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Female alternative reproductive behaviors: The effect of female group size on mate assessment and copying

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ABSTRACT

Extensive theoretical and empirical research has focused on male alternative reproductive tactics. In comparison, female alternative tactics have attracted little attention, and further theoretical and empirical research are needed. Using a game theoretical model, we examine female choice alternatives (1) by considering assessment errors in a novel and more realistic manner than done previously, and (2) for the first time, by highlighting the formation of groups of females as an important consequence of copying behavior. We consider two alternatives: direct assessment of male quality by females and female copying of the choice of other females. Assessment and copying are predicted to coexist under a wide variety of circumstances and copying is favored when females make assessment errors, when high-quality males are either common or very rare, and when female fitness declines with the number of other females choosing the same male. We also find that the frequency of copying at equilibrium is predicted to decrease when the presence of other females mating with the same male has a positive effect on female fitness (e.g. through increased male parental effort, decreased predation risk or cooperation among females). Female alternative choice tactics also influence the potential for sexual selection. In our model, when the frequency of copying females is low, the potential for sexual selection can be higher than in the absence of female copying. However, contrary to previous theory, we find that as copying females become more common than assessing females, the potential for sexual selection will be low as more females copy the mate choice of other copiers without assessment.

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1. Introduction

Extensive research has focused on explaining diversity within and between species. One of the most striking patterns of variation is the existence of discrete alternative phenotypes within a population. Alternative reproductive tactics represent a classic and well-studied example of such discrete variation (e.g. Gross, 1982, 1991; Gross and Charnov, 1980; Lank and Smith, 1987; Lank et al., 1995; Shuster, 1989; Shuster and Wade, 1991b; Shuster and Sassaman, 1997; Sinervo and Lively, 1996; Sinervo et al., 2000; Widemo, 1998; Widemo and Owens, 1995). Frequency-dependent selection and condition-dependent reproductive success are the most common mechanisms invoked to explain the coexistence of alternative reproductive behaviors (Gross, 1984, 1996; Lucas and Howard, 1995; Lucas et al., 1996; Rubenstein, 1980) and empirical evidence exists for both underlying mechanisms (reviewed in Shuster and Wade, 2003).

While most empirical and theoretical research on alternative reproductive tactics has focused on male alternatives, female alternative reproductive phenotypes certainly exist. For example, alternative female color morphs occur in a variety of damselfly species (Andres et al., 2002; Forbes, 1994; Van Gossum et al., 1999, 2001). In addition, genetically determined female throat-color and clutch size morphs have been observed in the side-blotched lizard, *Uta stansburiana* (Sinervo, 1999; Sinervo et al., 2000) and more subtle examples of female alternatives exist in the form of context-dependent female choice (Alonzo and Sinervo, 2001; Qvarnstrom, 2001; e.g. Sih and Krupa, 1992) and intra-specific brood parasitism (e.g. Ahlund and Andersson, 2001; Eadie and Lyon, 1998; Lyon, 1993).

Little empirical research and even less theoretical work have focused on understanding the factors that lead to discrete variation in female reproductive patterns. While general theory showing that frequency- and condition-dependent fitness can explain the stable coexistence of alternative phenotypes should also apply to females, it is less clear under which circumstances female traits will exhibit these patterns of fitness. Given the many differences between the sexes in reproductive traits and patterns of selection, theory devoted specifically to understanding the

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evolution of female alternatives is needed. The intent of this paper is to contribute to such a body of theory by examining the specific case of discrete variation in female choice tactics and ask when female alternatives are predicted to coexist.

Most models of intersexual selection assume the independence of females' mate choice (reviewed in Andersson, 1994; Jennions and Petrie, 1997). However, female choice may be non-independent for a variety of reasons (Galef and White, 2000; Godin et al., 2005; Westneat et al., 2000). One form of non-independent female mate choice that has received attention is copying, wherein a female copies the mating decisions of another female (Dugatkin, 1996a, b, 2005; Galef and White, 2000; Gibson and Hoglund, 1992; Losey et al., 1986; Pruett-Jones, 1992; Shuster and Wade, 1991a; Sirot, 2001; Stöhr, 1998; Wade and Pruett-Jones, 1990; Westneat et al., 2000). It has been suggested that copying may be favored when it reduces mate choice errors or various presumed costs of mate assessment (Dugatkin, 2005; Dugatkin and Godin, 1993; Gibson and Hoglund, 1992; Losey et al., 1986; Nordell and Valone, 1998; Pomiankowski, 1987; Pruett-Jones, 1992; Reynolds and Gross, 1990; Slagsvold et al., 1988; Stöhr, 1998).

However, non-independent female choice also has consequences. If we define a "group" as the assemblage of females that mate (simultaneously and/or sequentially) with a particular male, then it is apparent that copiers increase the size of the female groups they join, and this must be at the expense of other males with whom they might have mated. A recognized consequence of female mate choice copying is that variance in male mating success can be greatly increased, thereby influencing the opportunity for sexual selection and the evolution of preferred male traits (Agrawal, 2001; Kirkpatrick and Dugatkin, 1994; Laland, 1994; Wade and Pruett-Jones, 1990). Another consequence that has not been addressed in the literature is the effect that female group size might have on the fitness of females in those groups, and thus on the evolution of female mating tactics. The presence of other females can have a variety of fitness effects. Larger female group sizes can be costly if there are limitations on sperm availability, male parental care, critical habitat, or any divisible resource (that contributes to fitness) that becomes increasingly partitioned among more females in a group. Alternatively, larger group sizes could be beneficial when associated with increased male parental care, cooperative care among females, decreased individual risk of predation or mutualistic resource exploitation. In general, there are many potential costs and benefits to being part of a group. In this paper, we consider the net effect (positive or negative) of female group size on female fitness, and its consequences for the persistence of copying and assessment female choice alternatives. A priori, one might expect that a negative effect of female group size on female fitness might disfavor copying while a positive effect might favor copying depending of course on the relative costs and benefits of mate assessment as well. As we show below, these intuitions are not borne out.

We present a game-theoretic model of female alternative reproductive tactics, which, for the first time, highlights the formation of female groups as a biologically important consequence of copying. We are particularly interested in the conditions that permit the coexistence of mate assessment and copying behaviors, while accounting for the influence of female group size effects. We also consider the possibility that females make assessment errors, and examine how the frequency of high-quality males affects the costs and benefits of assessment and copying behaviors in females, because previous theory (Dugatkin, 2005) has shown these factors to influence alternative female choice tactics. We focus our analyses on two questions: (1) when are female alternative reproductive tactics predicted to coexist

and (2) how do female alternatives affect the distribution of mating success among males and hence the potential for sexual selection?

2. Model description

We imagine that females choose among males either through direct assessment and mate choice or by copying the mate choice of others. Active choice may incur a fitness cost (e.g. reduced fecundity due to energy or time lost), while copiers avoid that cost. For the purposes of our model, we follow Pruett-Jones (1992) and assume that this is a fixed cost that is paid by all assessors. While the latter assumption may not capture the dynamic nature of the costs and benefits associated with mate choice, it is the simplest possible assumption and helps to keep the model tractable. The main parameter of interest is the proportion of copying females in the population (c), and we focus on the conditions under which both female alternative reproductive tactics (assessing and copying) may coexist. Our model extends the model presented by Pruett-Jones (1992), which was chosen for its simplicity and tractability. We also incorporate some ideas from, and extend, the model presented by Dugatkin (2005), which itself is an extension of the Pruett-Jones (1992) model that considers errors.

Females are paired randomly, and the two females in a pair search together for males, both choosing the same male. Females mate once, with only one male. For "assessors" (females who evaluate male quality and make active choices accordingly), this assumption does not affect their probability of mating with a male since both females choose among males and pay assessment costs as if on their own. When a copier is paired with an assessor, the copier female always follows the choice of the assessor. The assessor female pays an assessment cost while the copier female does not. If the pair is composed of two copiers, these females choose a male at random and do not pay any assessment costs. The assumption of paired females is utilized, following the previous studies (Dugatkin, 2005 implicitly; Pruett-Jones, 1992 explicitly) that are here being extended, because it fosters the mathematical tractability of this dyadic game, without compromising the central biology: assessors choose independently, and copiers follow their lead. This assumption further implies that females only know what their paired female does, rather than having information about the mate choice other females in the population. Instead, assessor females choose independently and a copier female chooses based on the behavior of the one female she is copying. We also assume that copier females cannot preferentially copy the choice of assessor females. The importance of this will become evident in the discussion of female group size effects. More complex treatments of the decision-making process have been considered by Uehara et al. (2005) but their approach was applied only to a small number of females (three) choosing among two males. We wish to examine a population of females choosing among many males, and thus we have chosen simpler assumptions to retain tractability. Furthermore, these assumptions are consistent with the many biological systems in which females must directly observe the behavior of other females during copying rather than using other more indirect cues of female mating behavior.

We include three extensions of Pruett-Jones' (1992) model. (1) Following Dugatkin's (2005) use of two generic resources that differ in quality, males are here classified as either "high" or "low" quality, a proportion q being high quality. We assume that variation in male quality is maintained in the population ($0 < q < 1$). While male quality often varies continuously in real systems, the simplifying assumption of discrete quality classes

captures the essential biology (that males vary and this affects female fitness) while keeping the model tractable. The qualitative results reported here will apply to a wide variety of empirical systems as long as males vary in quality in a way that affects female fitness where q captures the relative availability of higher versus lower quality males. (2) We also consider that assessors sometimes make rejection or acceptance errors (with probabilities p_r and p_a , respectively). This treatment of assessment errors differs crucially from that of Dugatkin (2005). He assumed a single assessment error term representing the (predetermined) overall probability of ending up with the undesirable resource type (e.g. a low-quality male). Instead, we posit that individual assessment interactions are prone to errors. From this more basic, and more realistic, assumption we then derive the overall probability of ending up with each male quality type. As will be seen below, this leads to a higher (and dynamic) rate of acceptance errors, especially when high-quality males are rare, because individual interaction errors become compounded. (3) The number of females associated with each male (female group size) influences the fitness of each female. As described above, female copying affects the distribution of mating success among males, which can affect female fitness and the costs and benefits of mate choice copying. Due to these three extensions, we use some of the variables slightly differently than Pruett-Jones (1992). In our model, W is the fitness a female experiences by mating with a low-quality male, $W+f$ is the fitness of mating with a high-quality male, and k is the cost of assessment, paid by assessors only. We further introduce Z , the effect of female group size on the fitness of individual females. Female group size, and thus its effect, will differ between high (Z_H) and low-quality (Z_L) males as a result of female choice. All variables are defined in Table 1.

Assuming that rejection of a male always leads to a new search, then the probability, overall, that an assessor female ends up mating with a high-quality male is

$$P_H = q(1 - p_r) + ((qp_r + (1 - q)(1 - p_a))q(1 - pr)) + \dots,$$

which is equal to

$$P_H = q(1 - p_r) \left(\sum_{i=0}^{\infty} (qp_r + (1 - q)(1 - p_a))^i \right).$$

This simplifies to

$$P_H = \frac{(1 - p_r)q}{p_a + q - p_r q - p_a q}. \tag{1a}$$

Table 1
Variables used in the model of female alternative tactics

Variable	Definition
M, F	The numbers of males and pairs of females in the population
W	Fitness associated with mating with a low-quality male ($= 1$)
f	Additional fitness benefit of mating with a high-quality male
k	Fitness cost of assessing male quality
p_r	Probability of rejection error by assessor female
p_a	Probability of acceptance error by assessor female
q	Proportion of males that are high quality (low-quality $= 1 - q$)
c	Proportion of females in population that are copiers (c^* represents an equilibrium value of c)
Z_H	Average relative change in fitness due to presence of other females around a high-quality male (will be a function of c, q, p_a , and p_r)
Z_L	Average relative change in fitness due to presence of other females around a low-quality male (will be a function of c, q, p_a , and p_r)
$G(x)$	Function determining costs/benefits to a female due to the presence of other females mated with the same male
e	Shape parameter for $G(x)$ function

Similarly, the probability that an assessor mates with a low-quality male is

$$P_L = \frac{p_a(1 - q)}{p_a + q - p_r q - p_a q}. \tag{1b}$$

The average fitnesses of assessors, W_a and copiers, W_c will be:

$$W_a = P_H Z_H (W + f - k) + P_L Z_L (W - k), \tag{2a}$$

$$W_c = ((1 - c)P_H + cq)Z_H (W + f) + ((1 - c)P_L + c(1 - q))Z_L W. \tag{2b}$$

It is worth noting that random mating would only be favored over copying if there was no benefit associated with high-quality males (e.g. when $Z_H(W+f) < Z_L W$). Eqs. (2a) and (2b) also imply that copiers can generally invade a population of all assessors since, when rare, copiers have an equally high chance of mating with a high-quality male as assessor females yet they do not pay the cost of assessment. If a mixed ESS equilibrium of assessment and copying exists, it must occur at a point when the fitnesses of these two types of females are equal. Setting $W_a = W_c$ and solving for c (the frequency of copier females in the population) yields, with simplification:

$$c^* = \frac{k(p_a Z_L + q(Z_H - p_r Z_H - p_a Z_L))}{q(p_r + p_a - 1)(q - 1)(f + W)Z_H - WZ_L}. \tag{3}$$

While purposely general, this model is consistent with species where males are territorial and females search for males as well as with species where males search for females and females assess males prior to mating. Hence, our results should apply to a wide variety of systems in which females are capable of observing the mate choice of another female and male quality varies in a way that females can assess and that affects female fitness.

2.1. The simple case

Suppose that there are no errors in assessment by assessors ($p_r = p_a = 0$), and that there are no effects of female group size ($Z_H = Z_L = 1$). Then Eq. (3) simplifies to

$$c^* = \frac{k/f}{1 - q}. \tag{4}$$

This is the same result as found by Pruett-Jones (1992), except that we (like Dugatkin, 2005) also consider the frequency of high-quality males in the population, leading to the additional $(1 - q)$ term. The ratio of cost of assessment to the benefit of mating with high-quality males (k/f where $k < f$), scaled by the frequency of high-quality males (q where $q < 1$), determines the equilibrium frequencies of copiers and assessors in the population (Fig. 1).

When female group size does not affect female fitness, copying by females will be more frequent when high-quality males are common (q large) and the fitness benefit of mating with a high-quality male (f) is small compared to the cost of assessment and active mate choice (k). As shown in Fig. 1, copiers are favored increasingly as the proportion of high-quality males increases. Intuitively, when high-quality males are common, costly assessment of males is less beneficial. In fact, setting Eq. (4) equal to zero or one (the biological boundaries) and then attempting to solve for q shows that, for any non-zero level of costs and any finite level of benefits: (1) copiers (or more precisely random choosers when $c^* = 1$) will exclude assessors from the population when q equals or exceeds $1 - k/f$, and (2) copiers will always persist at some level in the population, since k/f cannot be less than or equal to zero. Explicitly considering the effect of the frequency of high-quality males increases the circumstances in which copying (or at the extreme random mating) is favored and

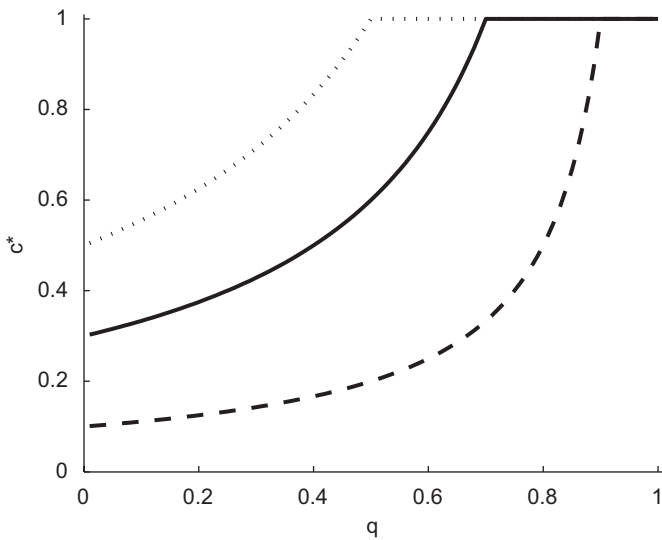


Fig. 1. The equilibrium proportion of copiers in the population (c^*) as a function of the proportion of high-quality males in the population (q) when assessors do not make errors. Shown for $k/f = 0.1$ (dashed line), 0.3 (solid line), and 0.5 (dotted line).

leads to the general prediction that the coexistence of mate assessment and female copying will be common.

2.2. Incorporating assessment errors

Suppose now that we let p_r and p_a take on values greater than zero (but for the moment still ignore female group size effects, i.e. $Z_H = Z_L = 1$). From Eq. (3), we have

$$c^* = \frac{k((1 - p_r - p_a)q + p_a)}{fq(p_r + p_a - 1)(q - 1)}. \quad (5)$$

Differentiating the right hand side of Eq. (5) with respect to p_a or p_r gives first partial derivatives that are positive for any biologically realistic parameter values. Thus, errors in assessment, either rejection or acceptance errors, decrease the frequency of assessors at equilibrium (since benefits are diminished but costs remain constant), and the resulting value of c^* is higher than without errors.

Interestingly, our consideration of assessment errors leads to a novel and qualitatively different relationship between the stable frequency of copiers (c^*) and the frequency of high-quality males (q , compare Figs. 1 and 2). As in the case with no errors, there is an upper threshold for q , beyond which only copiers (random choosers) exist in the population. However, assessors no longer have an advantage at very low values of q . When high-quality males are very rare, assessors still pay an assessment cost, but they rarely end up with a high-quality male since they often wind up making an acceptance error before they encounter a high-quality male. Thus, assessment errors increase the range of parameter space in which copiers are in the majority, and, surprisingly, random choice can be favored even when high-quality males are rare and when intuition would thus suggest that assessment would be very valuable.

Dugatkin (2005) also found that incorporating assessment error (thus reducing the benefits of assessment) increases the frequency of copying. However, he predicts a low frequency of copiers when the frequency of the preferred resource is low. Recall that Dugatkin (2005) uses a single fixed assessment error term representing the overall probability of selecting a resource type. In contrast, our biologically realistic manner of incorporating errors allows the overall probability of selecting a male type to be a

function of acceptance and rejection error rates and male frequency. This leads to the novel prediction of the U-shaped relationship between copying and male quality shown in Fig. 2. In fact, such a relationship could not result from the prior model because of the unrealistic implicit assumption that assessors (whether or not they correctly select it) are always successful in finding the good resource no matter how rare.

3. Effects of female group size

Suppose now that the number of females associated with a male ("group size") affects each female's expected fitness. Let $G(x)$ represent the change in fitness a focal female experiences due to the fact that a total of x pairs of females have chosen the same male as she has (x includes the pair to which a focal female belongs). For tractability, we choose a simple functional form, $G(x) = x^e$, where e is a scaling constant that can be negative (the presence of additional females is costly), zero (the presence of additional females has no effect on fitness), or positive (the presence of additional females is beneficial, Fig. 3).

To determine the average effect of female group size on female fitness (Z_H and Z_L), we need to derive the expected distribution of female group sizes in the population. Let $\pi(c)$ be the probability that a randomly selected pair of females mates with a high-quality male. A fraction c^2 of the pairs are made up of two copiers; the remaining proportion $(1 - c^2)$ of the pairs have one or two assessors. The former find a high-quality male only at random, that is, with probability q . The latter find a high-quality male with probability P_H . Thus, we have:

$$\pi(c) = P_H(1 - c^2) + qc^2. \quad (6)$$

If we have a total of F pairs of females in the population, then $\pi(c)F$ pairs of females mate with high-quality males, and $(1 - \pi(c))F$ pairs of females mate with low-quality males. Similarly, if we have M males in the population, then the numbers of high- and low-quality males are, respectively, qM and $(1 - q)M$. With these numbers defined, we can write $\Phi_i(x)$, the probability that a randomly selected male of quality i ($i = H$ or L) has a group of females of size x pairs, using the standard formula for binomial probabilities:

$$\Phi_H(x) = \frac{(\pi(c)F)!}{(x!(\pi(c)F - x)!)} \left(\frac{1}{qM}\right)^x \left(1 - \frac{1}{qM}\right)^{(\pi(c)F - x)}, \quad (7a)$$

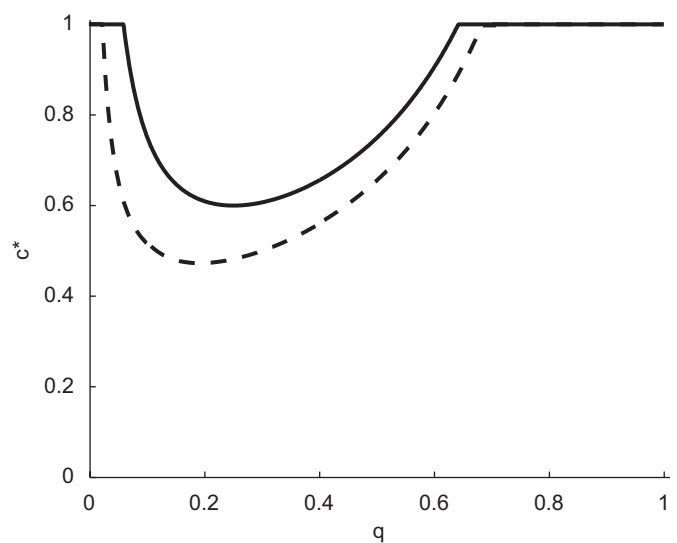


Fig. 2. The equilibrium proportion of copiers in the population (c^*) as a function of the proportion of high-quality males (q) when assessors make acceptance and rejection errors; dashed line: $p_a = p_r = 0.05$ and solid line: $p_a = p_r = 0.1$, $k/f = 0.3$.

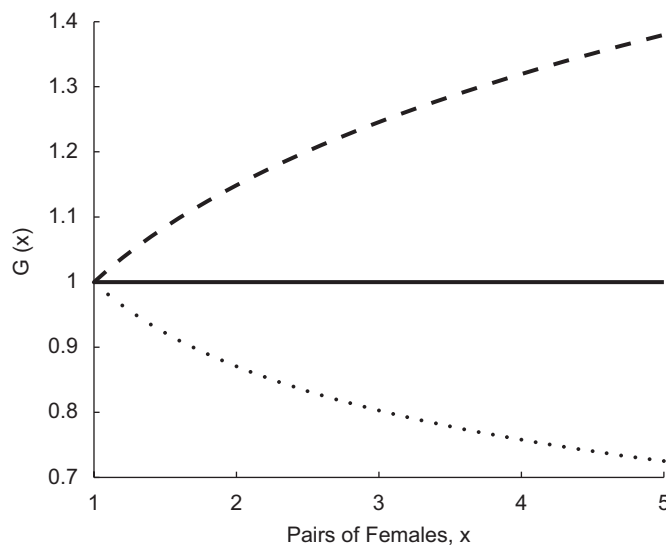


Fig. 3. The effect of female group size, x , on female fitness is described by the function $G(x) = x^e$. Representative values of the shape parameter, e , are shown; dashed line: $e = 0.2$, solid line: $e = 0$, and dotted line: $e = -0.2$.

$$\Phi_L(x) = \frac{((1 - \pi(c))F)!}{(x!((1 - \pi(c))F - x)!)} \left(\frac{1}{(1 - q)M}\right)^x \left(1 - \frac{1}{(1 - q)M}\right)^{((1 - \pi(c))F - x)} \quad (7b)$$

With Eqs. (6)–(7), we can thus write formulae for Z_H and Z_L , which are simply the means (expected values) of group size effects:

$$Z_H = \sum_{x=1}^{\pi(c)F} G(x)\Phi_H(x), \quad (8a)$$

$$Z_L = \sum_{x=1}^{(1 - \pi(c))F} G(x)\Phi_L(x). \quad (8b)$$

Although some males will likely experience a female group size of zero, no female can experience such a group size, thus the sums in Eqs. (8a) and (8b) begin at one, not at zero. Note that because of this fact, in practice, the probabilities $\Phi_i(x)$ must be rescaled such that the sum of such probabilities over the limits given in Eqs. (8a) and (8b) would be unity (as is required of any discrete probability distribution function).

Even though the functions we have chosen are simple, c^* , the equilibrium value of c , cannot be found analytically in this case. The reason is that the sums in Eqs. (8a) and (8b) only have defined upper limits when c is known, but c cannot be known without evaluating these sums. To derive predictions about this scenario, we thus adopted a numeric analysis of the model, which we present graphically. All analyses were performed in Mathematica and files can be provided on request. In the figures that follow, we present plots of the fitnesses of assessors and copiers as a function of c (using Eqs. (2a) and (2b) and (6)–(8) above). If copier fitness declines with c , and if the fitness functions have a point of intersection, then that point is a stable mixed ESS.

Fig. 4 shows how c^* varies with q and with the effects of females on each other, as encapsulated by the exponent e . Fig. 5 shows the distribution of female group sizes among males of high and low quality for the corresponding cases. W_c , the fitness of copiers, is always negatively frequency dependent. However, the fitness of assessors can be either negatively or positively frequency dependent, which is determined by whether e is negative or positive. When e is negative (Fig. 4A–B), females have

negative effects on each other's fitness. Assessor fitness is thus negatively frequency dependent, since the assessors tend to aggregate around the good males more than the copiers do (this is most pronounced for the cases when high-quality males are rare, Fig. 4A). For the same reason, assessor fitness is positively frequency dependent when e is positive (Fig. 4C–D). Paradoxically, assessor fitness is highest when e is positive and when high-quality males are rare (Fig. 4D), because the condition of few high-quality males results in the largest aggregations of females (Fig. 5D). Another interesting result is that, if females impact each other negatively, assessors do not dominate even if high-quality males are rare (Fig. 5A). This is because assessors hurt each other by aggregating in larger female groups around the few high-quality males that are in the population. This contrasts greatly with the simple cases (Figs. 1 and 2) in which assessors do very well relative to copiers when high-quality males are rare (e.g. compare to dashed lines in Figs. 1 and 2 at $q = 0.2$). It is also worth noting that the difference between the dashed and solid lines in Fig. 5 represents the expected distribution of mating success among high and low-quality males. When high-quality males are common, copying replaces assessment and high-quality males do not have a mating advantage. The potential for sexual selection on males is predicted to be highest when high-quality males are rare and the net effect of female group size on female fitness is positive (note in Fig. 5C that the curve for high-quality males is skewed farther right, while that of low-quality males is skewed farther left, resulting in the greatest discrepancy between average "harem" sizes).

4. Discussion

When we consider the effects of female group size and realistic errors on female alternative mate choice tactics, we find that female choice alternatives are predicted to be very common. Our model predicts the equilibrium frequency of copiers may often exceed that of assessing females (Figs. 1, 2, and 4). We also predict the presence of copiers even in situations where the assessment of males may be especially easy (e.g. leks: in terms of energetics, Gibson and Bachman, 1992; and predation risks, Höglund and

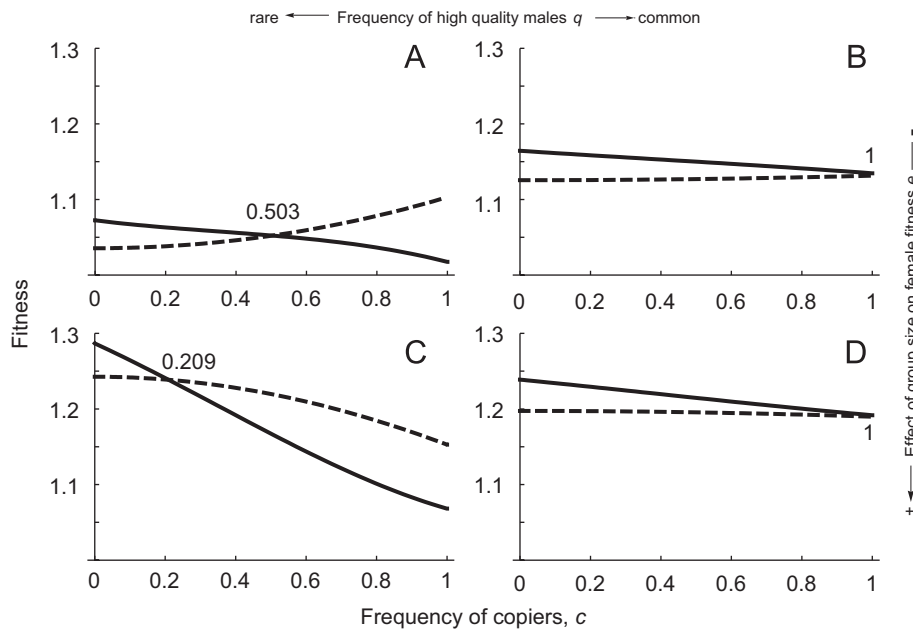


Fig. 4. Fitnesses of assessors (dashed lines, W_a) and copiers (solid lines, W_c) as a function of the proportion of copiers in the population. Fitnesses are shown for different values of q , the proportion of high-quality males (from left to right across the columns, $q = 0.2, 0.8$), and for different values of e , the exponent shaping the effects of female group size on female fitness (from top to bottom across the rows, $e = -0.3, 0.3$). The number shown within each plot is the equilibrium value c^* (where the lines cross, if an intersection exists). For all plots, $W = 1, f = 0.2, k = 0.04, p_r = p_a = 0.05, M = 100$ males, $F = 50$ pairs of females.

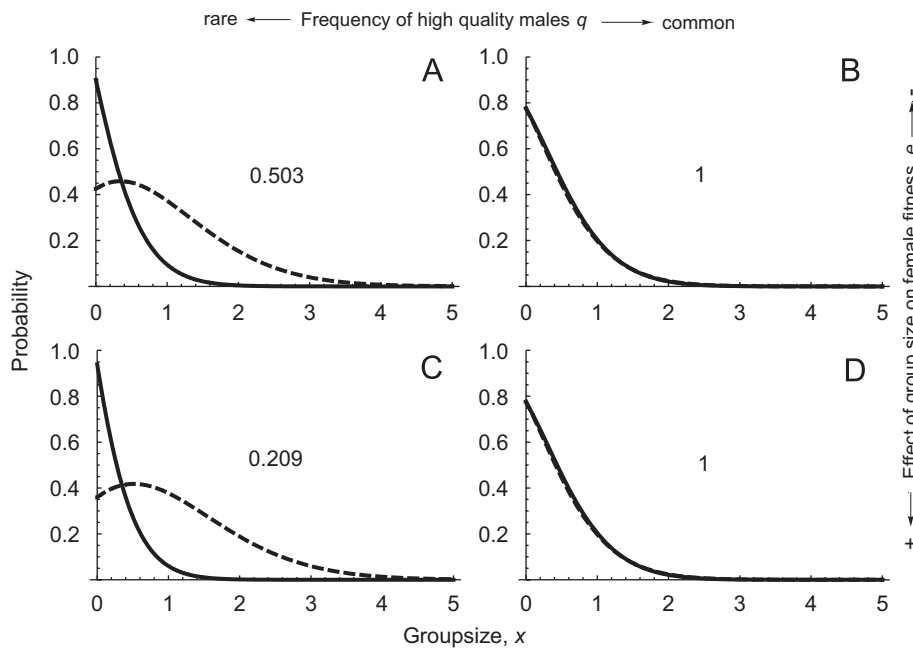


Fig. 5. Probability density functions for numbers of pairs of females per male at equilibrium, shown separately for high-quality (dashed lines) and low-quality (solid lines) males. Equilibrium values c^* are given in each plot. All parameter values are the same as the corresponding panels in Fig. 4. Note that for identical values of c^* and q , the female group size distributions are identical.

Alatalo, 1995) and intuition suggests that choosing might be favored. In fact, it is precisely when assessment is favored that we expect copying to coexist with assessment. We predict a homogenous population (of randomly mating females) only when assessment itself does not benefit females, and we never predict assessment without some copying. Our model implies that the propensity of mate choice copying in leks (reviewed in Jennions and Petrie, 1997) may be due less to reduced assessment costs

(which should actually favor assessment not copying) than to the ease of copying at a lekking aggregation.

While we predict that female copying may be common, it is operationally difficult to demonstrate, with most examples coming from relatively unnatural studies (but see Alonzo, 2008; Goulet and Goulet, 2006). Copying cannot be identified by simply examining female mating patterns with respect to male traits or other types of inferred “preference functions.” Instead we need

more information on how females move in space and select among males in the wild. We also must pay much greater attention to interactions among females and the effect of other females on female fitness. When we find patterns of mate choice that are hard to understand based on standard sexual selection theory (e.g. Bradbury et al., 1985), we should consider female copying and the effect of female group size on female fitness as potential explanations for these counter-intuitive patterns. In general, however, our model demonstrates that female copying can persist in a wide variety of circumstances and more generally that female choice alternatives may be more common than previously recognized. Further, empirical and theoretical research examining discrete variation in female choice behavior is certainly warranted.

Because little is known about the actual mechanisms of copying in wild populations, we have represented copying (and mate choice in general) in our model in a very simple manner. Females always select mates in pairs, and the two members of a pair always make the same selection. These assumptions certainly do not capture the diversity and complexity of mating systems observed in the wild. More complicated and potentially more realistic mechanisms can certainly be constructed (e.g. Uehara et al., 2005). However, the representation we used captures the essential aspects of copying and assessment: assessors tend to find high-quality males, and copiers benefit from the presence of assessors. As a result, our model is consistent with a wide variety of species where females move in small groups and select males that vary in quality. For example, in species where male parental care increases with mating success (i.e. $e > 0$) as in many fishes with paternal care, female mate choice copying is predicted to be common if low-quality males are rare. Altering our representation of copying and mate choice in an attempt to make it applicable to a particular system is unlikely to alter the predictions of our model qualitatively as long as the basic biology of the species is consistent with the general assumptions. While adding complexity to the copying process is possible, thus far it has made the full model (with errors and female group size effects) intractable. In general, our model predicts that female mate choice copying may be more common than previously predicted and occur in wide variety of mating systems. However, future theory should examine the effect of our assumptions regarding female copying and male quality in further detail.

The operational sex ratio (OSR) has been shown to influence alternative mating tactics of males (Lucas and Howard, 1995), and Jennions and Petrie (1997) suggest it may also influence alternative sampling tactics and mate-choice decisions of females. Our model, which permits independent variation of the number of males and females (parameters M and F) and thus OSR, lends limited support to these ideas. We find no effect of OSR in our first two scenarios. In our full model, female group sizes and OSR have pronounced effects on fitness and on the ESS copier frequency only when high-quality males are rare. The intuitive reason is that we only observe large aggregations of females—and hence, we only have many females experiencing the effects of female group size and/or OSR—when there are relatively few high-quality males for the assessors (and their copiers) to find. When the density of preferred mates is low, there can be increased distance, energetic and time costs to sampling (Real, 1990), and increased risk of failure to mate (Moller, 1992). Such increased assessment costs should lead to a reduction in choosiness according to Jennions and Petrie (1997) and a greater proportion of copiers in our model. However, a model in which OSR, assessment cost, and mating success are not independent parameters may be more appropriate for testing these ideas.

If copying reduces costs, we might expect females that are more sensitive to assessment costs to be more likely to copy.

Inexperienced females or those in poor condition should be more likely to copy (Pruett-Jones, 1992), and age-related changes in propensity to copy have been reported in several groups (Jennions and Petrie, 1997). Further theory on context- and condition-dependent alternative female choice tactics is needed. Because female copying directly affects female group size, it can increase the variance in male reproductive success. This effect of copying can be further amplified if copiers can serve as models for further copying. Modeling such an “information cascade” (Gibson and Bachman, 1992) would be a useful extension of the present model. Allowing copiers to copy each other would also draw attention to the consequences of acting on poor, or even deceptive, mate choice information.

We have shown that female group size effects can greatly influence the evolution of female alternative mating strategies. This raises the possibility that females might base their mating decisions on female group size itself. Recall that our definition of group size (the number of females that mate with a male) is broad enough to include both situations of simultaneous aggregations (e.g. joint nesting, harems, females at male leks) and multiple mating separated in time and/or space. Our model is well-suited to analysis of the latter situation, where multiple mating has fitness consequences but is not directly, or profitably, assessable. One promising extension of this model would be to incorporate female group assessment tactics.

Another important prediction of our model is that including the very realistic possibility of errors in female assessment leads to qualitatively different predictions. When female assessment is assumed to be perfect, copiers can coexist with assessor females but are only predicted to become common when high-quality males are common, and thus assessment has little advantage over random mating (Fig. 1). However, in the presence of assessment errors, copying is favored at both high and low frequencies of the preferred, high-quality males. This arises because of the compounding error that occurs as assessor females search for rare high-quality males. Assessment errors favor copying females that avoid the cost of assessment, which is highest when preferred males are rare.

It is also worth highlighting the important effect of the frequency of high-quality males (q) on the costs and benefits of assessment versus copying. This has been considered briefly in previous theory of female copying (Dugatkin, 2005) and clearly has a large effect on the outcome of our model (Figs. 1, 2, and 4). Furthermore, if male quality is heritable, then, in the presence of assessor females, high-quality males should increase in frequency between generations. However, our model predicts an increase in q will lead to an increase in the frequency of copying females (Fig. 4), leading to a decrease in the mating advantage of high-quality males (Fig. 5). A coevolutionary model of female choice alternatives and a male trait is an obvious extension of the theory we present here. In general, however, female copying should increase in frequency when high-quality males become more common and thus the mating advantage of these males may decrease over time (Fig. 5). When low in frequency, copying can increase the potential for sexual selection. However, in contrast to previous predictions (Wade and Pruett-Jones 1990), our model also illustrates that copying can decrease the potential for sexual selection on male traits when copying becomes more common (Fig. 5).

There has long been interest in the phenomenon of female choice, and the evolution of both female preferences and choosiness have clear theoretical importance (Jennions and Petrie, 1997). However, while we know something about the empirical benefits of female choice (e.g. Hill, 1991; Norris, 1993; Petrie, 1994), we still know nearly nothing about its costs. Our model, which hinges on the cost/benefit ratio to females of assessing

males, highlights the need for such empirical data. More generally, this model points to the importance of considering variability among females and their mating patterns as well as interactions among females. Female choice has been shown to be capable of both suppressing and generating male alternative reproductive behaviors in circumstances where the opposite would have been predicted by male intra-sexual mechanisms alone (Alonzo and Warner, 2000). Discrete variation in female choice will also affect inter- and intra-sexual interactions. The neglect of such complexity represents a clear gap in our theoretical understanding of sexual selection. Female alternative reproductive behaviors (of which copying is but one example) need to be integrated into our general view of alternative phenotypes. Our model also illustrates that female choice alternatives will affect the distribution of mating success among males. However, copying will not universally increase the potential for sexual selection as previously suggested. In general, our theory demonstrates that we must consider more carefully how variation among females might alter our understanding of female preference functions, the distribution of mating success among males and hence the potential for and dynamics of sexual selection.

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References

- Agrawal, A.F., 2001. The evolutionary consequences of mate copying on male traits. *Behav. Ecol. Sociobiol.* 51, 33–40.
- Ahlund, M., Andersson, M., 2001. Brood parasitism: female ducks can double their reproduction. *Nature* 414, 600–601.
- Alonzo, S.H., 2008. Female mate choice copying affects sexual selection in wild populations of the ocellated wrasse. *Anim. Behav.* 75, 1715–1723.
- Alonzo, S.H., Sinervo, B., 2001. Mate choice games, context-dependent good genes, and genetic cycles in the side-blotched lizard, *Uta stansburiana*. *Behav. Ecol. Sociobiol.* 49, 176–186.
- Alonzo, S.H., Warner, R.R., 2000. Female choice, conflict between the sexes and the evolution of male alternative reproductive behaviours. *Evol. Ecol. Res.* 2, 149–170.
- Andersson, M., 1994. *Sexual Selection*. Princeton University Press, Princeton, NJ.
- Andres, J.A., Sanchez-Guillen, R.A., Rivera, A.C., 2002. Evolution of female colour polymorphism in damselflies: testing the hypotheses. *Anim. Behav.* 63, 677–685.
- Bradbury, J.W., Vehrencamp, S.L., Gibson, R., 1985. Leks and the unanimity of female choice. In: Greenwood, P.J., et al. (Eds.), *Evolution: Essays in Honour of John Maynard Smith*. Cambridge University Press, Cambridge, pp. 301–314.
- Dugatkin, L.A., 1996a. Copying and mate choice. In: Heyes, C.M., Galef, B.G.J. (Eds.), *Social Learning in Animals: The Roots of Culture*. Academic Press, New York, pp. 85–105.
- Dugatkin, L.A., 1996b. Interface between culturally based preferences and genetic preferences: female mate choice in *Poecilia reticulata*. *Proc. Natl. Acad. Sci. USA* 93, 2770–2773.
- Dugatkin, L.A., 2005. Mistakes and the evolution of copying. *Ethol. Ecol. Evol.* 17, 327–333.
- Dugatkin, L.A., Godin, J.G.J., 1993. Female mate copying in the guppy (*Poecilia reticulata*)—age-dependent effects. *Behav. Ecol.* 4, 289–292.
- Eadie, J.M.A., Lyon, B.E., 1998. Cooperation, conflict, and creching behavior in Goldeneye Ducks. *Am. Nat.* 151, 397–408.
- Forbes, M., 1994. Tests of hypotheses for female-limited polymorphism in the Damselfly, *Enallagma boreale* Selys. *Anim. Behav.* 47, 724–726.
- Galef, B.G., White, D.J., 2000. Evidence of social effects on mate choice in vertebrates. *Behav. Process.* 51, 167–175.
- Gibson, R.M., Bachman, G.C., 1992. The costs of female choice in a lekking bird. *Behav. Ecol.* 3, 300–309.
- Gibson, R.M., Hoglund, J., 1992. Copying and sexual selection. *Trends Ecol. Evol.* 7, 229–232.
- Godin, J.G.J., Herdman, E.J.E., Dugatkin, L.A., 2005. Social influences on female mate choice in the guppy, *Poecilia reticulata*: generalized and repeatable trait-copying behaviour. *Anim. Behav.* 69, 999–1005.
- Goulet, D., Goulet, T.L., 2006. Nonindependent mating in a coral reef damselfish: evidence of mate choice copying in the wild. *Behav. Ecol.* 17, 998.
- Gross, M.R., 1982. Sneakers, satellites and parentals: polymorphic mating strategies in North American sunfishes. *Zeitschrift fuer Tierpsychologie* 60, 1–26.
- Gross, M.R., 1984. Sunfish, salmon, and the evolution of alternative reproductive strategies and tactics in fishes. In: Potts, G.W., Wootton, R.J. (Eds.), *Fish Reproduction: Strategies and Tactics*. Academic Press, London, pp. 55–75.
- Gross, M.R., 1991. Evolution of alternative reproductive strategies: frequency-dependent sexual selection in male Bluegill Sunfish. *Philos. Trans.: Biol. Sci.* 332, 59–66.
- Gross, M.R., 1996. Alternative reproductive strategies and tactics: diversity within the sexes. *Trends Ecol. Evol.* 11, 92–98.
- Gross, M.R., Charnov, E.L., 1980. Alternative male life histories in Bluegill Sunfish. *Proc. Natl. Acad. Sci.* 77, 6937–6940.
- Hill, G.E., 1991. Plumage coloration is a sexually selected indicator of male quality. *Nature* 350, 337–339.
- Höglund, J., Alatalo, R.V., 1995. *Leks*. Princeton University Press, Princeton.
- Jennions, M.D., Petrie, M., 1997. Variation in mate choice and mating preferences: a review of causes and consequences. *Biol. Rev.* 72, 283–327.
- Kirkpatrick, M., Dugatkin, L.A., 1994. Sexual selection and the evolutionary effects of copying mate choice. *Behav. Ecol. Sociobiol.* 34, 443–449.
- Laland, K.N., 1994. Sexual selection with a culturally transmitted mating preference. *Theor. Popul. Biol.* 45, 1–15.
- Lank, D.B., Smith, C.M., 1987. Conditional lekking in ruff (*Philomachus pugnax*). *Behav. Ecol. Sociobiol.* 20, 137–145.
- Lank, D.B., Smith, C.M., Hanotte, O., Burke, T., Cooke, F., 1995. Genetic polymorphism for alternative mating behaviour in lekking male ruff *Philomachus pugnax*. *Nature* 378, 59–62.
- Losey, G.S., Stanton, F.G., Telecky, T.M., Tyler, W.A., 1986. Copying others, an evolutionarily stable strategy for mate choice—a model. *Am. Nat.* 128, 653–664.
- Lucas, J.R., Howard, R.D., 1995. On alternative reproductive tactics in anurans: dynamic games with density and frequency dependence. *Am. Nat.* 146, 365–397.
- Lucas, J.R., Howard, R.D., Palmer, J.G., 1996. Callers and satellites: chorus behaviour in anurans as a stochastic dynamic game. *Anim. Behav.* 51, 501–518.
- Lyon, B.E., 1993. Conspecific brood parasitism as a flexible female reproductive tactic in American coots. *Anim. Behav.* 46, 911–928.
- Moller, A.P., 1992. Frequency of female copulations with multiple males and sexual selection. *Am. Nat.* 139, 1089–1101.
- Nordell, S.E., Valone, T.J., 1998. Mate choice copying as public information. *Ecol. Lett.* 1, 74–76.
- Norris, K., 1993. Heritable variation in a plumage indicator of viability in male great tits *Parus major*. *Nature* 362, 537–539.
- Petrie, M., 1994. Improved growth and survival of offspring of peacocks with more elaborate trains. *Nature* 371, 598–599.
- Pomiankowski, A., 1987. Sexual selection: the handicap principle does work—sometimes. *Proc. R. Soc. Lond. Ser. B, Biol. Sci.* 231, 123–145.
- Pruett-Jones, S., 1992. Independent versus nonindependent mate choice—do females copy each other. *Am. Nat.* 140, 1000–1009.
- Qvarnstrom, A., 2001. Context-dependent genetic benefits from mate choice. *Trends Ecol. Evol.* 16, 5–7.
- Real, L., 1990. Search theory and mate choice. I. Models of single-sex discrimination. *Am. Nat.* 136, 376–404.
- Reynolds, J.D., Gross, M.R., 1990. Costs and benefits of female mate choice: is there a lek paradox? *Am. Nat.* 136, 230–243.
- Rubenstein, D.I., 1980. On the evolution of alternative mating strategies. In: Staddon, J.E.R. (Ed.), *Limits to Action: The Allocation of Individual Behavior*. Academic Press, New York, pp. 65–100.
- Shuster, S.M., 1989. Male alternative reproductive strategies in marine isopod crustacean (*Paracerceis sculpta*): the use of genetic markers to measure differences in fertilization success among alpha beta and gamma males. *Evolution* 43, 1683–1698.
- Shuster, S.M., Sassaman, C., 1997. Genetic interaction between male mating strategy and sex ratio in a marine isopod. *Nature* 388, 373.
- Shuster, S.M., Wade, M.J., 1991a. Female copying and sexual selection in a marine isopod Crustacean, *Paracerceis sculpta*. *Anim. Behav.* 41, 1071–1078.
- Shuster, S.M., Wade, M.J., 1991b. Equal mating success among male reproductive strategies in a marine isopod. *Nature* 350, 608–610.
- Shuster, S.M., Wade, M.J., 2003. *Mating Systems and Strategies*. Princeton University Press, Princeton, NJ.
- Sih, A., Krupa, J.J., 1992. Predation risk, food deprivation and non-random mating by size in the stream water strider, *Aquarius remigis*. *Behav. Ecol. Sociobiol.* 31, 51–56.
- Sinervo, B., 1999. Mechanistic analysis of natural selection and a refinement of Lack's and Williams's Principles. *Am. Nat.* 154, 26–42.
- Sinervo, B., Lively, C.M., 1996. The rock-paper-scissors game and the evolution of alternative male strategies. *Nature* 380, 240–243.
- Sinervo, B., Svensson, E., Comendant, T., 2000. Density cycles and an offspring quantity and quality game driven by natural selection. *Nature* 406, 985–988.

- Siro, E., 2001. Mate-choice copying by females: the advantages of a prudent strategy. *J. Evol. Biol.* 14, 418–423.
- Slagsvold, T., Lifjeld, J.T., Stenmark, G., Breiehagen, T., 1988. On the cost of searching for a mate in female pied flycatchers *Ficedula hypoleuca*. *Anim. Behav.* 36, 433–442.
- Stöhr, S., 1998. Evolution of mate-choice copying: a dynamic model. *Anim. Behav.* 55, 893–903.
- Uehara, T., Yokomizo, H., Iwasa, Y., 2005. Mate-choice copying as Bayesian decision-making. *Am. Nat.* 165, 403–410.
- Van Gossum, H., Stoks, R., Matthysen, E., Valck, F., De Bruyn, L., 1999. Male choice for female colour morphs in *Ischnura elegans* (Odonata, Coenagrionidae): testing the hypotheses. *Anim. Behav.* 57, 1229–1232.
- Van Gossum, H., Stoks, R., De Bruyn, L., 2001. Frequency-dependent male mate harassment and intra-specific variation in its avoidance by females of the damselfly *Ischnura elegans*. *Behav. Ecol. Sociobiol.* 51, 69–75.
- Wade, M.J., Pruett-Jones, S.G., 1990. Female copying increases the variance in male mating success. *Proc. Natl. Acad. Sci. USA* 87, 5749–5753.
- Westneat, D.F., Walters, A., McCarthy, T.M., Hatch, M.I., Hein, W.K., 2000. Alternative mechanisms of nonindependent mate choice. *Anim. Behav.* 59, 467–476.
- Widemo, F., 1998. Alternative reproductive strategies in the ruff, *Philomachus pugnax*: a mixed ESS? *Anim. Behav.* 56, 329–336.
- Widemo, F., Owens, I.P.F., 1995. Lek size, male mating skew and the evolution of lekking. *Nature* 373, 148–151.