Underlined means are not significantly different from one another.

Table 2
Results of the experimental increases of sneakers at the nest

Variable	Observation			Statistic
	Before	During	After	
Sneakers at the nest	<u>5.75 (0.48)</u>	9.81 (0.56)	<u>6.53 (0.82)</u>	$\chi^2 = 20.78$ $p < .001$
Nesting-male responsiveness	<u>0.74 (0.06)</u>	0.15 (0.04)	<u>0.67 (0.06)</u>	$\chi^2 = 20.9$ $p < .001$
Female visits	<u>12.67 (1.55)</u>	18.87 (1.79)	<u>13.73 (1.33)</u>	$\chi^2 = 9.50$ $p < .001$
Females spawning	<u>2.60 (0.82)</u>	1.73 (0.61)	<u>4.00 (0.65)</u>	$\chi^2 = 7.153$ $p = .035$
Total spawns	<u>7.20 (1.54)</u>	3.33 (1.43)	<u>4.80 (1.34)</u>	$\chi^2 = 6.682$ $p = .040$
Spawns sneaked	<u>1.67 (0.70)</u>	<u>2.00 (0.81)</u>	<u>3.00 (0.86)</u>	$\chi^2 = 6.916$ $p = .393$
Pair spawns (nesting male success)	<u>4.20 (0.81)</u>	1.33 (0.66)	<u>3.13 (1.00)</u>	$\chi^2 = 12.100$ $p = .002$
Sneaks per sneaker (sneaker success)	<u>0.56 (0.13)</u>	0.20 (0.08)	<u>0.27 (0.11)</u>	$F = 3.5$ $p = .045$
Proportion of females spawning (female success)	<u>0.32 (0.05)</u>	0.09 (0.03)	<u>0.22 (0.06)</u>	$\chi^2 = 11.6$ $p = .003$
Chases	54.33 (5.95)	17.40 (3.53)	42.4 (6.12)	$\chi^2 = 24.4$ $p < .001$

Means are given with the standard error of the mean in parentheses. Underlined means are not significantly different from one another.

related with sneaker presence (Lejeune, 1985), so nests with many sneakers have had a higher past success than nests with fewer sneakers. Females prefer nests with a high past history of success but avoid spawning with sneakers (van den Berghe et al., 1987). Therefore nests with experimentally reduced sneaker numbers are preferred by females.

DISCUSSION

Nesting males reduce their own spawning rate in response to the presence of sneakers despite the fact that this reduces their immediate success. This reduction in mating ultimately leads to decreased sneaker presence and increased mating success. The fact that nesting males switch back and forth between responsiveness and unresponsiveness indicates these males are not simply inactive. In fact, males begin spawning immediately when the sneaker number at the nest is reduced, indicating no lack of ability to spawn. In unmanipulated nests, males also cycle naturally between periods of responsiveness and unresponsiveness. Given that males are able to spawn, it appears that males are actually altering their behavior in response to the spawning situation. Nesting males seem to choose the conditions under which to mate. Even if nesting male unresponsiveness is influenced by energy or sperm allocation, it still occurs in response to sneaker presence. This is distinct from energy or sperm depletion, where male spawning would be driven by internal, not external, conditions. Furthermore, nesting males may not only be avoiding high-competition spawning situations by reducing their immediate mating success, but they also experience increased future mating success. These observations and experiments support the idea of a trade-off occurring between present and future mating success. Although life-history trade-offs are well documented, this is the first demonstrated trade-off between present and future mating success that is generated by sexual conflict.

To demonstrate that this is an adaptive strategy, it should be shown that a nesting male using this strategy of unresponsiveness has greater overall mating success than a male that simply remains responsive to all females. However, all of the nesting males in this study cycled between responsiveness and unresponsiveness, and thus we have no direct measure of the mating success of the alternative. We do know that nesting male mating success is lower in the presence of sneakers (van den Berghe et al., 1989) and that past mating success at the nest is positively correlated with sneaker presence (Lejeune, 1985; Wernerus, 1985, 1988). Therefore, continuous responsiveness is expected to attract more sneakers, reducing nesting male mating success through increased sperm competition

and decreased attractiveness to females. In contrast, unresponsiveness decreases sneaker number, and previous studies have shown that experimental reductions of sneakers can increase mating rates threefold at the nest (van den Berghe et al., 1989). Thus, the decreased mating success caused by unresponsiveness may be compensated for by increased mating success as sneaker numbers decrease. In fact, it is possible that nesting males simply delay spawning and do not actually experience a decrease in total mating. As continued responsiveness would actually increase competition at the nest, it appears that this nesting male strategy, although decreasing short-term mating success, could actually have greater overall success than simply remaining responsive to females.

Although this behavior occurs in response to conflict between sneakers and nesting males, it causes conflict between the sexes. Nesting males, by becoming unresponsive, decrease female mating success. Therefore, intrasexual conflict creates conflict between the sexes. Females prefer nests with a high history of success, presumably to avoid nesting-male desertion, which causes the mating success to be extremely skewed among nests. Because few successful nests exist in the first place because of female choice patterns, female behavior actually generates the conflict between males. Female behavior, in turn, is driven by nesting-male desertion. Thus, conflict between the sexes over desertion creates conflict between males over sneaking; the resulting nesting-male behavior in turn causes conflict between females and nesting males. One of the major lessons from this study is that the reproductive behavior of this species can only be understood by simultaneous consideration of interactions between males and between the sexes.

Although the importance of intersexual conflict and intrasexual competition in determining mating systems is widely recognized, these processes are usually treated independently. In reality, the fitness of reproductive strategies will depend on the outcome of both within- and between-sex conflicts. Recent models examining multiple-linked dynamic programming games have indicated that conflict within and between the sexes can generate trade-offs between present and future fitness (Alonzo and Warner, in preparation). We have found evidence for a trade-off between present and future mating success in this species that is generated by conflict both within and between the sexes. These trade-offs, though similar to life-history trade-offs, are created by sexual conflict and reproductive behavior of other individuals in the population. We expect these types of trade-offs to be as common as sexual conflict and competition within a sex, and we suggest that by

considering trade-offs we will obtain a clearer understanding of reproductive behavior and mating systems in general.

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