

Dynamic games and field experiments examining intra- and intersexual conflict: explaining counterintuitive mating behavior in a Mediterranean wrasse, *Symphodus ocellatus*

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Intersexual conflict and intrasexual competition are widely recognized as playing critical roles in determining mating systems. Although they occur simultaneously in populations, 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. Using a modeling approach based on multiple, linked, dynamic state variable models, we examined the reproductive behavior of a Mediterranean wrasse, *Symphodus ocellatus*. We compared the predictions of models that examine only a single conflict interaction with those that consider multiple within- and between-sex conflicts simultaneously. The observed distribution of sneaker males and females among nests was compared with those predicted by the models. We found that the closest fit with empirical observations and experiments is given by the model that examines conflict between females, sneakers, and nesting males simultaneously. Removal of successful nests indicated that females join nests with few or no sneakers present, whereas sneakers join these nests only later, even though this leads to lower sneaker mating success. This behavior can be explained by observing that although sneakers would have higher fitness at nests where the spawning rate is greater, females would not be willing to spawn at these nests in the presence of sneakers. Presumably, once the nests have achieved high past success, females are willing to spawn in the presence of sneakers because of the associated decreased chance of nesting male desertion. *Key words*: dynamic game model, fish behavior, Labridae, mating systems, sexual conflict. [*Behav Ecol* 11:56–70 (2000)]

Impressive variation in mating systems exists within and between species. Theory has focused on explaining and predicting patterns of mating behavior (Arnold and Duvall, 1994; Clutton-Brock, 1991; Davies, 1989, 1992; Emlen and Oring, 1977; Hammerstein and Parker, 1987). Often, however, we remain unable to explain fully the behaviors we observe. Competition between males for access to mates or resources has long been recognized as an important force in the evolution of reproductive strategies. Male competition has been held responsible for the occurrence of extreme secondary sexual characteristics in some species and the stable coexistence of discrete alternative reproductive behaviors in others (Anderson, 1994). More recently, researchers have recognized the importance of interactions between the sexes on the evolution of mating systems. Clearly, both intra- and intersexual interactions are important factors in driving mating behavior. However, these interactions are usually considered in isolation. We suggest that in order to have a complete understanding of reproductive tactics in many species, intra- and intersexual interactions should be considered simultaneously. For example, males often compete between themselves for territories. Yet, female mating strategies will determine the type of territory with the highest mating success. The degree of female choosiness will dictate the distribution of success between males, and thus the degree to which males will compete for territories. However, female choosiness will be affected by the variation in male and territory quality. Thus, within-sex interac-

tions may set the stage for between-sex conflict. Just as easily, mate choice strategies can drive competition between males, and female choice can nullify predictions made when considering only the interactions between males.

Theoretical models have greatly enhanced our understanding of reproductive behavior (e.g., Arnold and Duvall, 1994; Curstinger, 1991; Davies, 1989; Gross, 1984; Hammerstein and Parker, 1987; Ims, 1988; Johnstone et al., 1996; Kirkpatrick, 1982, 1985, 1986; Maynard Smith, 1977, 1982; Maynard Smith and Price, 1973; Parker, 1979, 1984). However, models and empirical studies of sexual conflict and mate choice focus on the behavior and fitness of males and females, but tend to ignore the concurrent interactions between males (Anderson, 1994; Arnold and Duvall, 1994; Davies, 1989; Hammerstein and Parker, 1987; Janetos, 1980; Kirkpatrick, 1982, 1985, 1986; Losey et al., 1986; Parker, 1979, 1990, 1992, 1993; Real, 1990, 1991; but see Crowley, et al. 1991; Johnstone et al., 1996). In contrast, research and theories examining the evolution of alternative reproductive strategies focus primarily on within-sex games (Dawkins, 1980; Dunbar, 1983; Gross, 1984, 1991, 1996; Lucas and Howard, 1995; Lucas et al., 1996; Parker, 1990; Rubenstein, 1980; Waltz, 1982). Although these models have been useful in explaining the stable coexistence of alternative behaviors, patterns of parental care and female choice, they fail to fully explain the variation we observe in reproductive behaviors. Although game theoretic models do exist that examine interactions within and between multiple groups (Crowley et al., 1991; Hugie and Dill, 1994; Johnstone et al., 1996; Sih, 1998), this type of model has not been applied to mating systems. Further, our model examines conflict within and between the sexes simultaneously while also considering temporal dynamics and state dependence.

In a Mediterranean wrasse, *Symphodus ocellatus*, females ac-

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tively select spawning situations (Taborsky et al., 1987; van den Berghe et al., 1989; Wernerus, 1988). Small sneaker males compete through sperm competition while large males in the population court females, defend nests and provide parental care (Taborsky et al., 1987; Warner and Lejeune, 1985). Conflicts exist between and within the sexes and have the potential to influence reproductive behavior in this species. Although past research has clarified many aspects of the reproductive biology of this species, much about the mating behavior of *S. ocellatus* is not fully understood. For example, mating success is extremely skewed between nests, but this variation is not explained by any intrinsic nest or nesting male characteristic (Wernerus et al., 1989). Furthermore, although females prefer nests without sneakers, nests with the highest mating success also have the most sneakers present. To understand this counterintuitive distribution of mating between nests, we used a model to examine the known interactions within and between the sexes. We show that the only way to understand fully the complex interactions in *S. ocellatus*, and the mating behavior they exhibit, is to examine multiple conflicts within and between the sexes simultaneously. We compared predictions of models that examine a single interaction with those that consider conflict within and between the sexes simultaneously. We then compared these predictions to field observations and experiments. We have argued that the simultaneous consideration of conflicts within and between the sexes should give a more complete understanding of reproductive behavior. If this is the case, models examining inter- and intra-sexual interactions should explain observed behavior more fully than simpler models.

Study species

General information

S. ocellatus is found on rocky and seagrass substrates in shallow coastal waters (Fiedler, 1964; Voss, 1976). Estimates of adult densities range from 0.34 to 0.94 individual per square meter (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). Spawning is demersal (Fiedler, 1964; Lejeune, 1985). All females examined during the reproductive season had active gonads (Taborsky et al., 1987; Warner and Lejeune, 1985). Males in all size classes have active testes, but some adult males have been found with inactive testes in intermediate size classes (Taborsky et al., 1987). These males were not involved in reproductive behavior in that season (Taborsky et al., 1987). Mating occurs daily from sunrise to sunset (Lejeune, 1985). Individuals live 2–3 years (Lejeune, 1985; Warner and Lejeune, 1985), reaching a maximum of 8.5 cm standard length.

Male alternative reproductive behaviors

Observations of the males of this species have indicated that 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). Parental care includes fanning and defense of the eggs against conspecific and other egg predators (Fiedler, 1964; Lejeune, 1985) and ends upon hatching (Lejeune, 1985). Undefended eggs have no chance of survival (Alonzo, personal observation; van den Berghe et al., 1989). The nesting males go through a nest cycle of construction, spawning, and fanning the eggs (Lejeune, 1985). The nest cycle lasts on average 10 days (Fiedler, 1964; Lejeune, 1985; Wernerus, 1988; Wernerus et al., 1989). Males often change nesting sites between

cycles, moving from 10 cm to 10 m from their previous site (Fiedler, 1964; Wernerus, 1988; Wernerus et al., 1989). About one-third of all nests are deserted by the nesting male before the end of the nest cycle (Taborsky et al., 1987). The mating success of the nest seems to determine the probability of desertion, and male success varies greatly between days and between nest cycles (Wernerus, 1988; Wernerus et al., 1989). Nesting males tend to be the largest males (>8 cm) in the population, show distinct coloration during the breeding season (Warner and Lejeune, 1985; Taborsky et al., 1987), and are usually 2 years old (Alonzo, Taborsky, and Wirtz, in preparation).

Smaller males in the population perform typical sneaking behavior (Taborsky et al., 1987; Taborsky 1994). These males hover around actively spawning nests and attempt to join the nesting male's spawns (Lejeune, 1985; Wernerus, 1988; Taborsky et al., 1987). They have mature testes and sperm and are capable of fertilizing eggs (Warner and Lejeune, 1985). These males do not provide any care or defense of eggs (Taborsky et al., 1987). They also move freely between nests (Lejeune, 1985; Taborsky et al., 1987). These males tend to be the smallest adult males (4.5–8 cm) in the population and have a distinct color pattern on the opercules, but are otherwise indistinguishable from females (Taborsky et al., 1987; Warner and Lejeune, 1985). Males observed sneaking tend to be 1–2 years old (Warner and Lejeune, 1985). Sneaker males have larger testes than nesting males (Warner and Lejeune, 1985) and produce larger quantities of sperm per spawn (Alonzo and Warner, unpublished data). Recent evidence suggests that sneaking and nesting may actually be separate life histories (Alonzo, Taborsky, and Wirtz, in preparation) with similar mating success (Taborsky et al., 1987; Warner and Lejeune, 1985).

Female choice

Multiple studies on female choice in this species have failed to show any relationship between mating success and any intrinsic male or nest character, yet nesting male success varies greatly (van den Berghe et al., 1989; Wernerus, 1988; Wernerus et al., 1987, 1989). Females visit many nests and will spawn in only a few of those they visit (Taborsky et al., 1987). Females may visit and spawn in a single nest repeatedly through one day, but do not remain loyal to a given male between days or nest cycles (Taborsky et al., 1987). Females do, however, seem to spawn with a greater frequency in nests that have a recent history of high mating success (Wernerus, 1988) and prefer nests without sneaker males (van den Berghe et al., 1989). Thus, females do not choose males, but instead are choosing spawning situations (Wernerus, 1988; Wernerus et al., 1989).

Sexual conflict

The cost of sneaker males to nesting males is not only shared paternity, but reduced mating success (van den Berghe et al., 1989). There is also a strong correlation between previous mating success and the number of sneaker males at a nest (Lejeune, 1985; Wernerus, 1988). When sneaker males were experimentally removed, the mating success of a nest increased threefold (van den Berghe et al., 1989). The success of any remaining sneaker males also increased (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. Therefore, sneaking leads to conflict between females and sneaker males, between nesting and sneaker males, between females and nesting males, and even between individual sneaker males. Females are also in conflict with nesting males over their desertion of nests.

The distribution among nests of both females and sneakers is extremely skewed in *S. ocellatus* (Lejeune, 1985). A few nesting males have very high success. Although nest sites do not appear to be limiting in this species (Wernerus, 1988; Wernerus et al., 1989), the skewed distribution of mating in this species means that nesting males are in conflict with other nesting males for access to mates. These high-success nests attract females, presumably because of their low chance of nesting male desertion. However, these nests also attract sneakers which females attempt to avoid. Because females prefer nests with high levels of success to avoid desertion, females are not in conflict with one another over access to nests. Instead, females should prefer nests where many other females are also present. It seems counterintuitive that females would choose to spawn in nests with many sneakers present when many other nests exist with few or no sneakers. Similarly, the sneaker distribution greatly increases competition between sneakers. The observed distribution of both females and sneakers seems suboptimal for all groups involved. We use both field experiments and a dynamic game model to examine this counterintuitive observation.

The model

Basic model structure

We modeled the behavior of females, sneakers, and nesting males in three fitness equations linked by the fact that the fitness of each individual depends on the behavior adopted by others. For example, in each time period of the model, nesting males decide to desert or to remain at their current nest. This behavior generates a probability of desertion for each nest. Females choose between nests based on the probability of nesting male desertion and the number of sneakers present. Female choice generates the mating success associated with each type of nest. Sneakers distribute themselves between nests based on both female mating rate and competition with other sneakers. The solution of the sneaker fitness equation is used to generate the frequency distribution of sneakers. The three equations are therefore tightly linked, and the solution of one creates parameters that affect the behavior choices in another (Figure 1).

To model multiple dynamic game interactions simultaneously, we extended the basic structure of a dynamic programming game (Houston and McNamara, 1987; Mangel and Clark, 1988) to examine the interactions between three fitness functions (Alonzo and Warner, 1999). The fitness of sneaker and nesting males is separated into two equations because their behavior and life histories are distinct (Alonzo, Taborsky, and Wirtz, in preparation; Taborsky et al., 1987). Because we modeled their behavior separately, their relative frequencies are fixed at the level observed in the field. For every iteration of the model, the algorithm examines the solution of the fitness equation for females, sneakers, and nesting males. Then each of these solutions was used to generate parameters that are included in the next iteration of the three fitness equations. Therefore, the solution of one equation depends directly and indirectly on the solution of all three equations in the previous iterations. Iterations continue until all three solutions are stable.

Analysis of the model

The purpose of these models is to make predictions to be compared with field experiments and observations. We used knowledge of the system to form the model and choose realistic values for parameters whenever possible. For some parameters, such as survival rates, it is difficult to ascertain values in the field. For these parameters, we must make assumptions. However, parameter values will only affect predictions if they

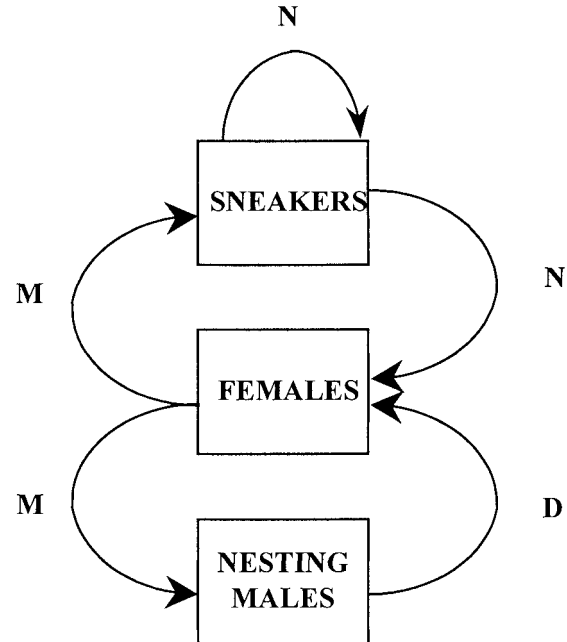


Figure 1

Multiple variables link the three dynamic programming equations. These links summarize the known interactions within and between the sexes in *Symphodus ocellatus*. *M* represents female spawning patterns, *N* indicates the number of sneakers at a nest, and *D* is the probability a nesting male will not desert his nest.

lead to different behaviors. In each of the equations described below we assume that survival (λ) does not differ between nests of different types. For any parameter that does differ between behavioral choices, we conducted sensitivity analyses (for details, see the appendix). Although this is a dynamic model, we assume that behavior is independent of the absolute time period (i.e., $t \ll T$). This type of analysis is generally valid when there is not a definite end to the time period under consideration and the model coefficients do not depend on time (Mangel and Clark, 1988).

We compared the predictions made by forms of the model that vary in whether they examine only within-sex conflict interactions or examine multiple conflict interactions simultaneously. First, we examined each fitness equation in isolation. Then we examined links between two groups such as between sneakers and females. Finally, we examined the predicted distribution of sneakers and females between nest types when conflict interactions within and between all three groups are considered. We then compared these qualitative predictions with field observations of sneaker and female distributions between nest types.

Nesting-male fitness equation

In the nesting-male fitness equation, males can either desert or stay at their current nest. Nests vary both in their age (day in the nest cycle) and the mating success males have experienced since the beginning of the nest's cycle. We refer to this as the nest state. Past mating success of a nest is $X(t)$, and the time in the nest cycle is $C(t)$. These two factors determine the state or type of nest a nesting male is experiencing. Each time period represents one day. If a male remains at a nest, he automatically increases his nest age by 1 day, or by remaining at a nest, $C(t+1) = C(t) + 1$, and his success, $X(t)$, changes as a function of the distribution of females between nests. In the field, mating success is extremely skewed in distribution, and males differ in success by orders of magnitude (Lejeune,

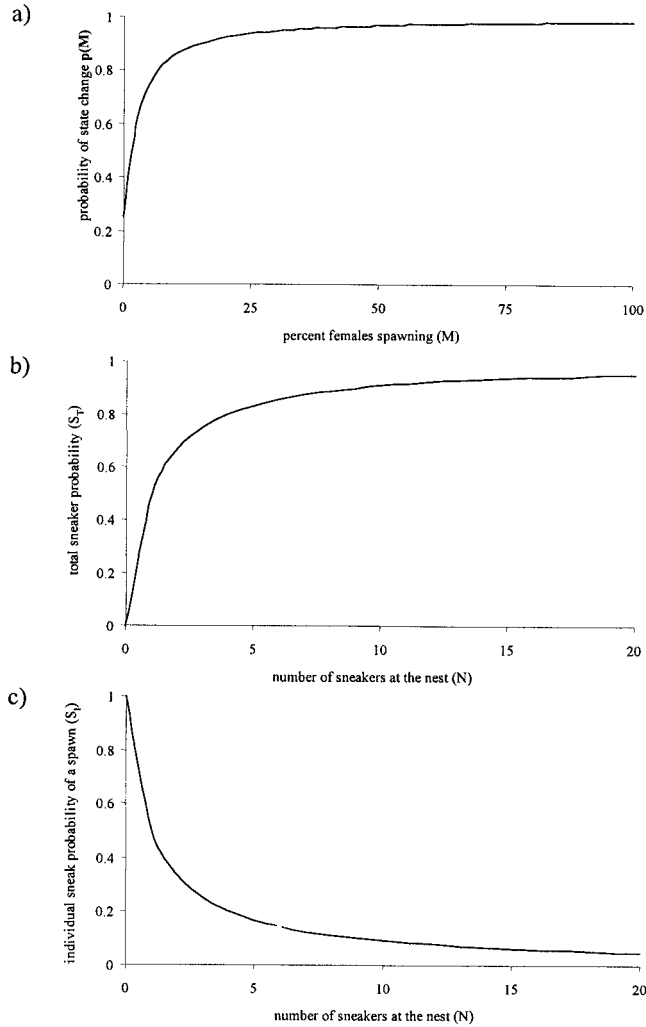


Figure 2

Functions used in the model. (a) The relationship between the percentage of females spawning in the male's nest type (M) and the probability a nesting will increase in success state, $p(M)$, is given by the equation $p = 1 - [1/(M + 1)]$, except $p = 0.01$ when $M = 0$ (where M is determined by the solution of the female fitness equation). (b) The relationship between the total number of sneakers at a nest (N_i) and the probability a female's spawn will be joined by a sneaker (S_T) is given by the relationship $S_T = 1 - [1/(N_i + 1)]$. (c) An individual sneaker's chance of sneaking each spawn decreases as a function of the number of sneakers at the nest. In the model, this relationship is given by the equation $S_i = 1/(N_i + 1)$.

1985; Wernerus et al., 1989). We assume $x = 0, 1, 2, 3, 4, 5$ and nest success is 10^x . We also assume that the mating success of a nest is to a certain extent stochastic. If females prefer that type of nest, the probability of changing success states will be high. In a given time period, males either stay at the same success state or increase by one state. Let $M(x, c)$ represent the mating rate at a nest in success state x and of age c . We assume mating rate is determined by the proportion of females preferring nests in state x and of age c . The probability, $p[M(x, c)]$, of changing x is an increasing function of mating rate [$M(x, c)$; Figure 2a]. Although nest state increases with mating rate, nesting males only gain fitness at the completion of the nest cycle. If a nesting male deserts his current nest, then he starts over in the next time period with zero past success ($x = 0$) and at the beginning of a new nest cycle (c

$= 1$). Nesting male survival between time periods (t) is λ , and T represents the final time period. Because males either remain at their present nest or start over at a new nest, we assume that survival is constant and does not depend on the behavior adopted. Let $F(x, c, t, T)$ represent the maximum expected fitness of a nesting male at a nest with success state x in day c of the nest cycle at time t . The reproductive value of deserting a nest [$V_{desert}(x, c, t, T)$] in state x and c days at time t into the nest cycle is

$$V_{desert}(x, c, t, T) = \lambda F(0, 1, t + 1, T), \quad (1)$$

and the reproductive value of staying with a nest [$V_{stay}(x, c, t, T)$] is

$$V_{stay}(x, c, t, T) = p(M(x, c))\lambda F(x', c + 1, t + 1, T) + (1 - p(M(x, c)))\lambda F(x, c + 1, t + 1, T) \text{ if } c < 10, \quad (2)$$

where

$$x' = \min[5, x + 1]$$

$$V_{stay}(x, c, t, T) = 10^x + \lambda F(0, 1, t + 1, T) \text{ if } c = 10,$$

and nesting-male fitness is

$$F(x, c, t, T) = \max[V_{desert}(x, c, t, T), V_{stay}(x, c, t, T)]. \quad (3)$$

The computer algorithm finds the behavior (desert or stay) for each nest state and time combination that leads to greater fitness for the nesting male. From the solution of this equation, we calculate $D(x, c)$, the probability the nesting male will stay with the nest until eggs spawned at this time period will develop (see appendix). $D(x, c)$ ranges from 0 to 1, where $D(x, c) = 1$ indicates the nest will not be deserted. We assume that males must start over with a new nest at the end of the tenth day in the nest cycle and eggs require 3 days to develop (Lejuene, 1985). Males only have immediate mating success when they complete a nest cycle. At that point they obtain fitness dependent on their past mating success represented by the state variable x .

If we solve Equation 3, independent of female or sneaker behavior, this is an optimality model (see appendix). If the female mating rate is equal across nests of different states, the model predicts that males will still desert nests with low past success if they are late in the nest cycle. If the mating success is higher at nests that have already had success, nesting male desertion of low-success nests becomes even more pronounced. Males desert nests after a few days if they have not been successful and start over (Kelly and Kennedy, 1993; Lejuene, 1985; Wernerus, 1988). Given the assumptions we have made, nesting males are predicted to desert low-success nests that are more than a few days into the nest cycle. At this point, we have not allowed for the fact that females, and as a result sneaker males, may alter their mating behavior in response to nesting male desertion and thus possibly alter this prediction.

Female fitness equation

We assume for simplicity that female choice is independent of female condition. The fitness associated with reproducing in a nest of type i depends on the probability the nesting male will stay with the nest until the eggs hatch (D_i), as well as the probability of spawning with a sneaker male. Females choose between nests that vary in their age and past mating success. These nest types (i) correspond directly to the above-described nest states (x, c) in the nesting-male fitness equation. The solution of the female fitness equation gives the female preference for different types of nests. As the number of sneaker males at a nest type increases (N_i), the probability a female will mate with a sneaker male [$N_i/(N_i + 1)$] also increases (Figure 2b). Nests vary in both the probability of desertion (D_i) and in the number of sneakers at the nest (N_i).

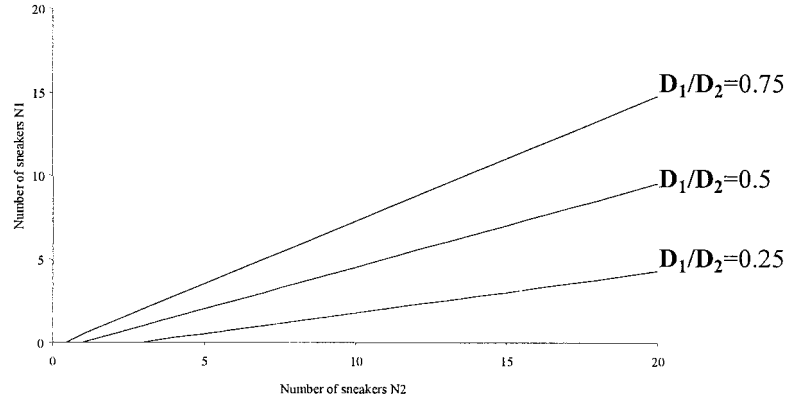


Figure 3

Females trade-off sneaker presence and nest desertion. The boundary sneaker number (N_1) increases with the number of sneakers at the other nest (N_2) and the relative probability that nest will not be deserted (D_1/D_2).

These parameters are given by the solution of the sneaker and nesting-male fitness equations. The reproductive success of spawning with only a nesting male (R_{NM}) is assumed to be higher on average than the reproductive success of spawning with sneakers (R_{SN}). Let λ denote survival during one time period, T , the final time period, and $G(t, T)$, the maximum expected reproductive success of a female mating at a nest with an associated probability of desertion (D_i) and sneaker presence (N_i). The reproductive value, $Y_i(t, T)$, of mating at any nest of type i is

$$Y_i(t, T) = D_i[R_{NM}/(N_i + 1) + N_i R_{SN}/(N_i + 1)] + \lambda G(t + 1, T) \quad (4)$$

and female fitness is

$$G(t, T) = \max_i \{Y_i(t, T)\}. \quad (5)$$

From the solution of this equation, the relative mating success at each nest type (proportion of females mating at each nest) can be calculated. For the female equation, we must make an assumption about the relative success of mating with a sneaker or nesting male. Although we do not actually know why females avoid sneakers, we assume that female reproductive success is for some reason lower when mating with sneaker males (i.e., $R_{NM} > R_{SN}$). We conducted sensitivity analyses to ensure that our conclusions were robust (for details see the appendix).

For females, there is clearly a potential tradeoff between desertion and sneaking. Female fitness increases as N_i decreases or D_i increases. The degree to which the number of sneakers present affects female fitness will depend on the relative reproductive success of mating with sneakers and nesting males. Females might, for example, be willing to spawn in the presence of sneakers if the chance of desertion were sufficiently low. In contrast, other nests might only be acceptable to females if few or no sneakers are present. In some cases, female fitness might be equal at nests where desertion probabilities and sneaker numbers differ. A nest with few or no sneakers might compensate for a higher chance of nest desertion. Two nest types will lead to equal success for females when

$$D_1[R_{NM}/(N_1 + 1) + N_1 R_{SN}/(N_1 + 1)] = D_2[R_{NM}/(N_2 + 1) + N_2 R_{SN}/(N_2 + 1)]. \quad (6)$$

For simplicity, assume that when females mate with sneakers, females achieve zero mating success ($R_{SN} = 0$) compared to mating with nesting males ($R_{NM} = 1$). Nest 1 will be acceptable despite a higher sneaker presence when

$$D_1/(N_1 + 1) = D_2/(N_2 + 1) \quad \text{or} \\ N_1 = (D_1/D_2)(N_2 + 1) - 1. \quad (7)$$

For females, as the relative probability of the nest not being deserted increases (D_1/D_2), the acceptable number of sneakers at that nest (N_1) increases as well (Figure 3). Females are predicted to prefer the nests that lead to the highest fitness given the trade-off between sneaker number and nest desertion.

Sneaker fitness equation

Sneakers choose between nests of different states, and nest states are determined by age and past mating success. These states correspond directly to the nest states in the nesting male and female fitness equations. Each nest type has an associated number of sneakers present, N_i , and expected mating rate, M_i . The reproductive value (Z_i) of reproducing at different nest types depends on M_i and N_i . If a male would have higher fitness at another nest, he will switch to that type of nest. If fitness at his current type of nest is higher or equal to other nests, then the male will not move between nests. If only some males leave the nest, we assume the identity of the male that moves is determined at random (but see Mangel and Roitberg, 1993). If different nest types lead to equal fitness, sneakers will distribute themselves equally between these nests. The individual probability of sneaking a spawn [$S_i = 1/(N_i + 1)$] is a function of the number of sneakers at the nest (Figure 2c). As before, let λ denote survival and T the final time period. Let $H(t, T)$ represent the maximum expected fitness of a sneaker at time t . The success of an individual sneaker, $Z_i(t, T)$, choosing a nest with an associated number of sneakers (N_i) and spawning rate (M_i) is

$$Z_i(t, T) = M_i/(N_i + 1) + \lambda H(t + 1, T), \quad (8)$$

and sneaker fitness is

$$H(t, T) = \max_i \{Z_i(t, T)\} \quad (9)$$

Female spawning (M_i) is predicted by the outcome of the female equation. The number of sneakers at a nest is generated by calculating the proportion of sneaker males choosing each nest type. One can easily see that if M_i remains the same, sneaker success will increase if the sneaker number (N_i) decreases.

The sneaker fitness equation incorporates interactions between sneakers. Therefore, this equation, even in isolation from the female or male nesting equation, is a game model. If we examine only sneaker male behavior, N_i varies while M_i is fixed. In this case, sneakers are predicted to distribute themselves in proportion to both competition from other sneakers

Table 1
A comparison of the model predictions

Model form	Sneakers	Females	Nest male
Equations solved separately	Ideal free distribution	Prefer low-desertion, no sneaker nests	Desert nests that are late cycle and low success
Female and sneaker	Evenly distributed among nests	Evenly distributed among nests	No prediction
Female and nesting male	No prediction	Prefer successful nests	Desert low-success nests mid-late cycle
The complete model	Sneak only at high-success nests	Spawn only at high-success nests	Desert all but high-success nests

and the female mating rate in an ideal free way. This means that sneakers will distribute themselves such that individual sneaker fitness, given by $M_i/(N_i + 1)$, is the same for all nest types. If female mating rate is the same between nests, then the number of sneakers at nests should be equal across nests. However, if mating rate varies, those nests with high mating rates are predicted to have many sneakers present, and those with few females present will have few or no sneakers present. Therefore, if female mating success is skewed between nests, sneaker competition could explain the skewed distribution of sneakers. If this is the case, the model predicts that the individual sneaker fitness should be the same across nests with different number of sneakers present.

Interactions between groups

In summary, females are predicted to trade-off desertion by nesting males with the cost of spawning with sneakers, and sneakers are predicted to distribute themselves between nests in proportion to the mating rate. If we examine both female and sneaker behavior simultaneously, these predictions change. Interactions between females and sneakers can be examined numerically (see appendix for details). If females are distributed between nests that differ in sneaker numbers, sneaker males are predicted to redistribute themselves, thus causing female preference to change. Interactions between sneakers and females only have a few possible stable distributions. If nests do not vary in desertion rates, females and sneakers are predicted to distribute themselves equally among nests. If nests differ in desertion probabilities, the only stable distribution of females and sneakers occurs where both females and sneakers spawn only at nests with the lowest chance of nesting male desertion. Any other distribution is unstable because as soon as sneakers join the nest, it becomes unattractive to females.

We have assumed that neither nesting males nor sneakers are directly affected by each other's presence. This is clearly an oversimplification because nesting males share paternity with sneakers, and sneakers require the parental care provided by nesting males. However, their fitness is connected by their effect on female choice. Past research has shown that the cost of sneakers to nesting males is as much through reduced mating success as shared spawns (van den Berghe et al., 1989). Although nesting males do direct aggression toward sneaker males, it has not been found to affect sneaker fitness (Taborsky 1994; Taborsky et al., 1987). For these reasons, we focus on the indirect interactions between sneakers and nesting males caused by female behavior.

Females prefer nests that nesting males will not desert. Nesting males prefer nests where their chance of obtaining success is high. Therefore, females and nesting males actually prefer the same kinds of nests. However, nesting males are always predicted to desert nests with low success that are not at the beginning of the nest cycle even if female spawning is the

same across nests. This causes females to prefer the nests that have already been successful. If the number of sneakers is equal across nests, then females will simply prefer nests with the least chance of being deserted. Therefore, if only females and nesting males interact, mating success will be skewed to nests in high success states.

In summary, the connections between groups can drastically alter the predictions made by the model. The interactions between sneakers, females, and nesting males can be examined using the dynamic state variable algorithm (see appendix). When we examine all of these interactions simultaneously, only one type of distribution leads to a stable solution of the model. The computer algorithm predicts that female and sneaker distributions will be extremely skewed such that the mating rate at nests with no past success is practically zero. Then males will never desert high-success nests, and females and sneakers will be distributed exclusively at the nests. This raises the question of how this distribution can ever exist if females almost never spawn at low-success nests. We have assumed that even unpreferred nests have a small chance of changing nest state (Figure 2a). The model predicts that if mating success is somewhat stochastic at the beginning of the nest cycle, then the few nests that get some success in the beginning by chance will become successful.

The mating distribution predicted by the complete model clearly differs from those predicted by simpler forms of the model (Table 1). When only interactions between sneakers were considered, we predicted a simple ideal free distribution of sneakers between nests. Interactions between sneakers and females alone predict an even distribution of sneakers and females between nests. Interactions between nesting males and females predict a somewhat skewed distribution of females between nests. In contrast, the complete model predicts that the distribution of females and sneakers should be extremely skewed among nests, and this distribution, though stable, will not lead to the highest immediate mating success available. The distributions of females and sneakers among nest observed in the field is extremely skewed (Lejeune, 1985; Wernerus et al., 1989) and can only be explained by the model that examines multiple conflict interactions within and between the sexes.

Given that only the complete model can predict the observed mating distribution, it is interesting to consider some of the more specific predictions of the complete model. As mentioned above, individual variation in nesting male success is completely driven by chance in the model. Therefore, it is possible that males become highly successful simply because they happen to achieve sufficient early mating success. The model also predicts that there will be a lag between a nest achieving mating success and the subsequent arrival of sneaker males. The state of the nest must first increase before sneakers can successfully mate at the nest. This also makes the

prediction that if we could experimentally increase the state of any nesting male sufficiently, he should become highly successful independent of his identity or quality. Finally, the skewed mating distribution and desertion behavior of nesting males is robust to large variation in parameter values (see appendix). This argues that the mating system, though extremely dynamic, is also very stable. By altering the state of a nest, we could manipulate the mating success of that nest, but the distribution of sneakers and females among nests when manipulated should quickly return to their premanipulation state. We examine some of these predictions below.

Experiments

Manipulation of the number of sneakers at a nest

The complete model predicts that the stable distribution of sneakers between nests will be suboptimal for both sneakers and females. However, the interactions within and between the sexes cause this distribution to be stable. Sneaker competition alone would predict that if the number of sneakers at the nest were altered, sneakers would redistribute themselves to the premanipulation level (Table 1). If the number of sneakers at a nest is decreased, mating success of the remaining sneakers should increase. The solution of the female equation also predicts that a reduction in the number of sneakers at the nest should increase female preference for that nest (Table 1). Similarly, if the number of sneakers at a nest increased, the mating success of females and sneakers should decrease. The sneaker-only model predicts that sneaker males will distribute themselves in an ideal free way between nests, whereas the complete model argues that sneaker distribution will be more skewed. When interactions between all groups are considered, sneaker males are predicted to occur in high numbers at those nests where females are willing to spawn in the presence of sneakers. This will occur at nests that have little chance of being deserted. We examined these predictions experimentally by manipulating the number of sneakers at a nest and observing the resulting mating success and behavior of females, sneaker, and nesting males. We also examined the premanipulation distribution of females and sneakers between nests.

Nest removal experiments

Theory that only examines interactions between sneakers predicts that males distribute themselves between nests in an ideal free way. To understand the fact that sneakers do not do this, one has to consider both the interactions between and within the sexes, as well as their temporal dynamics. From the model, we predict that nests must first achieve mating success before either the number of females or sneakers at the nest will increase. This is predicted despite the fact that sneakers have lower success at these nests than they would have at nests where there are fewer competitors. The question remains, how does this process begin?

This surprising prediction may be the result of a trade-off between present and future fitness for sneakers. The higher past success at a nest, the higher the probability that the nesting male will not desert. These nests are, as a result, very attractive to females. If sneakers go immediately to the nests with low past success, females may not spawn at these nests in the presence of sneakers. However, if sneakers join a nest once high mating rates have been established, females may spawn in the presence of sneakers. That is, females are likely to spawn in a nest with many sneakers if the undesirability of sneaking is counteracted by the higher probability that nesting males will provide parental care. By delaying sneaking activity in a nest, sneakers may manipulate the interaction between nesting males and females to their advantage. Accord-

ing to the model, the only distribution that is stable, given nesting male desertion, is to have a few nests with most of the spawning females and sneakers.

We tested this prediction by removing a successful nest and observing how the females and sneaker males redistributed themselves between remaining nests. We observed all of the nests in one area and then removed one nest with high female visitation rates and many sneakers. We conducted repeated observations on the remaining nests to determine the effect of the manipulation on sneaker distribution and the mating success of individual females, sneakers, and nesting males.

MATERIALS AND METHODS

We conducted all of the research under natural conditions near the University of Liège (Belgium) Marine Laboratory, La Station de Recherches Sous-Marin et Océanographique (STAR-RESO), located near Calvi, Corsica, France. A high density of *S. ocellatus* individuals is found in Revellata Bay near the research station. We made all of the observations on the rocky substrate within 200 m of shore at ≤ 15 m depth using SCUBA. We conducted research in May and June of 1996 and 1997. We caught nesting males before the reproductive season and marked individuals using a pattern of subcutaneous injections of alcian blue. We observed individual nests throughout the study area. We used the same protocol for all observations. We observed focal nests for 10 min and remained a minimum of 3 m from the nests. We also noted the identity of the nesting male (determined by the alcian blue mark) at the beginning of each observation. To determine the mating success of females, sneakers, and nesting males, we noted a variety of variables during each observation. We counted the number of sneakers present at the nest once every minute. We considered a sneaker male to be at the nest if he was within 3 m of the nest, oriented toward the nest, and not feeding. We also observed the number of females that visited a nest. We defined females to have visited a nest if they came within 10 cm of the nest. We also determined the number of females that spawned in the nest, the total number of times they spawned, and the number of spawns joined by a sneaker. Finally, we noted the number of chases directed by the nesting male toward sneaker males.

For all analyses, we represent female mating success by the proportion of females spawning per nest. 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. 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 we used variations on these measures.

Sneaker decreases

We randomly selected nests with a minimum of five sneakers present. We observed a nest for 10 min, noting the identity of the nesting male, the number of sneakers present, the number of females visiting and spawning in the nest, the total number of spawns, the total number of sneakers, and the number of chases as described above. After this observation, we caught sneakers using small, hand-held nets and held these males in a live bait bucket. After the number of sneakers present around the nest had been reduced significantly (a minimum reduction of three), we left the nest undisturbed for 5

min. We then observed the nest as described above. Subsequently, we released the captive males away from the nest. After a 30 min, we observed the nest a third and final time for 10 min. We conducted 20 replicates of 3 observations each. We performed controls by releasing any caught sneaker males immediately and conducting the three successive observations exactly as done for the experiment ($N = 5$).

Sneaker increases

To increase the number of sneakers at a nest, we removed a nearby nest with many sneakers. Therefore, we chose a pair of nests, both of which had sneakers present and which were in close proximity to one another (within 5 m). We observed the focal nest for 10 min. Following this observation, we covered the other nest. From pilot observations, it was apparent that it required 20–30 min 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. We conducted 20 replicates of 2 observations each. We performed five controls by following exactly the same protocol as above except covering an active nest that did not have sneakers present at the nest.

Nest removal experiments

To determine female and sneaker choice between nests, we observed the effect of removing a high-success nest on the distribution of sneakers and females between remaining nests. We chose sites where a number of nests existed within one area. We observed all nests within 10 m of the removed nest. These nests could be grouped by their past mating success. We observed all nests for 10 min before the manipulation. Some nests had zero mating in the first (premanipulation) observation and had no sneakers present. We classified these nests as zero-success nests. Other nests had a low mating rate and one or two sneakers present at the nest. We classified these nests as low past-success nests. Finally, we classified nests with many sneakers present as high past-success nests. We chose groups of nests that had one low past-success nest and two high past-success nests. We also observed the zero-success nests throughout the experiment.

We conducted all observations using the same protocol as described above. For each replicate of the experiment, we observed all nests three times: before any manipulation, a second time at least 30 min after the manipulation, and a third time at least 4 h after the manipulation. After the first set of observations, we covered one of the nests with high past success with a net. From pilot studies, we knew that both females and sneakers will desert a nest covered this way, while the nesting male will remain at the nest. Within 30 min of covering the nest, female visitation and sneaker presence is practically zero.

Analysis of the data

Sneaker decreases

We tested all variables for normality using a Kolmogorov-Smirnov test (Zar, 1996). We tested the assumption of equal variances using the Levene-Median test (Snedecor and Cochran, 1989). Because all variables deviated significantly from normal, we conducted a Friedman's nonparametric two-way ANOVA on each variable. We made pairwise comparisons using the Student-Newman-Keuls method (Zar, 1996).

Sneaker increases

We examined the effect of treatment by comparing the two observations. We assessed the normality of the differences us-

ing the Shapiro-Wilk test (Shapiro and Wilk, 1965; Zar, 1996). We attempted transformations if variables were significantly non-normal and performed a paired t test on the differences or transformed differences. We expected sneaker number to increase and therefore used a one-tailed t test. The success of females, nesting males, and sneakers is expected to decrease, as is female spawning rate, sneak rate, and total spawning rate. Because we made no predictions regarding the direction of change in chases or female visitation rate, these tests are two tailed.

We also examined the relationship between spawning rate and the number of sneakers at nests. In these analyses, we only used the premanipulation observations pooled between the two experiments. We calculated a simple linear regression between the number of sneakers at the nest and total spawning opportunities per sneaker (total spawns/number of sneakers present). The sneaker-only model predicted that this relationship should not have a slope significantly different from zero because sneakers are predicted to distribute themselves among nests in proportion to spawning rate.

Nest removal experiments

First, we examined changes in variables between the three observations for each nest type. This indicated how the frequency of females spawning and the number of sneakers at a nest changed as a result of the manipulation. We also compared variables at a given time between nest types. This analysis indicated the nest type that leads to higher individual fitness for each group at any given time. We tested for deviations from normality using a Kolmogorov-Smirnov test (Zar, 1996). We also tested for deviations from the assumption of equal variances using a Levene-Median test (Snedecor and Cochran, 1989). We made comparisons between the three observations using a repeated-measures ANOVA when variables met the assumptions of normality and equal variances. We used a Friedman's nonparametric ANOVA when variables deviated significantly from normality or had significantly unequal variances. We made pairwise comparisons using the Student-Newman-Keuls method (Zar, 1996). We made comparisons between low and high past-success nest types for each observation using a paired t test where variables did not deviate significantly from normal. If variables deviated significantly from normal, we performed a Wilcoxon signed-rank test. All of these tests were two tailed.

RESULTS

Sneaker decreases

The number of sneakers at the nest was significantly decreased by the manipulation and returned to the original level in the final observation. Female success, nesting-male success, and sneaker success all increased when the number of sneakers at the nest was decreased (Figure 4 and Table 2). Spawning rates, the number of females spawning, and sneak rates all increased with decreased sneaker number and then returned to premanipulation levels. No significant differences existed in female visitation rates (Table 2).

Sneaker increases

Sneaker success, female success, nesting-male success, spawning rates, and sneaking rates were square-root transformed to meet the assumptions of normality. Sneaker numbers increased significantly as a result of the manipulation. Sneaker, female, and nesting male success also decreased as a result of the manipulation (Figure 5 and Table 3). Spawning rates, chases, and sneak rate all decreased as a result of the manipulation, and female visitation rate did not change significantly.

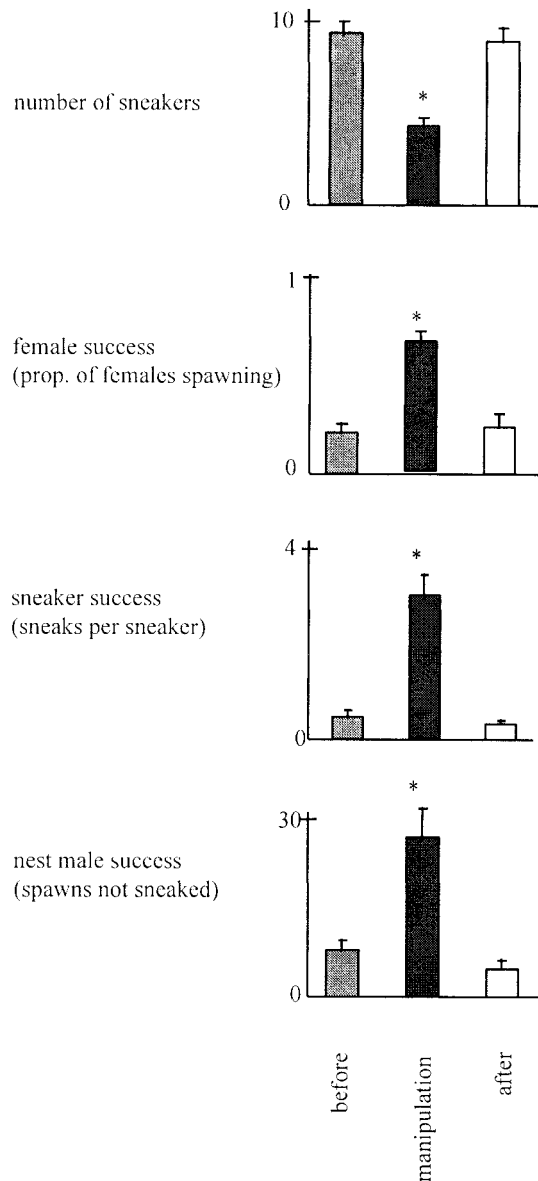


Figure 4
Sneaker decreases. When the number of sneakers at the nests is decreased, the mating success of all groups increases. The decrease in sneakers and increase in success is unstable, returning to the premanipulation level in the final observation.

Sneaker increase and decrease controls both indicated that when sneaker number was not manipulated, other variables remained unchanged as well ($N = 5$). In contrast to the prediction of an ideal free distribution based on the sneaker-only model, a significant relationship exists between sneaker presence and spawns per sneaker. This relationship is decreasing (Figure 6), with a slope and intercept significantly different from zero. This indicates that spawns per sneaker are not constant across nests, as predicted by the sneaker-only model, but instead decrease with increasing numbers of sneakers at the nest.

Nest removal experiments

Comparisons between observations

Variables for which we report F ratios did not deviate significantly from normality or equal variances. For all other variables, we report the χ^2 value from the Friedman's nonparametric ANOVA. At high past-success nests, the number of sneakers increased significantly after the manipulation (Table 4). In the final observation, the number of sneakers at the nest returned to the premanipulation level (Figure 7). No other variables differed significantly between observations for nests with high past-success (Table 5). Nests with low past-success did not experience an increase in the number of sneakers present in the first observation after the manipulation (Figure 7). However, in the final observation, the number of sneakers at the nest had increased significantly (Table 5). The total spawning and proportion of females spawning at the nest were highest in the second observation (Table 5). Comparisons made between zero past-success nests indicated that all variables remained unchanged by the manipulation at these nests. As a result, these nests were excluded from comparisons between nest types.

Comparison between nest types

The number of sneakers at the high past-success nests was significantly higher than the low past success nests in both the first (premanipulation) and second observation (Table 6 and Figure 7). However, the numbers of sneakers at the two nest types were not significantly different from the final observation (Table 6). Although significantly more females visited the high past-success nests in the pre- and first postmanipulation observations, an equal number of females visited both nest types in the final observation. Total spawns was significantly higher at the low-past success nests in the first postmanipulation observation, but in the final observation no differences in spawning were found. At first, mating success was higher for sneaker males at the low past-success nests, but then became equal in the final observation. Nesting male success fol-

Table 2
Results of sneaker decrease experiments ($n = 20$)

Variable	Observation (mean)			χ^2	p
	Before	During	After		
Sneaker number	8.30	3.85*	7.96	30.90	<.001
Female visitation rate	19.30	20.6	17.70	1.60	.45
Female spawning rate	3.95	13.1*	3.60	12.78	.002
Total spawning rate	6.95	27.85*	4.85	13.73	.001
Sneaking rates	3.55	11.35*	1.80	23.73	<.001
Female success	0.20	0.63*	0.23	12.90	.002
Sneaker success	0.44	2.96*	0.29	23.73	<.001
Nesting-male success	3.40	16.5*	3.05	10.98	.004
Chases	17.95	19.65*	11.05	7.60	.022

* Significantly different from other means.

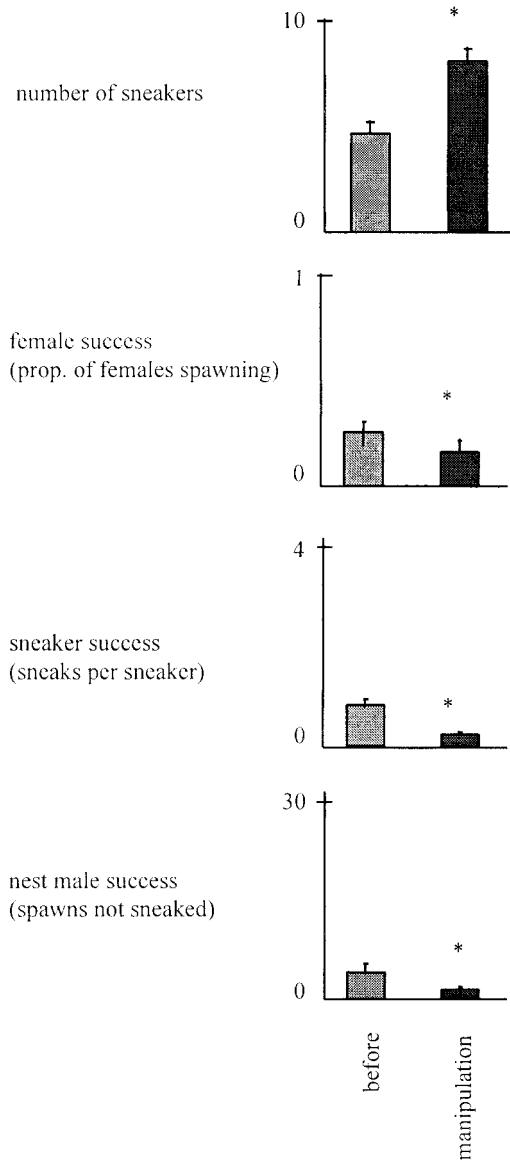


Figure 5
Sneaker increases. When the number of sneakers at the nest is increased, the mating success of all groups decreases significantly.

Table 3
Results of sneaker increase experiments ($n = 20$)

Variable	Observation (mean)		t	p
	Before	During		
Sneaker number	4.54	7.82	14.24	<.001
Female visitation rate ^a	14.25	16.20	1.89	.074
Female spawning rate	3.35	1.90	2.11	.024
Total spawning rate	6.90	3.20	2.24	.019
Sneaking rates	3.15	1.80	1.96	.033
Female success	0.24	0.16	2.75	.006
Sneaker success	0.75	0.22	4.42	<.001
Nesting-male success	3.75	1.40	1.81	.044
Chases	17.80	12.75	2.61	.017

^a Means are not significantly different from one another. All other means differ significantly from one another.

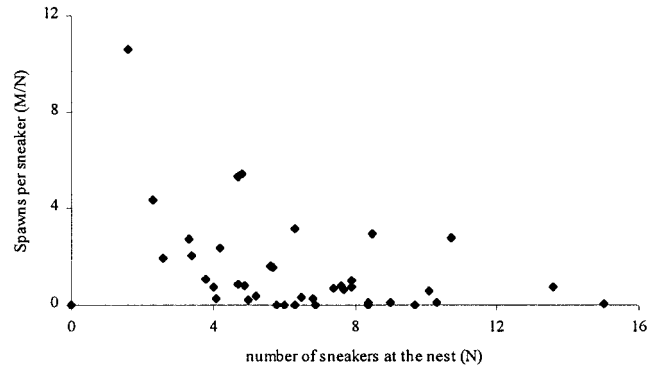


Figure 6
Sneaker males are not simply distributed in proportion to the total spawning rates at nests. If males were distributed in an ideal free way between nests, total spawns available per sneaker should be equal across nests. Instead, a significant negative relationship exists between spawns per sneaker and total sneaker number. The relationship is given by the equation $y = -0.26x + 3.08$, where both the negative slope ($t = -2.52, p = .016$) and the intercept ($t = 4.27, p = .0001$) are significantly different from zero.

lowed the same pattern. Female success was higher after the manipulation at the low past-success nest type, but then was not significantly different between nest types at the final observation.

Conclusions

Sneaker increase and decrease

By increasing the number of sneakers at the nest, the competition between sneakers is increased. However, the conflict between nesting males or females and sneakers is also increased due to a higher probability that any spawn will be sneaked. In addition, the conflict between the nesting male and female over sneaking is increased. In contrast, by decreasing the number of sneakers, the success of all individuals is increased, and the conflict between each group is decreased.

The fact that sneaker success is lower at the stable sneaker number than with fewer competitors can be explained by competition between sneakers (Sibly, 1983). However, the distribution of sneakers among nests is not explained by interactions between sneakers alone. Spawning rates at nests with many sneakers were lower than nests with fewer sneakers present (Figure 7). As predicted by the model, the existence of multiple simultaneous conflict interactions led to situations where all individuals involved have lower fitness.

Table 4
Comparisons between observations for high past-success nests

Variable	Observation, mean (SE)			Statistic	<i>p</i>
	Before	Post 1	Post 2		
Sneakers at the nest	6.55 (0.81)	10.91 (1.57)*	6.24 (0.65)	$\chi^2 = 15.5$	<.001
Female visits	14.17 (1.93)	16.08 (2.00)	14.83 (1.97)	$\chi^2 = 2.04$.36
Females spawning	1.00 (0.41)	1.58 (0.75)	3.42 (1.33)	$\chi^2 = 2.63$.27
Total spawns	1.83 (0.84)	2.25 (1.14)	5.50 (2.05)	$\chi^2 = 2.38$.31
Spawns sneaked	0.92 (0.53)	1.33 (0.86)	2.41 (0.80)	$\chi^2 = 1.13$.36
Pair spawns (nesting-male success)	0.92 (0.45)	0.92 (0.50)	3.08 (1.41)	$\chi^2 = 1.54$.46
Sneaks per sneaker (sneaker success)	0.15 (0.08)	0.13 (0.08)	0.44 (0.17)	$\chi^2 = 1.17$.58
Proportion of females spawning (female success)	0.11 (0.05)	0.10 (0.04)	0.22 (0.08)	$\chi^2 = 3.41$.18
Chases	16.00 (3.91)	13.42 (3.29)	17.08 (3.42)	$F = 0.417$.66

* Significantly different from other two means.

Nest removal experiments

After nest removal, the number of sneakers initially increased at nests that already had many sneakers present and did not change at the low past-success nest type. However, spawning rate and female mating success were higher at the nests with low past success. In other words, females and sneakers did not join the same nests, and sneaker success was higher at the nests to which sneakers did not redistribute. Immediately after the manipulation, low past-success nests had the same fre-

quency of sneaked spawns and lower competition with other sneakers as the high past-success nests. Yet sneakers did not move to these nests. In the final observation, both nests are equivalent in all variables. Sneakers are initially choosing nests that lead to lower immediate mating success. As the model predicts, although choosing the low past-success nest might lead to immediate higher mating success, this distribution would be unstable because females would be less likely to spawn there. However, once these nests have achieved high success, females are willing to spawn in the presence of sneakers. Presumably, this female preference occurs because of the decreased chance of nesting-male desertion.

DISCUSSION

The simultaneous resolution of multiple conflict interactions can explain the counterintuitive observation that sneakers delay sneaking at nests despite higher potential immediate mating success. It is possible that factors we have not considered could also explain this pattern of distribution. For example, sneakers could simply be unable to assess which nest would lead to higher fitness. Though this may be true, it is still clear that the examination of competition between males or female choice in isolation would not have fully explained the observed mating behavior in *S. ocellatus*. Furthermore, the experimental results are consistent with the natural pattern of success at nests. Given the models compared here, the distribution is best explained by the simultaneous resolution of multiple conflict interactions.

These multiple conflict interactions create trade-offs for both sneakers and females. Although similar to traditional life-history trade-offs (Roff, 1992; Stearns, 1992), these trade-offs are generated by sexual conflict. Females trade-off the cost, whatever it might be, of mating in the presence of sneakers with the cost of nesting male desertion. This trade-off enables sneakers to achieve mating success despite the fact that females prefer to spawn with nesting males. In fact, we predict that females are willing to spawn in the presence of sneakers because of nesting male desertion. Therefore, nesting male behavior leads, through female choice, to conflict between sneakers and nesting males. This counterintuitive pattern can only be understood by a careful analysis of all of these elements simultaneously.

Recent research into sexual conflict has indicated that conflict is a common force in many species (reviewed by Andersson, 1994). The consideration of sexual conflict has clearly

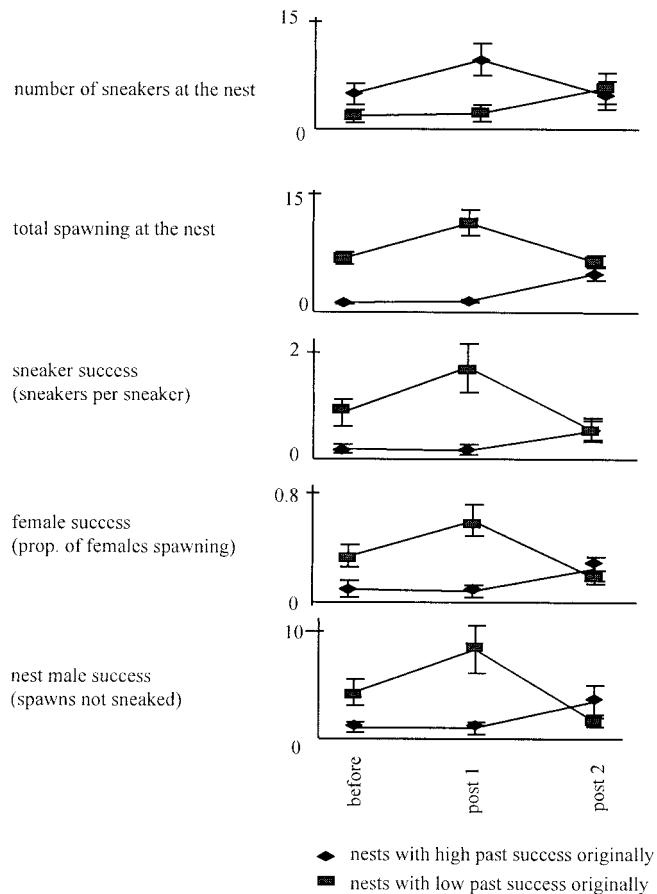


Figure 7
Results of nest removal experiment. Bars indicate SEs of mean.

Table 5
Comparisons between observations for low-success nest

Variable	Observation, mean (SE)			Statistic	<i>p</i>
	Before	Post 1	Post 2		
Sneakers at the nest	1.09 (0.09)	1.31 (0.13)	4.69 (0.80)*	$\chi^2 = 16.17$	<.001
Female visits	5.58 (1.04)	7.58 (2.10)	11.58 (2.57)	$F = 3.28$.057
Females spawning	2.17 (0.59)	3.67 (0.89)	2.33 (0.74)	$\chi^2 = 2.54$.25
Total spawns	4.75 (1.40)	9.33 (2.19)	4.67 (1.88)	$F = 2.84$.08
Spawns sneaked	0.92 (0.34)	1.92 (0.47)	3.17 (1.47)	$\chi^2 = 1.04$.60
Pair spawns (nesting-male success)	3.83 (1.13)	7.42 (1.96)*	1.50 (0.50)	$F = 6.42$.006
Sneaks per sneaker (sneaker success)	0.74 (0.21)	1.50 (0.41)	0.47 (0.18)	$\chi^2 = 2.79$.25
Proportion of females spawning (female success)	0.32 (0.07)	0.52 (0.04)*	0.19 (0.05)	$F = 3.61$.044
Chases	15.75 (3.53)	15.92 (3.57)	17.00 (3.69)	$\chi^2 = 0.17$.92

* Significantly different from other two means.

extended our theoretical and empirical understanding of mating systems and reproductive behavior (e.g., Clutton-Brock and Parker, 1992; Davies, 1989, 1992; Davies and Hatchwell, 1992; Hammerstein and Parker, 1987). Yet the simultaneous consideration of multiple conflict interactions can lead to a more complete understanding of the reproductive behavior of a species as well as variation in behavior between species. Clearly, a complete theory of mating systems and reproductive behavior must also consider the basic reproductive biology and ecology of a species. These basic elements will influence the costs and benefits and behavior and may even drive the conflict interactions. We argue that the simultaneous resolution of multiple conflicts within and between the sexes will drive mating behavior in most species.

Our understanding of mate choice has increased significantly in recent years (e.g., Andersson, 1994; Crowley et al., 1991; Janetos, 1980; Johnstone et al., 1996; Kirkpatrick, 1982, 1985, 1986; Kirkpatrick and Dugatkin, 1994; Losey et al., 1986; Real, 1990, 1991). However, if one is trying to understand female choice in a species, our research indicates that it is not

sufficient to consider only how female fitness is affected by different patterns of female choice. We must also allow for the fact that female choice will influence the fitness of male behavior. This in turn will alter female mating success. Similarly, the behavior of other females in the population may affect the fitness of female choice either directly or indirectly through their effect on male behavior. Whenever female choice drives male mating success, we must consider the interactions both within and between the sexes to fully explain patterns of female mate choice.

Although past research has determined the main mechanisms that can maintain alternative behaviors and documented patterns of expression (Austad, 1984; Caro and Bateson, 1986; Dominey, 1981, 1984; Dunbar, 1983; Gross, 1984, 1991, 1996), we have little understanding of how interactions between the sexes influence alternative reproductive behaviors. If we are interested in predicting the occurrence of alternative male reproductive strategies, we will need to consider the possible effect of female choice on male behavior (Alonzo and Warner, 1999; Henson and Warner, 1997). If female fitness is

Table 6
Comparisons between high and low past-success nests for each observation

Variable	Observation		
	Before	Post 1	Post 2
Sneakers at the nest	High>low $t = 6.59$ $p < .001$	High>low $W = -78$ $p < .001$	No difference $t = 1.27$ $p = .23$
Female visits	High>low $t = 5.33$ $p < .001$	High>low $t = 4.91$ $p < .001$	No difference $t = 1.15$ $p = .27$
Females spawning	No difference $t = -1.465$ $p = 0.17$	No difference $t = -1.66$ $p = .13$	No difference $t = 0.71$ $p = .49$
Total spawns	No difference $t = -1.57$ $p = .15$	Low>high $t = 2.54$ $p = .03$	No difference $t = .29$ $p = .77$
Spawns sneaked	No difference $W = 3$ $p = .9$	No difference $t = -0.70$ $p = .50$	No difference $t = 0.46$ $p = .66$
Pair spawns (nesting-male success)	Low>high $t = -2.11$ $p = .06$	Low>high $t = -2.86$ $p = .02$	No difference $W = -9$ $p = 6.438$
Sneaks per sneaker (sneaker success)	Low>high $t = -2.0$ $p = .03$	Low>high $t = -3.62$ $p = .004$	no difference $t = -0.12$ $p = .91$
Proportion of females spawning (female success)	Low>high $t = -2.40$ $p = .04$	Low>high $t = -3.53$ $p = .005$	No difference $t = -3.98$ $p = .002$
Chases	No difference $t = .052$ $p = .96$	No difference $t = -0.46$ $p = .66$	No difference $t = 0.02$ $p = .99$

affected by the type of male with whom they mate, female choice between alternatives alters the predictions made by considering interactions between males alone (Alonzo and Warner, 1999). There may also be situations where females are not affected by the presence or absence of male alternatives. Therefore, we need not only to ask how will female choice affect the evolution of male alternatives, but also question under what circumstances interactions between the sexes will not be important.

Clearly, there will be cases where a single conflict interaction can fully explain the observed reproductive behavior in a species. However, in other cases, such as *S. ocellatus*, multiple interactions within and between the sexes must be considered simultaneously in order to understand mating behavior. The skewed, suboptimal distribution of both females and sneakers between nests could only be explained through careful consideration of multiple interactions simultaneously. We also argue that a complete theory of reproductive behavior and the evolution of mating systems will need to consider the simultaneous resolution of multiple conflict interactions if our goal to fully predict and explain observed variation in behavior.

APPENDIX

Details of numerical methods

The game method

The computer algorithm solved each fitness equation separately. The nesting-male nests states (x, c) correspond directly to the nest types (i) that females and sneakers experience. Using the behavioral matrices resulting from the backward iteration, a forward simulation calculated the proportion of females preferring nest types, $M(x, c)$ or M_i , the proportion of sneakers preferring nest types, N_i , and the probability each nest state would be deserted, $D(x, c)$ or D_i . These values were then used in another backward iteration. This iteration procedure was continued until all behavioral matrices and variables did not change between successive iterations. This is the same as the behavior being stable against invasion. It is possible that a dynamic game can fail to converge to a stable solution. This was not a problem for this model as long as we used the stabilization method described below.

Stabilizing the model

We used a method proposed by McNamara et al. (1997) to stabilize dynamic state variable game models. This was especially necessary for the models examining multiple conflict interactions simultaneously. The change in behavior is damped between iterations. This is achieved by allowing only some portion (δ) of the population to change behavior. The damping increased as the number of iterations searching for a stable behavior increased ($\delta = 1/\text{number of runs}$). Thus, for any given iteration the behavior adopted by the population is $\pi_n = \delta B(\pi_{n-1}) + (1 - \delta)\pi_{n-1}$.

Game initiation

To begin the entire iteration procedure, we assumed that no nests were deserted (i.e., $D = 1$ for all nests) and that females and sneakers were evenly distributed between nests. Final results did not differ if other assumptions were made. We also had to make assumptions about the distribution of nest types at $t = 1$. For the results presented here, we assumed that males all started at $x = 0$ and $c = 1$ at $t = 1$. Female and sneaker behavior did not depend on state, and thus no assumptions needed to be made. Results presented are only for those time periods after which the nesting male state distribution had stabilized and was independent of the absolute value of t . The

nesting male state distribution for $t > 1$ was determined by the male behavior and the probability of changing success state, $p[M(x, c)]$. All distributions were calculated based on proportion of individuals in the state rather than simulating the actual number of individuals.

For the incomplete models, we made assumptions about the input parameters (M, D , or N) that were not an outcome of the model. For example, for the female-only fitness model, we solved only the female fitness equation and examined a variety of sneaker distributions and desertion probabilities. Similarly, for the sneaker and nesting-male interactions, we examined the effect of a variety of sneaker distributions on the solution of the linked female and nesting male fitness equations.

State variables

In the iterations presented, we always assumed that the maximum nest cycle value, c_{max} , was 10. This value is based on nest cycle duration in the field. Although changing the value drastically ($c_{max} \leq 2$ or $c_{max} \leq 100$) does alter the qualitative predictions, the exact number does not drive the predictions. With c_{max} slightly smaller or larger, the mating distribution remains skewed, and highly success nests are rare and never deserted by the nesting male. In the results presented here, we also assume that the maximum nest state, x_{max} , was always 5. However, we also examined situations where the maximum was smaller ($x_{max} = 2$) and larger ($x_{max} = 10$). With $x_{max} = 2$, the qualitative results hold, but the skew is less extreme because there are fewer nest states. Similarly, with $x_{max} = 10$, the highest nest state remains the rare and has high mating success. The skew is more apparent the more nest states that are considered. However, the qualitative results that the mating distribution is skewed and nesting males desert all but high-success nests are unaffected by the exact number of nest states.

Time variables

We always assumed that a time period $t \rightarrow t + 1$ represented one day. However, we always allowed T to be large enough that the behavior was independent of time. The maximum number of time periods required was $T = 1000$. The results we present are only for time periods $t \ll T$. We focus on time-independent behavior because we are interested in short-term changes in behavior at a nest. However, it would be interesting to examine in the future whether day in the nest cycle influences behavior patterns as well. We would expect individual behavior to change near the end of the reproductive season.

Reproductive success variables

For nesting males and sneakers, reproductive success is entirely determined by variables that are outcomes of the other fitness equations. For female reproductive success we always assumed $R_{SN} < R_{NM}$. Only the relative differences affect predictions. As a result, we assumed $R_T = 1$ and examined $R_{SN} < R_T$ in 0.1 intervals from 0 to 1. As long as $R_{SN} < R_{NM}$, the predictions did not differ. Even if $R_{SN} = 0$, females will mate in the presence of sneakers at high-success nests and nesting males desert all but high success nests. If $R_{SN} = R_{NM}$, females do not avoid sneakers, and the mating distribution is evenly distributed between all nests except low-success nests late in the cycle, which are deserted by the nesting male. We did not consider the case where $R_{SN} > R_{NM}$ because we know that females avoid mating with sneakers if at all possible.

Reproductive success functions

For individual and total sneak rates, we made assumptions about the form of the function (Figure 2). If the probability of state change (Figure 2a) for the nesting male is linear, mating becomes slightly less skewed in distribution, and nesting

males still desert all but the most successful nests. If total sneaker probability (Figure 2b) was linear with respect to the number of sneakers at the nest, females still were only willing to spawn in the presence of sneakers as long as $R_{SN} < R_{NM}$. Results did not differ greatly if sneak rate was a linear function of N . Females were still only willing to spawn in the presence of sneakers at high-success nests.

Survival probability

For the results presented here, we assumed that the survival probability was equal for all behaviors; we set $\lambda = 0.99$. We also ran the models with $\lambda = 0.95$, and the results remained the same. If survival is very low ($\lambda < 0.7$), then nesting males are less likely to desert nest with any success. However, observed survival probability during the reproductive season is very high.

Calculating $D(x, c)$

The solution of the nesting male fitness equation gives the behavior a male will adopt at every nest state and time combination. We also know the probability the male will change state $p[M(x, c)]$. From these two factors, we calculate the probability the nesting male will not desert the nest before eggs that are spawned in the present time period will hatch. In *S. ocellatus* it takes on average 3 days for eggs to develop (Lejeune, 1985). We assume for all of our calculations that the nesting male must remain with the nest for three time periods after the female spawns ($t + 3$). In every time period there is the probability, $p[M(x, c)]$ that the nesting male's success state will change. Let $b(x, c)$ be the behavior adopted by the nesting male and $p[M(x, c)]$ be the probability of increasing in success state if nest success state is x and time in the cycle is c . If the nesting male chooses to desert or reaches the end of a nest cycle, $b(x, c) = 0$; otherwise, $b(x, c) = 1$. If there are fewer than 3 days left in the nest cycle ($c > 7$), then the nest will certainly be deserted before the eggs can hatch, and $D = 0$. If $c < 7$, the total probability the male will remain with the nest for the next three time periods is

$$\begin{aligned}
 D = & b(x, c)(1 - p(M(x, c)))b(x, c + 1)(1 - p(M(x, c + 1))) \\
 & \times b(x, c + 2)(1 - p(M(x, c + 2)))b(x, c + 3) \\
 & + b(x, c)(1 - p(M(x, c)))b(x, c + 1)(1 - p(M(x, c + 1))) \\
 & \times b(x, c + 2)p(M(x, c + 2))b(x', c + 3) \\
 & + b(x, c)(1 - p(M(x, c)))b(x, c + 1)p(M(x, c + 1)) \\
 & \times b(x', c + 2)(1 - p(M(x', c + 2)))b(x', c + 3) \\
 & + b(x, c)p(M(x, c))b(x', c + 1)(1 - p(M(x', c + 1))) \\
 & \times b(x', c + 2)(1 - p(M(x', c + 2)))b(x', c + 3) \\
 & + b(x, c)(1 - p(M(x, c)))b(x, c + 1)p(M(x, c + 1)) \\
 & \times b(x', c + 2)p(M(x', c + 2))b(x'', c + 3) \\
 & + b(x, c)p(M(x, c))b(x', c + 1)p(M(x', c + 1)) \\
 & \times b(x'', c + 2)(1 - p(M(x'', c + 2)))b(x'', c + 3) \\
 & + b(x, c)p(M(x, c))b(x', c + 1)(1 - p(M(x', c + 1))) \\
 & \times b(x', c + 2)p(M(x', c + 2))b(x'', c + 3) \\
 & + b(x, c)p(M(x, c))b(x', c + 1)p(M(x', c + 1)) \\
 & \times b(x'', c + 2)p(M(x'', c + 2))b(x''', c + 3), \quad (A1)
 \end{aligned}$$

where

$$x' = \min\{5, x + 1\}.$$

If the nesting male deserts the nest in the current time period [$b(x, c) = 0$], then clearly $D = 0$. Otherwise, the desertion

probability depends both on the probability of changing success states, $p(M)$, and the behavior chosen by the male in each nest state.

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