

Predators, reproductive parasites, and the persistence of poor males on leks

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Lekking males are thought to face strong directional selection on secondary sexual traits. How variation in male traits can persist under these conditions remains problematic (the lek paradox). Here, we present several game-theoretic models that show that avoidance of costly and mobile predators, sneakers, or brood parasites (enemies) leads to variation in female choice. This can result in maintenance of variation in male quality. “Enemies” will congregate around higher quality males. Females must then trade-off the benefits of mating with high-quality males against the increased risk of enemies. At equilibrium, the models predict a positive correlation between the quality of a male and the proportions of both enemies and females visiting him. In the first model, we use this framework to predict the lowest quality male on the lek that will receive any matings. In the second model, we examine the influence of this female-enemy game on the maintenance of variation in male quality. Low-quality males are likely to persist when enemies are costly to females or occur at high density, and when there is some spatial structure on the lek, so that neighboring males are typically of similar quality. If enemies are more costly to males than to females, high-quality males may benefit from receiving fewer female visits. In the third model, we consider the special case when enemies are male reproductive parasites. These models illustrate the importance of considering the simultaneous decisions of multiple players in mate choice games. *Key words:* alternative reproductive tactics, genetic variation, harassment, predation risk, sexual selection. [*Behav Ecol* 17:97–107 (2006)]

Leks are male aggregations, usually at traditional sites, that are visited by females primarily for the purpose of obtaining fertilizations (Höglund and Alatalo, 1995). On leks, the mating decisions and mating success of both males and females can often be readily observed. Thus, lekking has become a model system for understanding both sexual selection and the benefits of group living. Because the costs of choice among lekking males should be low, leks offer particularly good systems for addressing questions of female mate choice. Many studies have shown female choice for certain male traits on leks (reviewed in Andersson, 1994; Höglund and Alatalo, 1995). However, this observation is somewhat paradoxical because variation in these traits should diminish rapidly due to the directional selection imposed by female choice. Nevertheless, female choice persists and so does variation in the male secondary sexual traits chosen by females. The maintenance of variation in the face of strong directional selection on a trait is a general problem in evolutionary biology. The combination of strong female choice with the persistence of variation in male secondary sexual characters on leks has led to this phenomenon being labeled the “lek paradox” (Borgia, 1979; Taylor and Williams, 1982).

Here, we focus on the lek paradox in the most narrow sense, which is the maintenance of variation in female choice and male quality on leks and similar male aggregations (e.g., aggregated nest sites of many fishes with exclusive paternal care—ocellated wrasse: Taborsky et al., 1987; blennies: Oliveira et al., 2002; Gonçalves et al., 2003; sunfish: Gross, 1984). Several different solutions to this paradox have been suggested. Variation in male traits could be maintained despite strong directional selection and the absence of direct benefits to female choice through nonlinear selection for exaggerated

traits (Pomiankowski and Møller, 1995, but see Rowe and Houle, 1996), cyclic evolution of sexually selected traits due to intrinsically unstable Fisher’s runaway processes (Iwasa and Pomiankowski, 1995), and condition dependence of sexually selected traits (Rowe and Houle, 1996).

Another possibility is that reproductive skew on leks is not as high as often thought because females also mate with low-quality males. In other words, variation in male traits persists because there is no strong directional selection on these. This may be for a number of different reasons. Randerson et al. (2000) suggested that simple errors in mate choice enable the maintenance of variation in mate quality. Females may not be as choosy as typically thought if, for example, there is high predation risk on the lek (Grafe, 1997). Females may also express age-specific preferences, which could increase variation in mate choice (Coleman et al., 2004). Further, females may choose for compatible, rather than good, genes so that each female has a different optimal mate (Mays and Hill, 2004; Neff and Pitcher, 2005; Roberts and Gosling, 2003). Selection for direct benefits, which may not necessarily correlate with indirect benefits, could also conceivably lead to variation in female choice (Kirkpatrick and Ryan, 1991; Reynolds and Gross, 1990; Williams, 1993). Although lekking males are typically not thought to provide direct benefits to choosing females, the latter may benefit from reduced costs associated with choosing particular males.

Males may differ in their risk to females in terms of predation (on females or eggs), reproductive parasitism, or harassment. If high-quality bourgeois (territorial) males attract large numbers of predators, reproductive parasites, harassing males, or pathogens (hereafter collectively referred to as enemies), then females must trade-off the genetic benefits of mating with high-quality bourgeois males against the costs imposed by enemies. High-quality males may be riskier because they are more conspicuous (Breden and Stoner, 1987) or because they harbor higher densities of sexually transmitted pathogens or ectoparasites (Kokko et al., 2002; Reynolds and Gross, 1990). Here, we suggest that high-quality males

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may also be risky to females because mobile enemies will tend to congregate around them, even if they are no more conspicuous than lower quality males. Although this may not be a universal phenomenon, it may explain variable female choice in many systems and offers one resolution of the lek paradox.

This argument assumes that mobile enemies can impose high costs on females. Clearly, predators on females or eggs will be costly. Brood parasites should also be costly to females if parasites kill or harm host offspring or if the costs of parental care increase with brood size (e.g., in fish: Sato, 1986; Wisenden, 1999; in birds: Tewksbury et al., 2002; in insects: Tallamy and Horton, 1990). Harassing males may impose energetic costs, disrupt matings, or injure females (e.g., Bro-Jørgensen, 2003; Magurran and Seghers, 1994; Schlupp et al., 2001; Shine et al., 2000; Stone, 1995; reviewed in Clutton-Brock and Parker, 1995). Finally, there is evidence that females avoid sneakers (Alonzo and Warner, 1999, 2000; van den Berghe et al., 1989; Warner and Hoffman, 1980; reviewed in Taborsky, 1994), suggesting that the latter are costly to females. Such costs may result from low genetic quality of sneakers (van den Berge et al., 1989), costs of harassment (for references, see above), nest predation (van den Berghe et al., 1989), or negative brood care responses of bourgeois males (Neff, 2003).

The argument that females attempt to avoid parasitic or harassing males when making decisions regarding mating on leks has been proposed previously (e.g., Alonzo and Warner, 2000; Clutton-Brock et al., 1992; Taborsky, 1994). However, this hypothesis has been rejected in several instances based on the observation that females tended to congregate around males that bear high risks of harassment or parasitism or because there was no correlation between harassment and mating (Carbone and Taborsky, 1995; Saether et al., 1999). Similarly, evidence for the influence of harassment on mate choice is equivocal. Some studies show a clear influence of harassment avoidance on mate choice (Carranza and Valencia, 1999; Fox, 2002; Hunter and Jones, 1999 and references therein), whereas others have found higher harassment rates on leks than off leks, and yet females strongly preferred males on the lek (Bro-Jørgensen, 2002, 2003; Saether et al., 1999). However, as also emphasized in several recent studies (e.g., Alonzo and Warner, 1999, 2000; Gonçalves et al., 2003; Oliveira et al., 2002), we argue that the decisions of mobile enemies, which would also be expected to congregate around males that are preferred by females (Arak, 1982), have largely been ignored. Here, we extend this logic to examine the consequences of decisions by females and mobile enemies on the maintenance of variation in male quality and male reproductive tactics.

We first present a simple model in which bourgeois males are ranked according to quality. We use this model to predict the number of males that receive female visits, one measure of the functional size of the lek, and the number of female visits received by each male, a measure of reproductive skew. In a second model, we examine the consequences of female-enemy interactions on the success of bourgeois males. We examine when low-quality males are able to persist on a lek and when males might even benefit from receiving fewer female visits. In a third model, we examine the consequences of the female-enemy game when enemies are male reproductive parasites.

In all models, all females have the same preference function in the absence of enemies, that is, they all prefer the highest quality males. Because the distribution of enemies will follow that of females, this leads to some females preferring the "good" males as expected and some visiting the low-quality males because they present a smaller risk. We show that this can promote the existence of "poor" males, despite a unimodal distribution of female mating preference for indirect (genetic) benefits in the population.

THE MODELS

The model is based on predator-prey habitat selection games (e.g., Hugie and Dill, 1994; Sih, 1998). The model assumes that all females rank males in the same way. We do not explicitly model the evolution of traits used by females in ranking but assume that ranking is based on some trait that is an index, or otherwise an honest signal of relative quality, where quality is some measure of "good genes" (sensu Andersson, 1994). In the absence of enemies, females that mate with high-quality males produce offspring with greater viability than females that mate with low-quality males. Variation in male quality and female preferences are assumed to be heritable. In the first model, females could also benefit from choosing high-quality males because their sons will also be attractive. In the second and third models, however, we solve for equilibrium conditions in which the fitnesses of high- and low-quality males and of females that choose each are equal. At equilibrium, the benefits of producing more attractive sons are exactly balanced by the costs of enemies also attracted to these sons. Nevertheless, runaway selection resulting from covariance between female preference and male characters may still have an influence on the rate at which the equilibrium is approached and on the evolution of characters used by females to assess quality.

In general, we model a game between females and enemies, which may be any of the predators on females, predators on both males and females, egg predators (when fertilization is external), brood parasites, or males pursuing parasitic or coercive alternative reproductive tactics. We then examine the consequences of this game for female and enemy behavior and bourgeois male mating success. Although we include the dynamics of bourgeois males in the model, it is not formally a three-player game because the frequencies of good and poor males have no influence on the decisions of females and enemies (except in the trivial case when there are no poor males).

We first derive a model that predicts the lowest quality male above which bourgeois males can expect to receive visits from females and enemies. Then, we use a simplified version of this model to predict how interactions between females and enemies influence the frequency of high- and low-quality bourgeois males. In these first two models, enemies are assumed to be members of a different species (or different class, e.g., juveniles) than the bourgeois males and females. Finally, we develop an extension of the second model that is specific for male reproductive parasites, in which we also solve for the equilibrium proportions of bourgeois and parasitic males. This results in two major changes to the model. First, sneakers may impose no costs on females. Second, sneakers must exist in equilibrium with bourgeois males, so that there are four possible types of males (good bourgeois male, poor bourgeois male, sneaker that parasitizes good bourgeois males, and sneaker that parasitizes poor bourgeois males).

As described above, bourgeois males vary in quality (q_i), where i is the ranking of each male in terms of quality ($i = 1$ to i_{\max}), with $i = 1$ representing the highest quality male (or males, in the case of the final two models). In the first model, the number of males on the lek is equal to i_{\max} .

Females choose to mate only with bourgeois males of a given quality; the proportion choosing each male type, i , is f_i . The density of females visiting the lek (or the visitation rate) is n_f . Note that females are not time or sperm limited and can therefore always find their chosen male.

We assume that future reproductive success is equal for all females. Furthermore, at equilibrium, the fitness of an average male and an average female offspring must be the same. If variation in male types and female choice are to persist as

mixed evolutionarily stable strategies (ESSs), the average fitness of good and poor males and of females that choose each must also be equal. Therefore, the relative fitness of a female visiting male i , in the absence of enemies, is simply q_i , the number of viable offspring of either sex that she can expect to produce from mating with that male. Enemies reduce this value in a negative exponential fashion as follows:

$$W_{fi} = q_i e^{-\gamma p_i n_p}. \quad (1)$$

The parameter γ describes the costliness of each enemy, p_i is the proportion of enemies that choose male i , and n_p is the total density of enemies. The cost of enemies is in terms of reduced clutch size, either directly (e.g., predation on eggs or on the female) or indirectly (e.g., increased energetic expenditures result in a higher probability of clutch failure), resulting from interactions with enemies.

In this model, enemies wait at a particular male for females to arrive. They then compete by scramble competition for access to v resources provided by females. The payoff to an enemy that chooses male i is

$$W_{pi} = \frac{v f_i n_f}{p_i n_p} \quad (2)$$

From Equation 2, the fitnesses of enemies visiting a male of type i versus type $i + 1$ are equal when $p_i/p_{i+1} = f_i/f_{i+1}$, as in the basic continuous input ideal-free distribution (Fretwell and Lucas, 1970). Replacing p_i with f_i in Equation 1, we can solve for the lowest quality male, i^* that will receive any female visits (i.e., for which $f_i > 0$). The last rank to receive any female visits is the largest integer with a value less than i_{crit} , where i_{crit} satisfies the following equality:

$$\gamma n_p = - \sum_{i=1}^{i_{\text{crit}}} \ln \left(\frac{q_{i_{\text{crit}}}}{q_i} \right) \quad (3)$$

Thus, i^* gives one measure of functional lek size, the number of males at the lek site that mate. From this, it is apparent that functional lek size increases with increasing costliness (γ) and density (n_p) of enemies.

The proportion of mates gained by each rank is

$$f(i) = \frac{1}{i^*} - \frac{\ln \left(\frac{q_{i^*}}{q_i} \right)}{\gamma n_p} + \frac{\sum_{i=1}^{i^*} \ln \left(\frac{q_{i^*}}{q_i} \right)}{i^* \gamma n_p}. \quad (4)$$

To find analytical solutions for these conditions, let us assume that, on the lek in question, relative male quality and rank are related according to the following negative exponential function:

$$q(i) = e^{-\lambda(i-1)}. \quad (5)$$

This function describes a population with few males of very high quality and many males of poorer quality, as might be expected if, for example, poor-quality males cluster around a small number of attractive males (Beehler and Foster, 1988). It yields positive values for male quality even for very low-ranked males. Using a linear function instead of Equation 5 does not change the qualitative results of the model, although quantitative predictions change, and maximum lek size becomes constrained by the condition that male quality must be ≥ 0 .

In Equation 5, the quality of the top-ranked male is standardized to 1, and the difference in quality between adjoining ranks increases with increasing λ . Substituting Equation 5 into Equation 3 and solving for i_{crit} , we find that the value of i^* is the largest integer with a value less than

$$i_{\text{crit}} = \frac{\lambda + \sqrt{\lambda^2 + 8\lambda\gamma n_p}}{2\lambda}. \quad (6)$$

If there are at least i^* males on the lek, the proportion of females visiting each male from $i = 1$ to i^* is found by substituting Equations 5 and 6 into Equation 4:

$$f(i) = \frac{1}{i^*} + \frac{\lambda(1 - 2i + i^*)}{2\gamma n_p}. \quad (7)$$

From Equations 6 and 7, predicted functional lek size increases, and the proportion of females visiting the highest ranked individual decreases as the costliness and density of enemies increase (increasing γ and n_p ; Figure 1) and the difference in quality between adjacent ranks (λ) decreases.

Female decisions and the maintenance of variation in male quality

In this model, we assume that there are only two classes of males: high- and low-quality males (good and poor males). We assume infinite (or very large) populations of males, females, and enemies. This does not necessarily mean that leks are very large as the population may be subdivided into many leks. Therefore, rather than using densities of males, females, and enemies, we model the number of these per lek. We assume that any vacancies on leks are immediately replaced, so that the numbers of male and female types on the lek do not change with predation. The proportion of bourgeois males of each type i is denoted m_i , and the total number of males on the lek is n_m . We assume that males are unrelated, only gain matings on leks, all leks are identical, choice is not based on a condition-dependent trait, and males do not change in quality over their lifetime; thus, if good and poor males are to persist in the population, they must have equal fitnesses at equilibrium. Violation of some or all of these assumptions is likely in many real systems, which may facilitate the maintenance of variation in natural populations; however, we sought to explore whether avoidance of enemies alone could explain persistence in variation in male traits and set

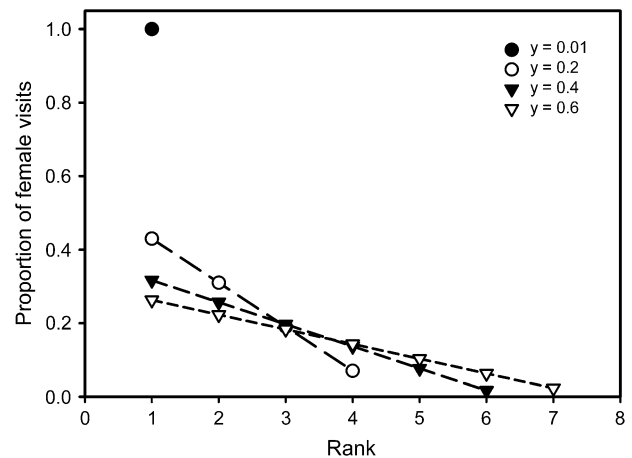


Figure 1

The proportion of female visits received according to male rank (i), when male quality $q(i)$ and rank are related according to the function $q(i) = e^{-\lambda(i-1)}$. Results are shown for increasing costliness of enemies to females, γ . As costliness to females increases, a larger number of males receive visits, while high-quality males receive fewer visits. Enemies follow the same distribution as females. $\lambda = 0.24$, $n_p = 10$.

up stringent conditions under which the persistence of such variation was unlikely.

There may be several males of each quality present on the lek, and females and enemies that prefer males of a particular type may have several males from which to choose. In the case of females, we assumed that females are divided evenly among the $n_m m_i$ males. In the case of enemies, we considered that they might be able to exploit more than one male. However, it is unlikely that, if enemies can exploit several males, they would restrict themselves to only one type if males of the other type were available.

To address exploitation of multiple males, we assume that there is some spatial structure on the lek, so that good and poor males are not distributed randomly. As will be shown later, this assumption is necessary for poor males to persist when more than one male may be exploited. We use the following asymptotic function to model the proportion of the total number of males of each type (or enemies or females visiting those males) around a given male.

$$k_{ji}(A) = \frac{A}{g_{ji} + A}, \quad A = \pi r^2. \quad (8)$$

As search radius increases, the value of $k_{ji}(A)$ approaches 1. The value g_{ji} is a measure of clustering. When g_{ji} is small, most males of type j are near males of type i . Specifically, when $g_{12} > g_{11}$ and $g_{21} > g_{22}$, males tend to be clustered with others of the same type as themselves. In spatially explicit simulations (not shown), the values of g_{12} and g_{21} tended to be similar, so we simplify our models by assuming that these are the same. The value, g_{12} , can also be thought of as a measure of spatial separation between male types. For example, very high levels of g_{12} are equivalent to having several leks in close proximity, linked by the same pool of choosing females (e.g., ruffs, Höglund et al., 1998).

In order for females to be able to choose among males differing in risk, enemies must not be able to efficiently search and exploit the entire lek. Otherwise, barring differences in intrinsic risk (e.g., some males may be in intrinsically safer locations), risk of enemies would be equal among males, and females should not consider risk in their decisions. Therefore, we assume that enemies can only search a limited area, defined as πr^2 , where r is the search radius and which may encompass several bourgeois males. Enemies can exploit any female that visits a bourgeois male within their search area. Thus, the search area defines a neighborhood of interactions with enemies for a given male and for females visiting that male.

Because enemies have a limited search area and because we assume that there is usually a spatial structure to the lek, enemies must choose where to focus their searching efforts (i.e., enemies of good males exploit regions where good males are frequent) when they first arrive on the lek. If there is no spatial structure to the lek, all enemies choose a random location (i.e., there is no difference between choosing poor or good male areas). The number of enemies in the neighborhood of a bourgeois male of type i is

$$E_i = \sum_j n_p p_j k_{ji}(A) \quad (9)$$

A similar approach could be used in the earlier model. However, this would involve making specific assumptions regarding the position of each member of the lek with respect to the others. Allowing enemies to focus on only one male could be considered to be an extreme form of the spatial structure discussed above, in that an enemy on a male of type i cannot exploit males of other types.

Enemies reduce the fitnesses of both females and males, as in Equation 1, but may affect each sex differently. For exam-

ple, females may be less affected by sneakers than are bourgeois males, while females may be more at risk from some types of predators (e.g., if females and males differ in size). The parameters x and y denote the effects of increasing local density of enemies on bourgeois male and female fitnesses, respectively.

If a female mates with a male of type i , her fitness is

$$W_{fi}(f, m, p) = \begin{cases} q_i e^{-yE_i} & \text{if } m_i > 0 \\ 0 & \text{if } m_i = 0 \end{cases}. \quad (10)$$

The fitness of a male of type i is

$$W_{mi}(f, m, p) = \frac{f_i n_f}{m_i n_m} q_i e^{-xE_i}. \quad (11)$$

Enemies gain resources of value, v , from each female, the value of which has no influence on the model predictions. We assume that enemies compete with one another for access to females. Again, assuming an even or random distribution of females among bourgeois males of a given type, the fitness of an enemy exploiting males of type i is

$$W_{pi}(f, m, p) = \frac{v \sum_j n_f f_j k_{ji}(A)}{E_i}. \quad (12)$$

For simplicity, we divide the populations of males, females, and enemies into two types: "high quality" and "low quality" ($i = 1$ and $i = 2$, respectively; $m_2 = 1 - m_1$). Low-quality females and enemies refer to those that choose males of low quality. We search for the equilibrium where

$$W_{f1} = W_{f2}, \quad (13a)$$

$$W_{p1} = W_{p2}, \quad (13b)$$

$$W_{m1} = W_{m2}. \quad (13c)$$

Some females and enemies should choose to associate with low-quality bourgeois males, and low-quality bourgeois males should persist (i.e., the equilibrium is $m_2^* > 0$, $f_2^* > 0$, $p_2^* > 0$), when

$$\frac{q_2}{q_1} > e^{\frac{y n_p A (g_{11} - g_{12})}{(g_{11} + A)(g_{12} + A)}}. \quad (14)$$

A homogenous male population is only expected when enemies are not costly to females or are relatively rare, when all poor males are of very low quality, or when there is no spatial structure on the lek. Spatial clumping has a strong effect on the model. As can be seen from Inequality 14, if there is no spatial heterogeneity of male types (i.e., $g_{12} = g_{11}$), good males will always do better than poor males and poor males will go extinct. Specifically, good males must be more likely to have good males as neighbors than do poor males.

When q_2/q_1 is greater than the right-hand side of Inequality 14 and less than 1, there is an equilibrium described by the following:

$$p_2^* = \frac{(g_{22} + A) \left[y n_p A (g_{11} - g_{12}) + \ln \left(\frac{q_1}{q_2} \right) (g_{11} + A)(g_{12} + A) \right]}{y n_p A [2g_{11}g_{22} - g_{12}(g_{11} + g_{22}) + A(g_{11} + g_{22} - 2g_{12})]}. \quad (15a)$$

$$f_2^* = p_2^* \quad (15b)$$

$$m_2^* = \frac{q_2 f_2^* e^{-x E_2}}{q_1 (1 - f_2^*) e^{-x E_1} + q_2 f_2^* e^{-x E_2}}. \quad (15c)$$

These equilibrium frequencies of enemies, females, and males (p_2^* , f_2^* , and m_2^*) are evolutionarily stable under replicator dynamics (Figure 2). On Figure 2, we show the best response curves for females and enemies (i.e., for a given frequency of females visiting low-quality males, the best response curve for enemies is the frequency of enemies visiting poor males, which yields the highest fitness). The intersection of these curves represents the equilibrium frequencies of enemies and females visiting poor males and, as shown in Figure 2, any perturbation from this equilibrium will return to it. There are also unstable equilibria at $f_2 = p_2 = 0$ and $f_2 = p_2 = 1$. A population perturbed from these equilibria will move away from them.

The frequency of female visits to poor males increases with increasing cost of enemies on females (Equation 15b; Figure 3a). The distribution of enemies exactly matches that of females (Equation 15b). The proportion of females visiting poor males increases with increasing clustering of good males (decreasing g_{11}) and decreases with increasing clustering of poor males (decreasing g_{22}). The effect of the spatial separation between male types on visitation of poor males interacts with search radius of enemies. If good and poor males are equally clustered, or if poor males are more clustered than good males, the proportion of females visiting poor males increases with increasing separation between poor and good males (Figure 4a). On the other hand, if good males are more clustered, visitation of poor males increases with increasing separation between poor and good males when search radii are large but decreases when search radii are small (Figure 4b). In general, the proportion of females and enemies visiting poor males increases with search radius at small radii but decreases as the search radius begins to encompass a large proportion of males on the lek (thereby reducing the effects of spatial structure) (Figure 4).

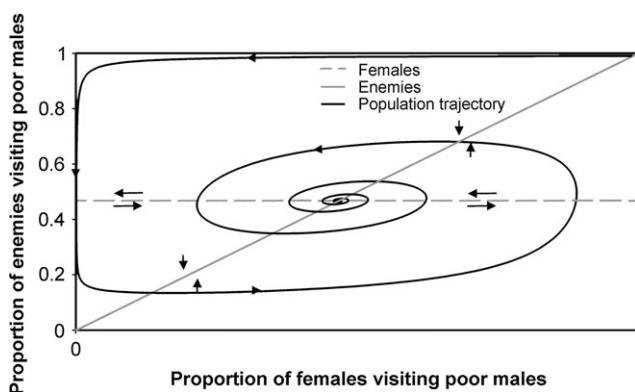


Figure 2

Best response curves for females (dashed gray line) and enemies (solid gray line). Along these lines, the fitness payoffs for choosing good or poor bourgeois males are equal. If perturbed from these lines, the population frequencies change as indicated by arrows. There are three equilibria: a stable equilibrium at the intersection of these lines and unstable equilibria at choosing only good males and choosing only poor males. The stable equilibrium is an attractor under replicator dynamics, as shown for an example population evolving toward this equilibrium from initial frequencies of 99% of enemies and females choosing poor males (black line; direction of population trajectory indicated by arrows along line). Thus, this equilibrium qualifies as an ESS.

When the effects of enemies on female fitness and the per-female increment in male fitness are similar, or when enemies have little effect on male fitness, the frequency of poor males closely matches the frequency of females that will visit them. If, on the other hand, males are much more strongly affected by enemies than are females (i.e., x is high and y is low), the frequency of poor males will be much higher than the frequency of females that will visit them (Figure 3b). Indeed, well more than 50% of the male population may be composed of poor males (Figure 3b). This is because females and enemies will tend to congregate at high-quality males if females experience few costs from high enemy densities. This can lead to drastic reductions in the fitness of good males. Indeed, the effects of enemies on the fitness of good males can be so severe that good males would do better if fewer females visited

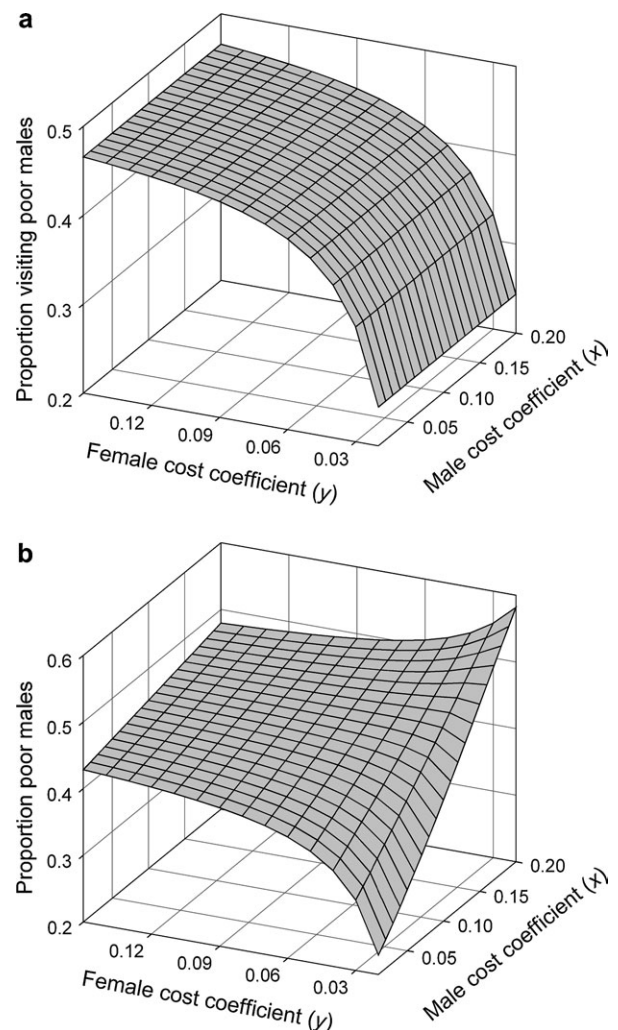


Figure 3

Evolutionarily stable proportions of females and enemies (a) choosing poor bourgeois males (or, in the case of enemies, regions of high densities of poor bourgeois males). As the results are exactly the same for females and enemies, only one result is shown. In panel (b), we show the proportion of bourgeois males that are of low quality at equilibrium. All results are plotted against increasing cost of enemies to females (y) and males (x). Costliness to males has no effect on the decisions of females or enemies, but high costliness to males leads to a high proportion of poor males in the population. Note that values of female cost coefficient increase from right to left.

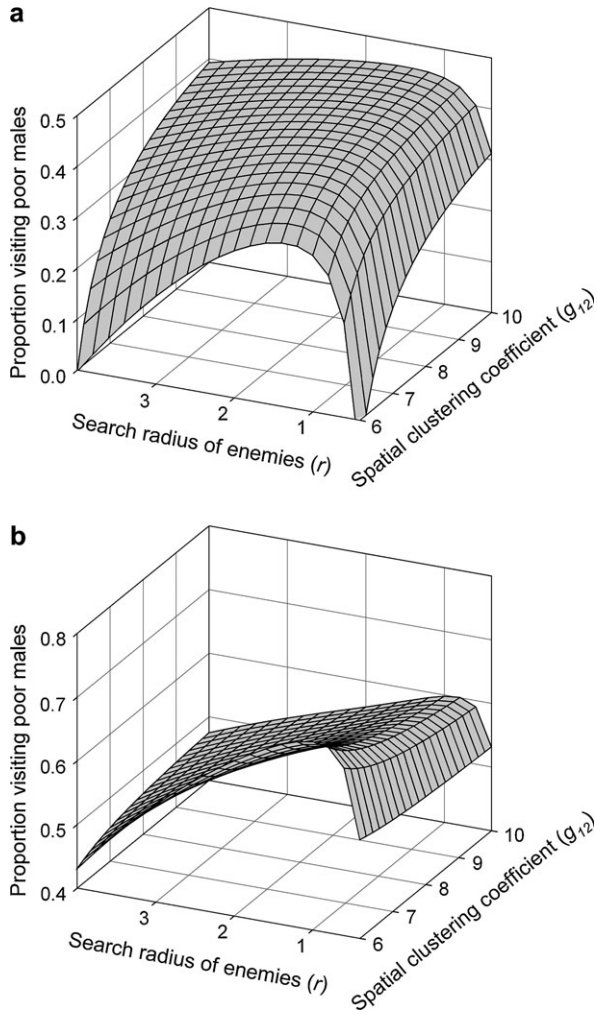


Figure 4

Influence of the spatial structure of the lek and the searching behavior of enemies on the evolutionarily stable proportions of females and enemies choosing poor bourgeois males (or, in the case of enemies, regions of high densities of poor bourgeois males). The results are exactly the same for females and enemies, so only one result is shown. In (a), the good and poor males are equally clustered (i.e., $g_{11} = g_{22}$). In (b), good males are more tightly clustered than poor males (i.e., $g_{11} < g_{22}$). All results are plotted against increasing distance between males of different types (g_{12}) and search radius of enemies (r). Note that values of search radius of enemies increase from right to left.

them, because they would then experience lower rates of visitation by enemies. This would be the case when

$$x > \frac{y(g_{12} + A)[A(g_{11} + g_{22} - 2g_{12}) - g_{12}(g_{11} + g_{22}) + 2g_{11}g_{22}]}{(g_{11} - g_{12}) \left[\ln\left(\frac{q_1}{q_2}\right)(g_{12} + A)(g_{22} + A) - \gamma n_p A(g_{22} - g_{12}) \right]} \quad (16)$$

The relative costs of enemies on males and females also influence reproductive skew, as measured by the per capita mating frequency or female visitation rate of good and poor males (not their relative fitnesses, as these must be equal). The relative success of a good male to a poor male is

$$\rho = \left(\frac{q_2}{q_1}\right)^{1-\frac{x}{y}} \quad (17)$$

Skew increases as the relative cost to males versus that to females increases. Skew also increases as the quality of poor males decreases.

A model with parasitic males

Enemies may be reproductive parasites of males, such as sneakers or satellites. For these parasitic males to influence female mating decisions, they must persist in equilibrium with the good and poor bourgeois males. Furthermore, such males may impose no costs on females (or even benefit females if they are of high quality). Here, we derive a model specific to male reproductive parasites. We consider parasitic and bourgeois tactics to represent a genetic polymorphism, with equal fitness at equilibrium (e.g., ruffs, Lank et al., 1995, and possibly *Lamprologus callipterus* (Teleostei, Cichlidae), Taborsky, 2001). We recognize that in many other cases, alternative reproductive tactics represent a conditional strategy (Gross, 1996), but we do not consider state- and status-dependent decisions further in this model.

The neighborhood number of parasitic males is the same as in Equation 9. However, n_p and n_m are replaced by sn_m and $(1-s)n_m$, respectively, where s is the proportion of males that pursue sneaking. Bourgeois and parasitic males compete for fertilizations. We model scramble competition but do not specify whether this is sperm competition or premating competition (where F would represent the average success of each tactic over many female visits). Each female produces b eggs. The fertilization success per female of each tactic is influenced by their relative competitive ability (C_p and C_m for parasitic and bourgeois males, respectively). Here, we consider that all bourgeois males (high and low quality, which, to reiterate, are measures of the number of viable offspring males can sire) have similar competitive abilities. The fertilization success of bourgeois males (of high and low quality) and parasitic males (visiting bourgeois males of high and low quality) are as follows:

$$F_{mi} = \frac{bC_m}{C_m + C_p E_i} \quad (18a)$$

$$F_{pi} = \frac{bC_p}{C_m + C_p E_i} \quad (18b)$$

The total fertilization success of a bourgeois male is then simply

$$W_{mi} = \frac{f_i n_p}{(1-s)m_i n_m} q_i F_{mi} \quad (19)$$

The total fertilization success of a parasitic male of quality q_s is

$$W_{pi}(f, m, p) = A q_s \sum_j g_{ij} f_j n_f F_{pi} \quad (20)$$

The total fitness of a female is

$$W_{fi}(f, m, p, s) = b \left(\frac{q_i C_m}{C_m + C_p E_i} + \frac{q_s C_p E_i}{C_m + C_p E_i} \right) \quad (21)$$

Standardizing the competitive ability of parasitic males (C_p) to 1 and the quality of good bourgeois males (q_1) to 1, we first solve for when poor bourgeois males will persist. Poor bourgeois males will persist in the population when parasitic males are present and

$$q_2 > \frac{q_1(g_{11} + A) - q_s(g_{11} - g_{12})}{g_{12} + A}. \quad (22)$$

Parasitic males will persist in the system, if poor bourgeois males are also present, when

$$C_m < \frac{q_s A n_m (q_2 - q_s) [f_2^* (g_{11} - g_{12}) + g_{12} + A]}{(g_{22} + A)(g_{12} + A) [f_2^* q_s (q_1 - q_2) + q_1 (q_2 - q_s)]}, \quad (23)$$

where f_2^* is the equilibrium proportion of females choosing poor bourgeois males (see below, Equation 25). Note that the quality of poor bourgeois males influences whether parasitic males can invade the system. When there is a large difference in quality among bourgeois males, parasitic males are more likely to persist.

If poor bourgeois males are not present, parasitic males can still persist in the system when

$$C_m < \frac{q_s A n_m}{q_1 (g_{11} + A)}. \quad (24)$$

If $q_s < q_1$, $q_s < q_2$ and Inequalities 22 and 23 are satisfied, there is a stable equilibrium, with some mixture of good and poor bourgeois males and parasitic males, and unstable equilibria at $m_2 = 0$ and $m_2 = 1$. If $q_s > q_1$ and $q_s > q_2$, the equilibrium mixture of good and poor bourgeois males is unstable, and there are stable equilibria at $m_2 = 0$ and $m_2 = 1$. Finally, if $q_s > q_2$ but $q_s < q_1$, Inequality 22 cannot be satisfied, and the only (stable) equilibrium is $m_2 = 0$. We verified the stability of these equilibria using replicator dynamic simulations (results not presented).

To simplify the presentation of results, we assume that $g_{11} = g_{22} = G$ subsequently. In other words, clustering is the same for good and poor males (although good and poor males are spatially separated). The equilibrium proportion of females choosing poor bourgeois males is

$$f_2^* = \frac{A(1 - q_2) + G(1 - q_s) - g_{12}(q_2 - q_s)}{(G - g_{12})(q_2 - q_s)}. \quad (25)$$

As in the general model, more females visit poor bourgeois males when the cost to females of parasitic males is high (i.e., the quality of parasitic males, q_s , is low) and when spatial clustering is high.

The equilibrium proportion of all males that pursue the parasitic tactic is

$$s^* = 1 - \frac{C_m(G + A)(g_{12} + A)[q_s f_2^* (1 - q_2) + q_2 - q_s]}{q_s n_m A (q_2 - q_s) [f_2^* (G - g_{12}) + (g_{12} + A)]}. \quad (26)$$

The proportion of parasitic males increases with increasing competitive ability of parasitic males (lower C_m), higher quality of these males, decreased spatial separation of poor and good males (lower g_{12}), and a larger search radius (Figure 5).

Of the s^* parasitic males, the equilibrium proportion that will visit poor bourgeois males is

$$p_2^* = \left(\{C_m(1 - q_2)(G + A)(g_{12} + A) + s^* A n_m [A(1 - q_2) + G(1 - q_s) - g_{12}(q_2 - q_s)]\} (G + A) \right) / (s^* A n_m (G - g_{12})(1 + q_2 - 2q_s)). \quad (27)$$

The equilibrium proportion of parasitic males visiting poor males is always less than that of females doing the same. As the competitive ability of both types of bourgeois males increases, fewer parasitic males visit low-quality bourgeois males. As the competitive ability of bourgeois males increases, the fre-

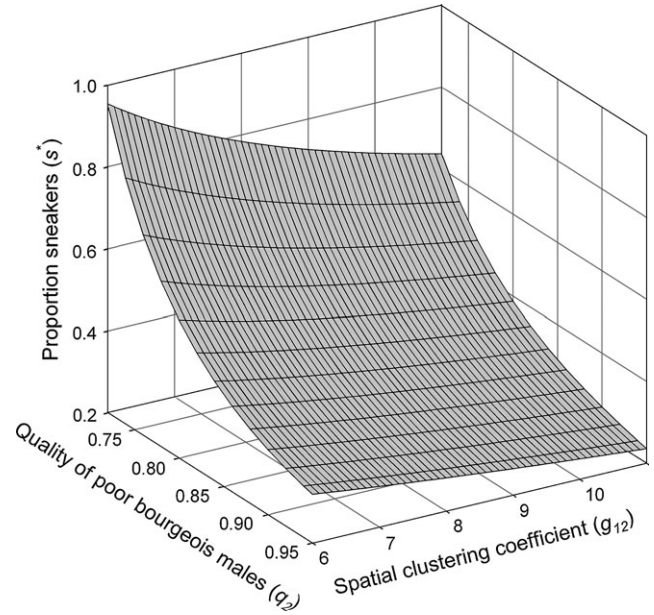


Figure 5

Evolutionarily stable proportion of males that pursue parasitic reproductive tactics plotted against the quality of poor bourgeois males (q_2) and the degree of spatial clustering of bourgeois male types (G). Values for q_2 range from those approaching the quality of parasitic males ($q_s = 0.6$) to that of good bourgeois males ($q_1 = 1$).

quency of parasitic males decreases, so that parasitic males experience less competition from other parasitic males. As the search radius and degree of spatial clustering increase, more parasitic males visit poor bourgeois males.

The equilibrium proportion of bourgeois males that are poor is

$$m_2^* = \frac{f_2^* q_2 (q_1 - q_s)}{f_2^* q_s (q_1 - q_2) + q_1 (q_2 - q_s)}. \quad (28)$$

In the previous model, the influence of the costliness of parasitic males to females on the frequency of poor males depended on the cost of parasitic males to bourgeois males. In contrast, in this model, the equilibrium proportion of poor males always increases as the costliness of parasitic males to females increases (q_s decreases). Interestingly, the relative competitive ability of bourgeois males (which is a measure of the cost of parasitic males to bourgeois males and is the same for both good and poor bourgeois males) has no influence on the equilibrium frequency of poor bourgeois males. Poor bourgeois males become more frequent as their quality, relative to that of good males, increases. However, this is only true when parasitic males are present. From Equation 26, the frequency of parasitic males in the population (s^*) decreases as the difference in quality between bourgeois males decreases. When differences between bourgeois males are small, there may be no parasitic males at equilibrium. Consequently, poor bourgeois males cannot persist. The only other factor that influences the frequency of poor males is the degree of spatial clustering on the lek. As before, when male types are highly clustered, poor males are more frequent, and in the absence of clustering, poor bourgeois males cannot persist.

Unlike in the previous model, bourgeois males could never do better by receiving fewer female visits. This is despite the cost of parasitic males weighing more heavily on bourgeois males than females. The cost to bourgeois males is purely in

terms of scramble competition in this model. However, if we modify the present model to include additional costs (by reducing the payoff by e^{-xL_i}), we find a result similar to that in the previous model: good males could do better if they received fewer females when x is very high (unpublished modeling results).

As in the previous model, the relative success of good bourgeois males is influenced by the relative costliness of parasitic males. The ratio of female visits to each good male to that to each poor male is as follows:

$$\rho = \frac{q_2(q_1 - q_s)}{q_1(q_2 - q_s)} \quad (29)$$

DISCUSSION

Our models demonstrate that the pressure of enemies, including predators of breeding males and females, egg predators, or parasitic males or females, can lead to a stable mixed distribution of female mate choices, so that some females choose to mate with low-quality males (or, alternatively, all females choose to mate with low-quality males sometimes) despite uniform assessment of genetic quality by females. We found that low-quality males can persist in such a system, sometimes at very high frequencies. However, some degree of spatial clustering is necessary for poor males to persist. Thus, our model provides one solution to the so-called lek paradox, in which uniform female preferences should lead to the rapid elimination of variation in male quality in the population (Borgia, 1979; Taylor and Williams, 1982). In our model, the intrinsic ranking of males in the absence of enemies is uniform, and uniform choice and the elimination of poor males will occur whenever Inequality 14 or 22 is not satisfied. However, when the cost of enemies to females is high, poor males persist. In addition, in a version of the model considering male reproductive parasites, the opportunity to choose between bourgeois males differing in quality also increased the probability that relatively low-quality parasitic males persisted in the population. Thus, female-enemy games can have a strong influence on the maintenance of low-quality males, be they bourgeois or parasitic males.

The importance of predation and harassment risk has been widely considered in the evolution of mating systems. However, previous considerations of the role of predation risk (or risk of harassment) in lekking systems have focused on its effects on female choosiness or choice for conspicuous signals, the duration of males' attendance on leks, and on the benefits males and females may gain from dilution of predation or harassment (Boyko et al., 2004; Carbone and Taborsky, 1995; Höglund and Alatalo, 1995; Saether et al., 1999). Predation risk has also been discussed with regard to the evolution of leks (reviewed in Höglund and Alatalo, 1995). All individuals potentially may gain from dilution or vigilance effects of staying in a group. This may often be the case for animals foraging in groups (Krause and Ruxton, 2002); however, empirical support for predation risk as a driving force in lek evolution is ambiguous (Bro-Jørgensen, 2002; Gibson et al., 2002; Höglund and Alatalo, 1995). Predation risk may also influence mate choice, by increasing search costs for females, and lead to reduced choosiness by females (Jennions and Petrie, 1997). Our models differ from the aforementioned explorations of the role of predation or other risks in lekking because females that mate with low-quality males do so because there is a direct, immediate cost in terms of increased harassment or predation to mating with higher quality males, not because of increased costs of choosiness.

We found that some sort of spatial structure within the lek or constraint on the ability to exploit more than one male is necessary for poor males to persist. That is, the area encompassed by the search radius of an enemy must contain either only one male or a higher density of good or of poor males than expected under a random distribution. In particular, clustering of good males results in a larger proportion of females and enemies choosing poor males. This is intuitive as clustering of good males results in high densities of enemies in such clusters. Keeping the distribution of good males constant, clustering of poor males reduces the proportion of females and enemies choosing poor males. This is likely because, when poor males are dispersed, the number of neighbors of poor males is overall low, so the pressure of enemies is reduced.

When the search radius of enemies is small, an increasing proportion of females and enemies choose poor males as search radius increases. However, as search radius increases, the effects of spatial heterogeneity decrease (because a large proportion of all males on the lek can be searched by any enemy), so that the proportion of females and enemies visiting poor males declines and may be zero when the search radius of enemies is very large.

Spatial structure appears to be common on leks (Fiske et al., 1998). For example, high-quality males often are concentrated in more central parts of the lek (Fiske et al., 1998; Kokko et al., 1998). This spatial clustering has been presumed to result from settlement decisions and monopolization by good and poor males (Höglund and Alatalo, 1995); our models suggest that lower quality males deciding where to settle may have to trade-off benefits of settling near good males (Beehler and Foster, 1988; Höglund and Robertson, 1990) with vulnerability to enemies that are also attracted to these "hotshots." Avoidance of high-quality males may ultimately yield higher fitness for low-quality males if females and enemies are free to move among males and enemies are very costly to males, as shown in Figure 3.

The relative costliness of enemies to males and females strongly influences reproductive skew and the abundance of good and poor males. Predation risk may differ between males and females if there is sexual size dimorphism. Costs of brood parasites will be higher for the sex that invests more in brood care. Egg predators may also be more costly to females if the remating rate of females is lower than that of males. Sneakers and other competitors for matings should be more costly to males than to females, who still gain parentage. When the costs of enemies on males are much higher than those on females (but enemies are still sufficiently costly to females so that either Inequality 14 or 22 is satisfied), then poor males should be particularly common, at least in our second model. This is because most females choose high-quality males, leading to high densities of enemies around these males. This suggests an interesting extension to the model. If the cost of enemies to males is particularly high, compared with that to females, it may benefit males, particularly high-quality ones, to occasionally not mate with or even chase away receptive females, if, by doing so, they can reduce the frequency of enemies nearby (Inequality 16, also suggested by Alonzo and Warner, 1999). Males commonly chase away receptive females (Alonzo and Warner, 1999; Gonçalves et al., 2003; Oliveira et al., 2002; Saether et al., 1999), even in systems where males are not expected to be choosy. There is evidence for male mate choice in a lekking cichlid (Werner and Lotem, 2003). The authors also hypothesize that courtship behavior may be costly due to, for example, increased predation risk. Hence, more female visits would be dangerous as outlined in our models. As our models are currently formulated, refusing females could not be evolutionarily stable because males that

did so would pay the cost of engaging in fewer fertilizations while reducing the number of enemies attacking all males of the same quality. However, if enemies have information on the quality and probability of female visitation for each male, these males probably could benefit from refusing female visits.

Differences in costs to bourgeois males and females should be particularly high when enemies are male reproductive parasites, although our third model suggests that the cost to bourgeois males is never high enough that they would gain from refusing female visits. Reproductive parasites should be more costly to bourgeois males because these lose fertilizations, while females still gain offspring. Indeed, parasitic males may not necessarily impose any quality cost on females or even be of higher quality (e.g., coho salmon: Gross, 1991, 1996; side-blotched lizard: Zamudio and Sinervo, 2000). Not surprisingly, however, we find that parasitic males must be costly if female-enemy games are to lead to the maintenance of low-quality bourgeois males. Whether costly parasitic males can themselves persist in the population is influenced by the difference in quality between high- and low-quality bourgeois males, with parasitic males being rarer and less likely to persist when there is little difference in quality between bourgeois male types (Figure 5). Parasitic males are also less likely to persist if their quality is low (Equation 26). Thus, we expect complex effects of the relative quality of good and poor bourgeois males and reproductive parasites. Counterintuitively, this means that, in populations with relatively little difference in quality among bourgeois males, females may be less likely to visit the poorer quality bourgeois males because parasitic males are not present. On the other hand, if there are large differences in quality, poorer quality bourgeois males also cannot persist, because females will not choose them, despite the lower risk of parasitism.

In the second model, the distribution of females and enemies is always the same. In the third model, however, the proportion of parasitic males that visit low-quality bourgeois males is lower than the proportion of females doing so. This is because parasitic males scramble for fertilization not only with other parasitic males but also with the bourgeois males. Indeed, the distribution of all male competitors (or, more accurately, competitive weights; Sutherland and Parker, 1985) does match that of females. Good and poor bourgeois males have the same competitive weight. Therefore, for the distribution of competitive weights to match that of females, the distribution of parasitic males must shift toward good bourgeois males. An increase in the search radius, the overall number of males, or the relative competitive abilities of parasitic versus bourgeois males results in the distribution of parasitic males approaching that of females (i.e., an increasing proportion of parasitic males visits areas with high densities of low-quality bourgeois males). This is because each bourgeois male makes up an increasingly small proportion of the total competitive weight. Interestingly, the distribution of females is not influenced by overall parasitic male density or competitive ability. Intuitively, one might expect that females would shift to visiting high-quality males if parasites were rare or poor competitors. However, because a larger proportion of the parasitic males visit high-quality bourgeois males, the relative net benefit of visiting good or poor males remains unchanged for females.

At equilibrium, there should always be a positive correlation between enemy density and female visitation. Such a distribution of harassing males, particularly on bird and ungulate leks, has been offered as evidence against the role of harassment in the mating decisions of females because females appear to prefer riskier males despite higher harassment (Bro-Jørgensen, 2002; Carbone and Taborsky, 1995; Saether et al., 1999). However, this interpretation ignores the decision of the harassing

males, which are also free to move. Several other recent studies have suggested a similar reason as that given here for such a correlation (Alonzo and Warner, 1999, 2000; Gonçalves et al., 2003; Reynolds and Côté, 1995). Here, we have extended this reasoning to produce general models of the female-enemy game and examine the influence of this game on the frequency and behavior of males.

Experimental evidence for the importance of interactions between mobile enemies and females on the decisions of both comes largely from colonially breeding fishes in which females also gain the direct benefit of paternal care, rather than those on true leks. However, mobile enemies are present on true leks and have been invoked as an influence on lek structure (e.g., egg predators on lekking cichlids: McKaye, 1983, 1984; Nshombo, 1991). Gonçalves et al. (2003) found that sneaker peacock blennies (*Salaria pavo*) preferred to approach larger (presumably higher quality) males in the absence of females but, when females were presented alongside the less preferred (usually smaller) males, spent more time with the latter. The density of enemies (sneakers) at a given nest influences the spawning decisions of females of a Mediterranean wrasse (*Symphodus ocellatus*). All else being equal, females appear to prefer nests without sneakers (Alonzo and Warner, 2000; van den Berghe et al., 1989) or to spawn with bourgeois nest owners when satellites and sneakers are present (Taborsky, 1994). Decreasing the density of sneakers resulted in a higher rate of female spawning but not visitation. However, there is a positive correlation between male mating success and sneaker density (Alonzo and Warner, 2000). Thus, there is evidence from this species that the observed positive correlation occurs in spite of female avoidance of sneakers, as predicted by both our model and theirs (Alonzo and Warner, 2000). Extending this logic, we suggest that relative enemy density could be a source of information regarding the relative intrinsic qualities of males on a lek.

These models show that a female-enemy game can alter patterns of female mate choice leading to reduced reproductive skew and the persistence of poor males. The proportion of poor males in the population even increases with increasing costliness of enemies to females. Thus, enemy avoidance is a plausible solution to the lek paradox in some cases. Furthermore, the models suggest that it can be favorable for good males to refuse receptive females under certain conditions. These insights are counterintuitive from the perspective of fixed enemy densities, rather than enemies being players in the game. There are other players that have not been considered in these models. In our models, bourgeois males do not make decisions, although their frequency changes as a result of the female-enemy game. We and others (Alonzo and Warner, 1999; Gonçalves et al., 2003; Oliveira et al., 2002) have suggested that one way they may influence the game is by rejecting some females. Another likely response of bourgeois males is to alter defense of the territory or provide information regarding territory safety (e.g., Warner and Dill, 2000). Incorporating the decisions of all players in the mate choice game would provide a more complete understanding of mating success and mate choice on leks.

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