

# Female mate assessment and choice behavior affect the frequency of alternative male mating tactics

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Explanations for the existence of alternative male mating tactics focus primarily on male–male competition. Mating systems, however, are composed of interactions both within and between the sexes, and the role of female behavior in shaping male mating tactics should not be overlooked. By using a dynamic state variable game model, I examine how female mate assessment and choice behavior affect the frequency of alternative male mating tactics. When females can accurately assess the quality of males, only males with high quality are likely to be chosen as mates, and thus, lower-quality males gain little fitness from courting females. This leads lower-quality males to switch to an alternative mating tactic that attempts to circumvent female mate choice. In contrast, if the abilities of females to accurately assess males are constrained by assessment costs, imperfect information, or time constraints, or if the pool of available males is smaller, then lower-quality males are increasingly chosen as mates and they less often use alternative mating tactics. Thus, female behavior shapes the frequency of alternative male mating tactics. A consequence of this game between the sexes is that male behavior (i.e., increased alternative mating tactics) decreases the benefits females might otherwise gain from lower assessment costs, clearer signals of male quality, more time to choose a mate, and more males from which to choose a mate. *Key words:* alternative mating tactics, dynamic game, mate assessment, mate choice. [*Behav Ecol* 15:239–247 (2004)]

Alternative male mating tactics appear to be relatively common (Henson and Warner, 1997; Taborsky 1994, 2001) and have been extensively studied, in part because they illustrate how intraspecific variation in behavior can shape the dynamics of complex systems. In many taxa, some males use a “bourgeois” or “courting” mating tactic, in which they invest in establishing territories or building nests and attempt to gain fertilizations by courting females, whereas other males use a “parasitic” or “sneaking” tactic, in which they attempt to force or steal fertilizations (for review, see Arak, 1984; Dominey, 1984; Dunbar, 1982; Taborsky, 1994, 2001). In some species, males facultatively or ontogenetically switch between these tactics (Clutton-Brock et al., 1979; De Fraipoint et al., 1993; Howard, 1978; Le Bouef, 1972; Magnhagen, 1992), and in other species the tactics appear to be fixed for an individual’s lifetime (Gross, 1982).

Attempts to examine how these alternative male mating tactics coexist have largely focused on male–male competition. One explanation for the existence of parasitic mating tactics may be that dominant males exclude subordinate males from using the bourgeois mating tactic (Dominey, 1984). Thus, the frequency of a parasitic male mating tactic may be sensitive to the density of males and the operational sex ratio (Crespi, 1988). Alternatively, female mate preferences may support the existence of parasitic mating tactics. Alonzo and Warner (2000) showed that female preferences for alternative male tactics (e.g., nonterritorial versus territorial males) can either exclude some male tactics or support the coexistence of alternative male tactics. Hughie and Lank (1997) showed that a female preference to spawn in presence of other males could select for

the existence of a male satellite tactic and for resident males to recruit and tolerate the presence of satellite males.

This article is the first to examine how female mate assessment behavior and the resulting accuracy of female mate choices affect the frequency of alternative male mating tactics in a mating system. I assume that females prefer to mate with high-quality males, but their ability to choose the best available male is constrained by the costs and time required to assess males and the imperfect information received from assessing males (Luttbeg, 2002). I examine how the number of available males, costs of assessment, imperfect information, and time constraints modify female mate assessment behavior, which in turn affects the frequency of alternative male mating tactics. If females choose their mates based on some preference for male traits, which they often do because of genetic or material benefits (Andersson, 1994) or nonadaptive sensory biases (Ryan, 1990), and they are very good at choosing the male that best matches their preferences, then only males with the most preferred traits can expect to gain reproductive success by courting females. Males without the preferred traits should thus adopt an alternative sneaking tactic that attempts to subvert female mate choice. However, as female mate choice becomes less accurate, the probability that a lower-quality male will be chosen as a mate increases, and fewer males should resort to a sneaking mating tactic. To test this idea and its potential impact on the evolution of mating systems, I develop a dynamic state variable game model in which males compete for fertilizations and female behavior both modifies and is modified by male–male competition.

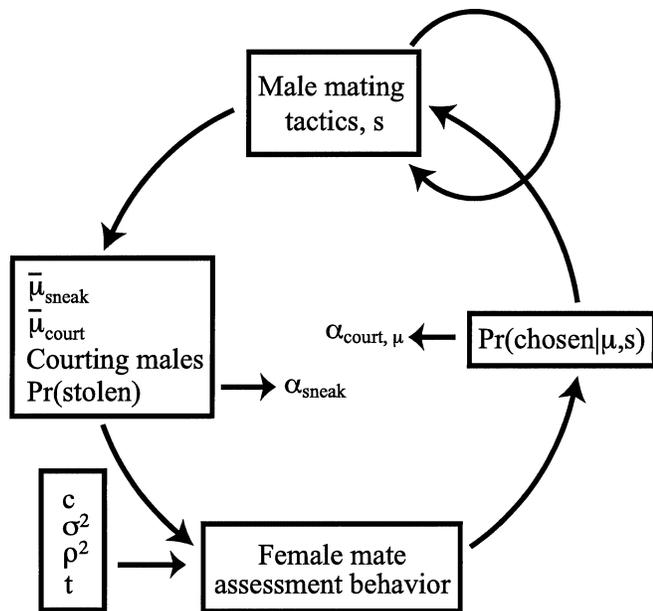
## METHODS

In the model I assume that males are attempting to maximize reproductive success and females are attempting to have their eggs fertilized by a high-quality male while minimizing assessment costs. Each male has a quality drawn from a normal distribution ( $\bar{\mu}$ ,  $\rho^2$ ) that is fixed for the duration of the model. I assume that male quality is a heritable trait that determines

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Received 17 August 2002; revised 1 April 2003; accepted 21 April 2003.



**Figure 1**

A flowchart of the games between males and between males and females. The details for each step are given in the Methods section. The mating tactic that a male uses depends on whether his quality exceeds the switching point ( $s$ ) between mating tactics. The switching point is shaped by an intrasexual game (represented by the clockwise arrow), and determines the average quality of courting ( $\bar{\mu}_{\text{court}}$ ) and sneaking ( $\bar{\mu}_{\text{sneak}}$ ) males, the pool of courting males, and the probability ( $\text{Pr}$ ) that a fertilization will be stolen. Expected male fitness from the sneaking tactic ( $\alpha_{\text{sneak}}$ ) is determined by the ratio of males using the two mating tactics, and the probability fertilizations are stolen. Female mate assessment behavior is shaped by the previous parameters and by assessment costs ( $c$ ), signal variance ( $\sigma^2$ ), variance in male quality ( $\rho^2$ ), and time limitations ( $t$ ). Female behavior determines the probability that a male of a given quality would be chosen as a mate if he uses the courting tactic, which is the expected male fitness from the courting tactic ( $\alpha_{\text{court}, \mu}$ ). Expected male fitness from the two mating tactics then modifies the game between males.

female fitness from mating. Genetic variance in male quality might be maintained by the capture of genetic variance as sexually selected male traits evolve condition dependence (Rowe and Houle, 1996). Each male uses one of two mating tactics for the duration of the model. He uses either a courting tactic in which he establishes a territory and courts females in an attempt to be chosen as a mate, or a sneaking tactic in which he is uniformly distributed among courting males and attempts to steal fertilizations. The expected payoff of the courting tactic depends on a male's quality, the frequencies of the male mating tactics, and female mate assessment behavior. The expected payoff of the sneaking tactic depends on the frequencies of the male mating tactics.

Females are attempting to increase their fitness by mating with males with high quality. The probability that a male will be chosen as a mate decreases with decreasing male quality. Thus, the courting tactic will have a lower expected benefit for low-quality males compared with high-quality males, and males using the courting tactic will have higher quality than males using the sneaking tactic. Therefore, females prefer to mate with courting males. They are attempting to discriminate which courting male has the highest quality, but they must pay an assessment cost to receive information about a male's quality. How much information females gather

before choosing a mate depends on the frequency of male mating tactics and environmental factors, such as the costs of assessing males and the clarity of information received.

Thus, there is a state-dependent game between males, in which a male's quality (a state variable) affects the probability that he will be chosen as mate over other males and in which the frequencies of the two male mating tactics affect their expected payoffs. I assume that courting males can mate with multiple females, thus there is no competition or game between females. There is also a game between the sexes in which the frequencies of male mating tactics shape the benefits females receive from assessing and choosing a mate, and female mate assessment behaviors shape the relative payoffs of the two male mating tactics.

The evolutionarily stable strategy (ESS) for this model occurs when both the frequencies of male mating tactics and female mate assessment behavior stabilize. Because a male's mating tactic depends on his quality, the ESS is a switching point (Dominey, 1984; Gross, 1996), with males using the courting tactic if their quality exceeds the switching point and using sneaking tactic if their quality is below the switching point. I use dynamic game modeling techniques and a best response approach to find the ESS switching point (Clark and Mangel, 2000; Houston and McNamara, 1999). The best response approach finds the best response strategy of male  $n$ ,  $\pi_n$ , to the strategy adopted by the rest of the population,  $\pi_{n-1}$ . When  $\pi_n = \pi_{n-1}$ , there is no strategy that male  $n$  can use that can do better than the strategy being used by the population, and that strategy is an ESS.

The dynamics of the model are complex because the behaviors of males and females are interdependent (Figure 1). I will first describe the dynamics and expected payoff of the male sneaking tactic. Then, I will describe female mate assessment behavior and the resulting expected payoff of the male courting tactic. I will finish by describing the manipulations that I performed and the metrics that I used to examine how relative female fitness and selection on male quality are affected by the game between males and females.

### The male sneaking tactic

By using the best response approach, I first set a population switching point,  $s$  (for a list and description of all of the parameters and symbols, see Table 1). The population switching point,  $s$ , indirectly determines the size of the pool of courting males, the probability that a fertilization will be stolen by a sneaking male, and the average quality of courting and sneaking males (Figure 1). As  $s$  increases, fewer males have a level of quality that exceeds the switching point, and thus, the ratio of sneaking males to courting males increases. I assume that sneaking males are uniformly distributed among courting males and they provide no benefits to courting males. I also assume that the probability that a fertilization is stolen is a function of the ratio of the number of sneaking males,  $m_s$ , to the number of courting males,  $m_c$ ,

$$\text{Pr}(\text{stolen}) = \frac{\ln\left(\frac{m_s}{m_c} + 1\right)}{b}, \quad (1)$$

and  $b$  sets the magnitude of the probability. As the ratio of sneaking males to courting males increases, the probability a fertilization is stolen increases, but the per capita probability of a sneaker male stealing a fertilization decreases. This matches a situation in which a larger group of sneaker males is better able to overwhelm a courting male's defenses, but sneaking males compete with each other. I set  $b = 4.621$ , so that  $\text{Pr}(\text{stolen}) = 0.15$  when  $m_s/m_c = 1$ . Changing  $b$  alters the frequency of mating tactics but does not qualitatively change

the reported results. I assume that the sneaking male fertilizes all of the eggs when the fertilization is stolen. Because sneaking males are uniformly distributed across courting males, expected fitness of the sneaking tactic per female is

$$\alpha_{\text{sneak}} = \text{Pr}(\text{stolen})/m_s. \quad (2)$$

If instead I had assumed that when a fertilization is stolen some portion of the eggs are fertilized by the courting male, then the expected fitness from the sneaking and courting tactics would have been decreased and increased respectively.

Male quality is normally distributed ( $\bar{\mu}$ ,  $\rho^2$ ). Thus, the distributions of courting and sneaking male quality are normal distributions truncated below and above  $s$ , respectively. As  $s$  varies, the mean quality of courting and sneaking males are

$$\bar{\mu}_{\text{court}} = \frac{1}{\sqrt{2\pi}} \int_{\mu=s}^{\infty} \mu e^{-\mu^2/2} d\mu \quad (3)$$

$$\bar{\mu}_{\text{sneak}} = \frac{1}{\sqrt{2\pi}} \int_{\mu=-\infty}^s \mu e^{-\mu^2/2} d\mu, \quad (4)$$

which I calculate by using approximations (Abramowitz and Stegun, 1972).

### Female mate assessment behavior

Female mate assessment behavior is indirectly modified by  $s$ , because  $s$  modifies the average quality of courting and sneaking males, the size of the pool of courting males, and the probability that a fertilization will be stolen. Female behavior is also modified by assessment costs ( $c$ ), signal variance ( $\sigma^2$ ), variance in male quality ( $\rho^2$ ), and how much time they have before a mate must be chosen (Figure 1). Because I am assuming females are attempting to choose a high-quality mate and they have incomplete information about the quality of males, females need a rule for how they will gather information and choose a mate. I assume that females use a comparative Bayes mate choice rule (Luttbegg, 1996). The comparative Bayes model has been shown to be a successful mate choice rule that is robust to varying environmental conditions (Luttbegg, 2002).

Females have a limited number of time steps during which they can gather information about males and choose a mate. During each time step, females decide whether to pay an assessment cost and receive new information about one male's quality or choose a mate based upon their current information. Female mate choice behavior evolves in the presence of a distribution of male quality. If the distribution of male quality is fairly constant over time, it would be maladaptive for females to estimate that all male qualities are equally likely. Thus, I assume that before a female has encountered a male, her estimate of that male's quality closely matches the population distribution of courting male quality. The mean of this prior estimate is  $\bar{\mu}_{\text{court}}$ , the mean quality of courting males. I assume that the variance in her prior estimate of male  $i$ ,  $\rho_i^2$ , equals  $\rho^2$ , the variance in male quality for the whole population, which in all cases is three. How much this prior estimate affects the females estimate of a male after she has gained new information about the male depends on the relative sizes of the estimate variance,  $\rho^2$ , and the signal variance,  $\sigma^2$ . If signal variance is smaller than the estimate variance, the prior estimate has a relatively small effect on the posterior estimate after new information is received.

These prior estimates are used to estimate the expected fitness of choosing a courting male. Because I assume that female fitness equals the quality of the male with which they

**Table 1**  
Parameters and symbols in the model

$\mu$	actual quality of a male
$\bar{\mu}_{\text{court}}$	average quality of courting males
$\bar{\mu}_{\text{sneak}}$	average quality of sneaking males
$\hat{\mu}_i$	mean of a female's estimate of male $i$ 's quality
$\rho_i^2$	variance in a female's estimate of male $i$ 's quality
$\sigma^2$	variance in the distribution of signals a female can perceive from a male
$s$	switching point, male quality at which males switch between mating tactics
$s^*$	evolutionarily stable switching point
$m_s$	number of sneaking males
$m_c$	number of courting males
$b$	sets the probability fertilizations are stolen
$\alpha_{\text{sneak}}$	expected male fitness from sneaking
$\alpha_{\text{court},\mu}$	expected male fitness from courting, given a male quality of $\mu$
$c$	assessment cost paid by females each time they assess a male
$f_{\text{mate},i}$	expected female fitness from mating with male $i$
$F_{\text{mate}}$	maximum expected female fitness from mating with any available male
$A$	number of assessments done by a female
$\Psi_f$	average relative female fitness/average female fitness from random mate selection
$\Psi_m$	average quality of mating males/average male quality

mate minus assessment costs, the expected fitness gained from choosing a courting male  $i$  with an estimated quality  $\hat{\mu}_i$  is

$$f_{\text{mate},i} = (1 - \text{Pr}(\text{stolen}))\hat{\mu}_i + \text{Pr}(\text{stolen})\bar{\mu}_{\text{sneak}}. \quad (5)$$

The first term is the expected fitness of mating with the chosen male times the probability that the courtship will not be stolen. The second term is the expected fitness of mating with a sneaking male times the probability that the courtship will be stolen. Variance in the female's estimate of the male's quality can be ignored because her estimate is symmetric and fitness function is linear. The highest expected benefit from mating with any of the courting males is

$$F_{\text{mate}} = \max(f_{\text{mate},i}). \quad (6)$$

If a female chooses to assess a male, she pays an assessment cost ( $c$ ), which is subtracted from the benefit she receives when she chooses a mate, and she receives a signal that gives her information about the quality of that male. Because of errors in the male's production of the signal and the female's perception of the signal, a signal as perceived by a female does not give her perfect information about the quality of the male that produced the signal. A range of male qualities can produce the received signal, which is represented with a normal distribution with variance equal to the signal variance ( $\sigma^2$ ). A more reliable signal has a smaller signal variance and smaller range of male qualities could produce the received signal. The new information in the received signal is combined with the female's prior estimate of the male by using Bayesian updating to produce a new estimate of the male's quality. In the next time step, the female again decides whether to gather information or choose a mate. This continues until a mate is chosen or the time limit is reached, at which point the male associated with  $F_{\text{mate}}$  is chosen. The details of how females estimate the benefit of assessing a male and decide whether to gather more information or choose a mate are given in Luttbegg (1996, 2002). For this model, the important outcomes of the

comparative Bayes rule are that females tend to make more accurate mate choice decisions (i.e., chosen males better match female preferences) when assessment costs are low, signals from males are clear (i.e., signal variance is low), time is abundant, and when choosing from a larger pool of males.

### The male courting tactic

The switching point ( $s$ ), the number of males courting, and female mate assessment and choice behavior combine to form the probability that a courting male of a given quality will be chosen as a mate (Figure 1). I assume that males do not assess the qualities or tactics of other males, and therefore, the expected payoff of the courting tactic is based on the expected distributions of male qualities and tactics. I use simulations to calculate the probability that a focal courting male with quality  $\mu_i$  will be chosen as a mate in a population of nonfocal males using a switching point  $s$ . I assign the focal male a quality ranging from eight to 13 at intervals of 0.25, and vary  $s$  from 8.125–12.875 at intervals of 0.25. The qualities of nonfocal males are drawn from a normal distribution (mean = 10, variance = 3), and these males court if their quality exceeds  $s$  and sneak if it does not. For each combination of  $\mu_i$  and  $s$ , I simulate 2000 females, choosing a mate from the pool of focal and nonfocal males, and measure  $\Pr(\text{chosen} | \mu_i, s)$  as the number of times the focal male was chosen divided by the number of simulations. For a male with quality  $\mu_i$  in a population using switching point  $s$ , the expected fitness of the courting tactic per female is

$$\alpha_{\text{court},\mu} = [1 - \Pr(\text{stolen})] \Pr(\text{chosen} | \mu, s). \quad (7)$$

Comparing  $\alpha_{\text{sneak}}$  (equation 2) and  $\alpha_{\text{court},\mu}$ , I find the level of  $\mu$  at which the focal male should switch between courting and sneaking tactics given a population switching point of  $s$ . Following the best response approach, when the optimal switching point for the focal male matches the population switching point, the focal male has no alternative switching point that can successfully invade the population, and that switching point ( $s^*$ ) is an ESS. In some cases, a series of consecutive switching points matched these conditions, and I repeated simulations at a finer grain until a single point emerged as an ESS. The reported ESS should be viewed as estimates that depend on the scale at which I searched.

### Further metrics

One major factor in this model is that the probability a male will be chosen as a mate changes as variables such as the cost of assessment change. To illustrate these changes, I present the probability that a courting male with a given quality, ranging from 10–15 at steps of 0.25, is chosen as a mate as various factors change. These presented probabilities do not incorporate the changes in female behavior and the corresponding changes in the probabilities a courting male is chosen that do occur in the model. The probabilities come from 1000 simulations in which I record how many times a focal courting male with an assigned quality was chosen from a pool of males composed of the focal courting male and nonfocal males with qualities drawn from  $N(10,3)$  and using the appropriate mating tactic given their quality and  $s$ . I arbitrarily set  $s = 10$ , pool size = 10,  $c = 0.05$ ,  $\sigma^2 = 2$ , and a time limit to 50, and then vary each to show their effects on the probability a male is chosen by a female.

Finally, I examine how relative female fitness and selection on male quality are affected by the game between males and females. I isolate the effects of male behavior on relative female fitness and selection on male quality by comparing the results

of simulations in which  $s^*$  is allowed to vary or is held fixed (5000 simulations of each). By holding  $s^*$  fixed, I prevent males from responding to changes in female mate choice behavior, thus eliminating the game. I vary factors such as the costs of assessment and signal variance, and run simulations in which a female chooses a mate from an assembled pool of males, with their qualities randomly drawn from a normal distribution (mean = 10, variance = 3) and using the appropriate mating tactic given their quality and  $s$ . I measure relative female fitness as the fitness achieved by females (with costs of assessment subtracted) divided by the expected fitness from a random mate selection (i.e., the average quality of males in that simulation):

$$\psi_f = \frac{(1 - \Pr(\text{stolen}))\mu_{\text{chosen}} + \Pr(\text{stolen})\mu_{\text{sneaker}} - Ac}{\sum_{i=1}^N \mu_i / N}, \quad (8)$$

with  $A$  being the number of assessments conducted and  $N$  the number of males in the population. I measure the selection differential on male quality as the quality of males that mated with a female, which can be the quality of a sneaking male, divided by the average quality of males in a simulation

$$\psi_m = \frac{(1 - \Pr(\text{stolen}))\mu_{\text{chosen}} + \Pr(\text{stolen})\mu_{\text{sneaker}}}{\sum_{i=1}^N \mu_i / N}. \quad (9)$$

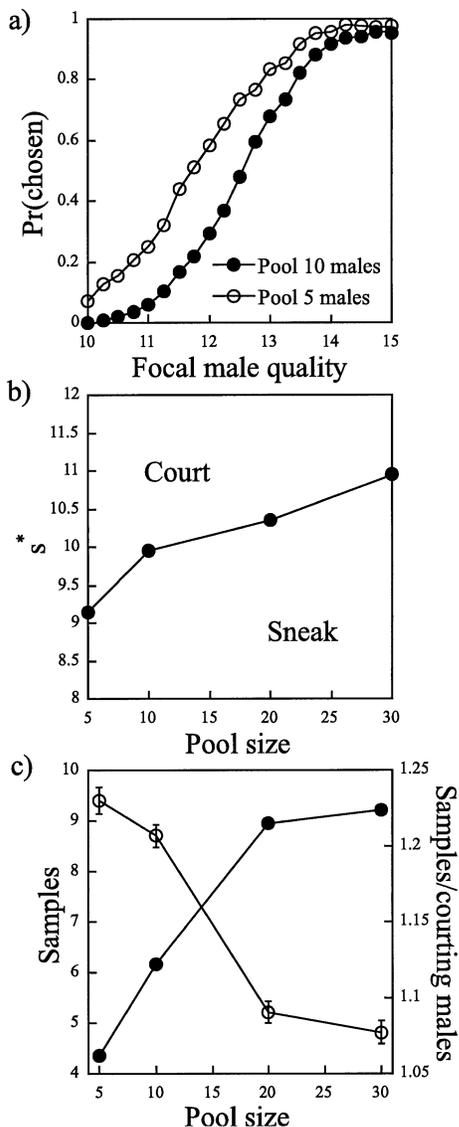
## RESULTS

I sequentially vary pool size, cost of assessment, signal variance, and time limits and show how the probability males are chosen, the ESS switching point  $s^*$ , and female assessment behavior are affected. I also show how relative female fitness and selection on male quality are affected by the varying parameter and whether or not males are changing their mating tactic in response to the varying parameter.

### Pool of males

For all males the probability of being chosen by a female decreases as the pool of males increases, but the decrease is proportionally more for males with average to low quality (Figure 2a). This causes the ESS switching point between male mating tactics,  $s^*$ , to increase (Figure 2b), which creates a mating system in which a greater proportion of males are sneaking. This matches previous studies that have found that the occurrence of a sneaking tactic increases as the operational sex ratio of males to females increases (Crespi, 1988). Females respond by assessing more males, but they assess each courting male fewer times (Figure 2c).

The game between males and females shapes how an increase in the pool of males affects relative female fitness and selection on male quality. If males are not responding to changes in the pool size and the resulting changes in female behavior (i.e.,  $s$  is fixed), then relative female fitness increases as the pool of males increases (Figure 3a). However, if males do respond (i.e.,  $s^*$  increases with pool size) (Figure 2b), then the increase in relative female fitness is reduced and can even decrease when the pool of males becomes large. This is caused by female mate choice being subverted by the increasing proportion of males using the sneaking tactic as the pool of males increases. Thus, for females there may be an optimal male pool size that balances the benefits of having many males to choose from against the costs of increased pressure from sneaking males. Females may control the size of the pool of males by selecting the size of groups or leks of males they visit (Alatalo et al., 1992; Höglund et al., 1993). Selection on male



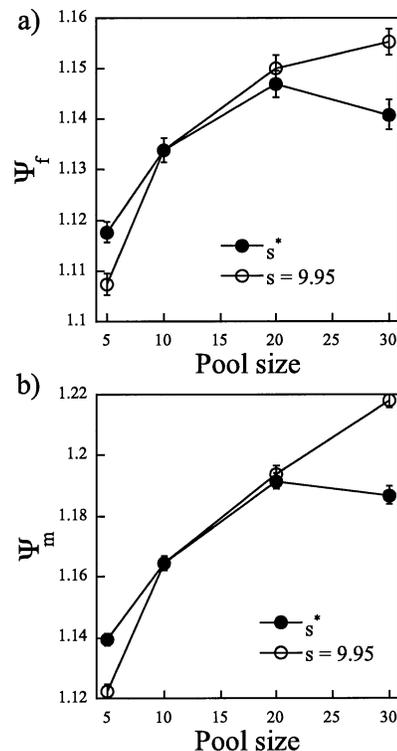
**Figure 2**  
The effects of male pool size on male mating tactics and female behavior. (a) The probability a courting male of given quality is chosen as a mate as the male pool size varies. (b)  $s^*$  as the male pool size varies, with  $c = 0.05$ ,  $\sigma^2 = 3.0$ , and a time limit of 50. (c) The average number of samples (empty circles with SE bars) and number of samples per courting males (solid circles) conducted by females from 5000 simulations given  $s^*$ .

quality also increases as the pool of males increases, but less so when males are responding by changing their behavior (i.e.,  $s^*$  increases with pool size) (Figure 3b).

**Cost of assessment**

For a male of low to average quality, the probability of being chosen as a mate decreases as the cost of assessment decreases (Figure 4a). This causes  $s^*$  to increase as the cost of assessment decreases (Figure 4b). The result is a mating system in which a larger proportion of males sneak and females are conducting more assessments per courting male as assessment costs decrease (Figure 4c).

Relative female fitness (Figure 5a) and selection on male quality (Figure 5b) both increase as assessment costs decrease, but the magnitudes of the increases are reduced by changes in



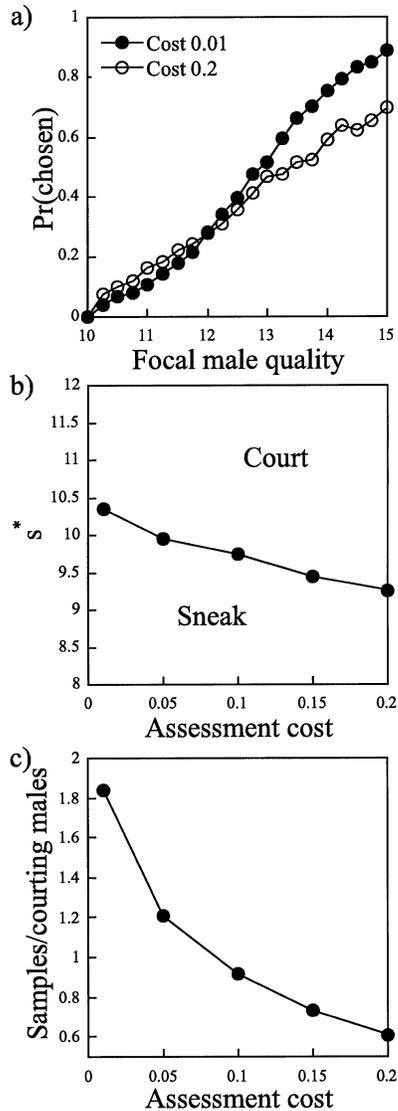
**Figure 3**  
The effects of male pool size on relative female fitness and selection on male quality. Average relative female fitness (a) and selection on male quality (b) (both with SE bars) from 5000 simulations as the male pool size varies, given males are using  $s^*$  or using  $s$  fixed at 9.95 ( $s^*$  for a pool of 10 males).

$s^*$ . Thus, selection for mechanisms that reduce female assessment costs, such as better perception of long distance signals, and the corresponding selection on male quality might both be reduced by the changes in male mating tactics that would accompany reductions in assessment costs.

**Signal variance**

As the signals from which females gain information about male quality become clearer and more accurate (i.e., signal variance,  $\sigma^2$ , decreases), the probability that a low-quality male will be chosen as a mate decreases (Figure 6a). This matches Johnstone and Earn’s (1999) finding that males of low quality become increasingly likely to be chosen as a mate as signal variance increases, but males of intermediate qualities are most likely to be chosen at intermediate levels of signal variance. The decreasing probability that low-quality males will be chosen as mates cause  $s^*$  to increase with decreasing signal variance (Figure 6b). The result is a mating system in which a larger proportion of males sneak and females are conducting fewer assessments per courting male as signal variance decreases (Figure 6c).

Relative female fitness (Figure 7a) and selection on male quality (Figure 7b) increase as signal variance decreases if males are not responding behaviorally (i.e.  $s$  is fixed). However, when  $s^*$  increases as signal variance decreases (Figure 6b), relative female fitness and selection on male quality both decrease slightly when signals become very clear. Selection for females to obtain clearer signals, perhaps by the type of signals they require from males or improvements in their perception or processing of male signals, and sexual selection on male

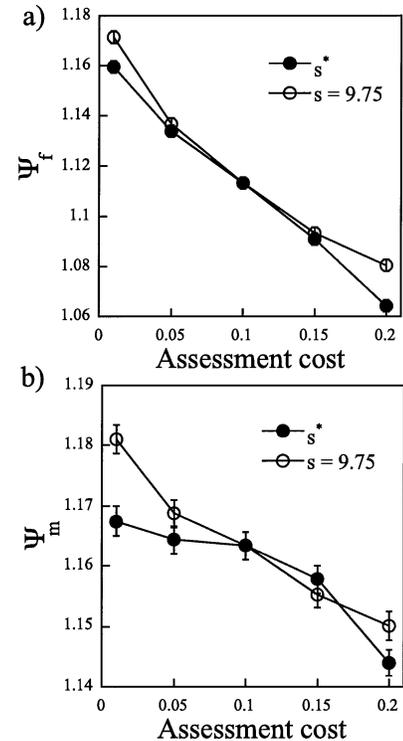


**Figure 4**  
The effects of assessment cost on male mating tactics and female behavior. (a) The probability a courting male of given quality is chosen as a mate as the assessment cost varies. (b)  $s^*$  as the assessment cost varies, with a pool of 10 males,  $\sigma^2 = 3.0$ , and a limit of 50 time steps. (c) The average number of samples per courting males (solid circles) conducted by females from 5000 simulations given  $s^*$ .

traits are both weakened by the resulting increase in male sneaking behavior.

#### Time available

As time available for choosing a mate increases, the probability that a male with average quality will be chosen as a mate decreases, whereas it increases strongly for high-quality males (Figure 8a). This causes  $s^*$  to increase as available time increases (Figure 8b). As time available increases, the resulting mating system is one in which a greater proportion of males use the sneaking tactic and females conduct more assessments per courting male (Figure 8c). Relative female fitness (Figure 9a) and selection on male quality (Figure 9b) both increase as time available for choosing a mate increases, but the magnitude of the changes are reduced by changes in  $s^*$ .

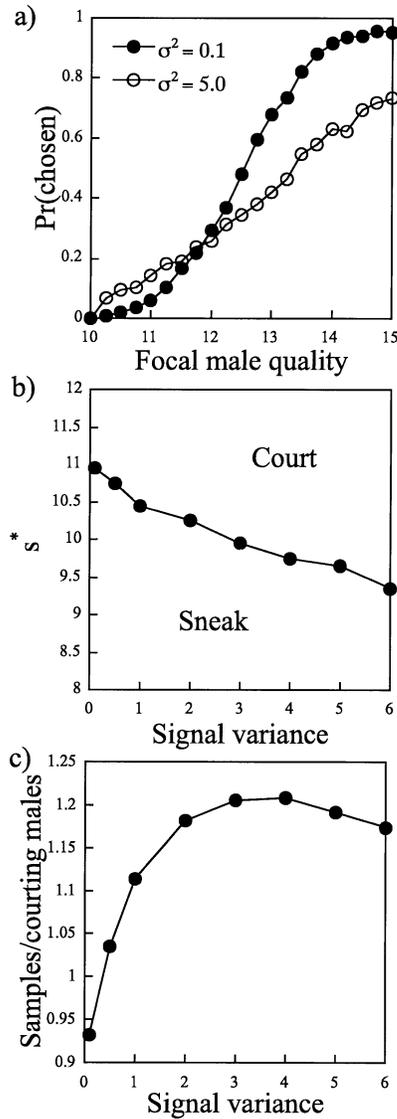


**Figure 5**  
The effects of assessment cost on relative female fitness and selection on male quality. Average relative female fitness (a) and selection on male quality (b) (both with SE bars) from 5000 simulations as the assessment cost varies, given males are using  $s^*$  or using  $s$  fixed at 9.75 ( $s^*$  for an assessment cost of 0.1).

#### DISCUSSION

I have shown that factors that shape how accurately females can assess and choose mates indirectly affect the frequency of alternative male mating tactics. When females in the model could accurately assess and choose mates, males with low to average quality were unlikely to have success courting females and in response used a sneaking mating tactic that attempts to circumvent female mate choice. However, if the accuracy of female mate assessment and choice were constrained by assessment costs, inaccurate information, and time constraints, or if the pool of males was smaller, then lower-quality courting males were chosen increasingly more often by females, and as a result, these males less often used the sneaking tactic. Thus, how well females can assess and choose mates affects the frequency of alternative male mating tactics.

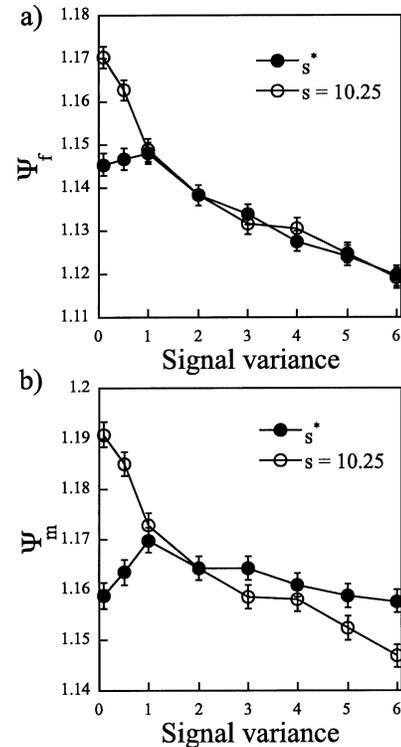
I have also shown that female fitness and how it is affected by changes in assessment costs, the accuracy of information, time constraints, and the size of the pool of males are altered by how males respond to those changes. It is commonly assumed or shown in models that females benefit from cheap and accurate assessment of potential mates (Kokko, 1997; Sullivan, 1994), having abundant time to assess and choose a mate (Real, 1990; Sullivan, 1994) and choosing a mate from a large pool of males (Alatalo et al., 1992; Bednekoff, 2002; Höglund et al., 1993). I have shown, however, that changes in male behavior may weaken or reverse these benefits for females. For example, when I fixed male mating tactics by holding the switching point between alternative male mating tactics constant, average female fitness increased as signals of male quality became more accurate. However, when male mating tactics were allowed to vary, average relative female fitness declined slightly as signals



**Figure 6**  
The effects of signal variance on male mating tactics and female behavior. (a) The probability a courting male of given quality is chosen as a mate as the signal variance varies. (b)  $s^*$  as the signal variance varies, with a pool of 10 males,  $c = 0.05$ , and a limit of 50 time steps. (c) The average number of samples per courting males (solid circles) conducted by females from 5000 simulations given  $s^*$ .

of male quality became more accurate, because lower-quality males were switching to the sneaking tactic and more fertilization were being stolen by sneaking males (Figure 7a). Thus, selection for females to reduce assessment costs, receive more accurate signals of male quality, have more time to choose mates, and choose mates from larger pools of males are all reduced by the male behavioral responses that would accompany these changes. How females assess and choose mates is not only shaped by environmental factors, such as the cost of assessment, but also by male tactics. This result is missed in models that focus only on female behavior.

There are, however, caveats to the results about selection on assessment costs, signal variance, and time constraints. The conclusions are based on looking at female fitness while varying parameters for the whole population. For example, Figure 7a shows that average female fitness increases as signals from males become less reliable. However, this analysis can

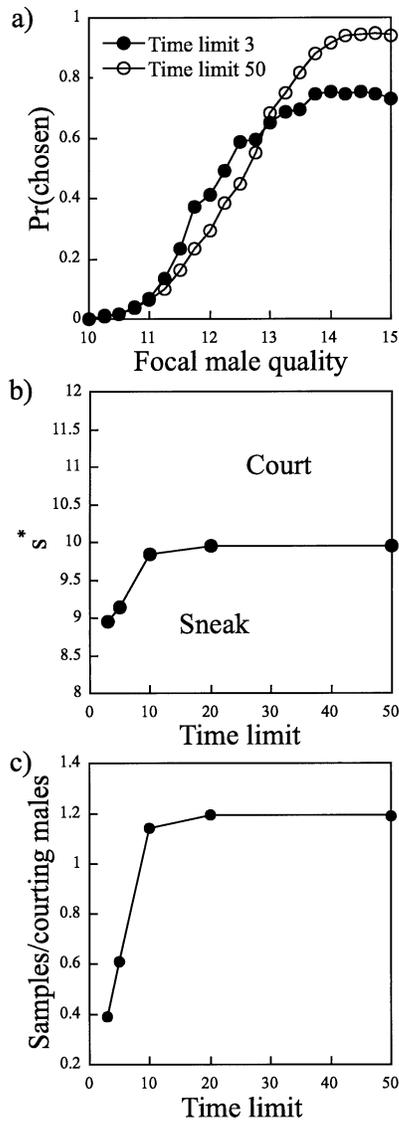


**Figure 7**  
The effects of signal variance on relative female fitness and selection on male quality. Average relative female fitness (a) and selection on male quality (b) (both with SE bars) from 5000 simulations as the signal variance varies, given males are using  $s^*$  or using  $s$  fixed at 10.25 ( $s^*$  for a signal variance of 2.0).

not clearly tell us whether selection on females should favor the evolution of male signals that are slightly less than perfect, because each female would presumably increase her fitness if she could assess males more accurately than other females in the population. Thus, the marginal fitness gains of females more accurately assessing and choosing a mate than other females might drive the system toward more reduced assessment costs, more accurate signals of male quality, and more abundant time to choose mates than would happen if all females were equal. This should weaken but not eliminate the effects of male behavior on the benefits females receive from lower assessment costs, clearer signals, and weaker time limitations.

This dynamic, however, may not be true for selection on pool size. Assuming that females can choose between visiting pools of males of different sizes and males base their mating tactics on the size of the pool they are occupying, then male responses to the size of the pool (i.e., a greater proportion of males sneaking in larger pools of males) may cause females to avoid visiting larger pools of males (Figure 3a). This result is not constrained by the game between females as described above, because a female does not benefit by visiting larger pools than other females. Thus, females may prefer to choose mates from pools of intermediate size.

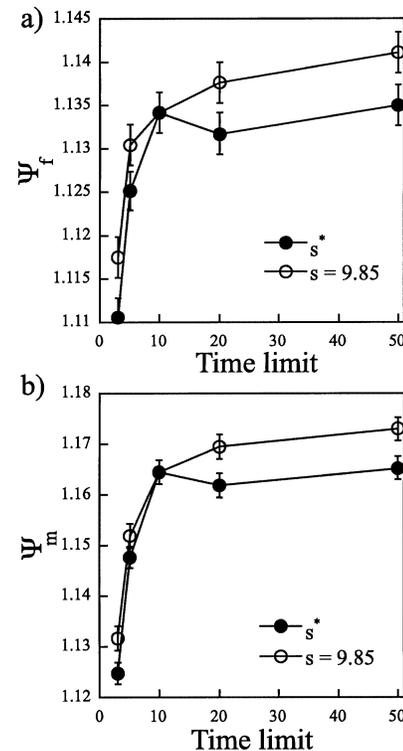
The conclusions of this model could apply to many systems in which females choose mates based on male quality and male alternative mating tactics either encourage or attempt to circumvent female mate choice. The model specifically addressed how the frequency male sneaking tactics are affected by how accurately and thoroughly females assess and choose mates. However, the conclusions should also hold for any alternative male mating tactic that attempts to circumvent



**Figure 8**  
The effects of time limitations on male mating tactics and female behavior. (a) The probability a courting male of given quality is chosen as a mate as the time limitation varies. (b)  $s^*$  as the signal variance varies, with a pool of 10 males,  $c = 0.05$ , and  $\sigma^2 = 3.0$ . (c) The average number of samples per courting males (solid circles) conducted by females from 5000 simulations given  $s^*$ .

female mate choice, such as forced copulations or female mimicry (Bisazza et al., 2001; Clutton-Brock and Parker, 1995). Other assumptions should affect the relative frequencies of male mating tactics and how responsive females are to changes in the frequencies of male mating tactics, but have little effect on my overall conclusion. I assumed that the sneaking male fertilized all of eggs when a fertilization was stolen. Alternatively, sperm competition could determine the fraction of eggs fertilized by the chosen and sneaking males. As the fraction of eggs fertilized by the sneaking male is reduced, the expected male benefit from sneaking tactic would be reduced, and thus, the frequency of the tactic would be reduced. In addition, the detrimental effect of male sneaking on female fitness would be reduced, and thus, females would be less responsive to changes in the frequency of the alternative male mating tactics.

I assumed that only the quality of the male that fertilizes the



**Figure 9**  
The effects of time limitations on relative female fitness and selection on male quality. Average relative female fitness (a) and selection on male quality (b) (both with SE bars) from 5000 simulations as the time limitation varies, given males are using  $s^*$  or using  $s$  fixed at 9.85 ( $s^*$  for a time limitation of 10).

eggs affects a female's fitness. Alternatively, female fitness could be affected by direct benefits from the chosen male, regardless of whether he fertilized the female's eggs or not. This would be the case if the effect of male quality on female fitness is owing to the male's parental abilities (Forsgren, 1997; Hoelzer, 1989). Similar to sperm competition that favors the chosen male, these direct benefits would lower the detrimental effect of sneaking on female fitness and, thus, reduce female responsiveness to changes in the frequency of male mating tactics, unless the chosen male reduces his level of parental care when sneaking occurs. However, unlike sperm competition, this would not directly lower the male expected benefit from sneaking.

Another assumption was that a male's mating tactic depends on his quality relative to the switching point between alternative tactics. Alternatively, a male's mating tactic could depend on his estimate of the quality and tactics of other males, based either on directly observing these male or on the behavior of females (Magnhagen, 1998). This would complicate the dynamics of the game between males, but I believe would not alter the general conclusions from this model.

Finally, I assumed that females were not competing for mates. When a male was chosen as a mate, he remained available for other females. Alternatively, if males were limited to a single mate, females would be competing to quickly choose higher-quality males, and this would require a mate choice rule that incorporates female competition. Another consequence would be an increased probability that average- to low-quality males would be eventually chosen as a mate. This would lower the switching point between male mating tactics and make the sneaking tactic less common. However, the sneaking tactic

would still be more common when females accurately choose mates, particularly if females that choose a mate earlier are more fecund (Price et al., 1988).

Mating systems are complex systems shaped by the behaviors and interactions of individuals with different states and traits. Any alteration in the behaviors of some individuals may cascade through the population and alter the shape of a mating system. I have shown that the frequency of alternative male mating tactics can be shaped by female mate assessment and choice behavior. Thus, understanding the causes of alternative male mating tactics would be aided by a better understanding of how females assess and choose mates. Unfortunately, generally very little is known about issues such as how females assess potential mates, whether encounters with males are random or controlled by the female, or how females respond to changes in assessment costs or signal clarity (Gibson and Langen, 1996). By taking advantage of seasonal changes or population differences in female mate choice behavior it should be possible to investigate how changes in female behavior affect male mating tactics.

I thank Suzanne Alonzo, Shane Richards, Michael Taborsky, Mary Towner, Marlene Zuk, and an anonymous reviewer for helpful comments on this article. This work was conducted as part of the Evidence Project Working Group supported by the National Center for Ecological Analysis and Synthesis, a Center funded by NSF (grant DEB-0072909), the University of California, and the Santa Barbara campus.

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