Behav Ecol Sociobiol (1998) 44: 91–98

ORIGINAL ARTICLE

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Measuring mate choice using correlation: the effect of female sampling behaviour

Received: 18 May 1998 / Accepted after revision: 18 July 1998

Abstract For intersexual selection to occur, it is necessary that females choose between males. It is now well appreciated that constraints exist, which preclude females sampling all the available males in a population. These constraints are likely to have caused the evolution of sampling rules (such as the "best-of-*n*" rule) by which females sample males. Here we investigate the impact of female subsampling of the male population, not on the evolution of sampling behaviour, but on the population-level correlation between a male trait and currencies such as reproductive success. This study is important as it illustrates when population-level correlations can be safely used to infer the presence and strength of sexual selection in the field. We find that the correlation between a male trait and a mate choice variable rises steeply as the number of males sampled by each female increases, flattening above seven to ten males sampled. This shape is found to be remarkably robust, and little affected by, for example, the mate choice variable used, by noise in assessment, by sampling behaviour depending on female quality, or by population size. The only variable found to have a large impact is male clumping according to their "quality". If females are sampling about four males, the maximum correlation that can be found at the population level is in the range 0.4–0.6, perhaps as little as 0.1 if males are strongly clumped. A recent review of the literature suggests that four is the average number of males that females sample. Thus, the absence of a strong correlation cannot by itself be used to infer that sexual selection is weak, as it may be due to females sampling few males.

Key words Mate choice · Sexual selection · Correlation · Mate sampling · Decision rules

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Introduction

The elaborate secondary sexual traits of many species have interested behavioural scientists for many years. Darwin originally suggested that these structures may be used by females to discriminate between males (Darwin 1871). In the last 15–20 years, the study of sexual selection and mate choice has been one of the major endeavours of behavioural ecology and it has been successful in identifying the roles played by ornaments of various species (Andersson 1994).

There has been interest recently in the behavioural mechanism by which females choose males (see review by Gibson and Langen 1996). Intuitively, a female's choosiness should be affected by three different variables: the cost of searching for mates, the benefits to be gained from continued searching (which will be related to the variance in male quality) and a female's own quality (because low-quality individuals have less to gain from being choosy) (Gibson and Langen 1996; Real 1990, 1991). The evolution of optimal decision making by females has been investigated by a number of people, following the seminal paper by Janetos (1980), who suggested that females use a "best-of-*n*-males" strategy to choose. The particular strategy used by females is still open to considerable debate (Gibson and Langen 1996; Luttbeg 1996; Real 1990, 1991).

This investigation is not concerned with optimal mate choice tactics by females: we assume that females do choose (using a "best-of-*n*" strategy). We are instead interested in investigating the impact of varying the *n*, in the best-of-*n* strategy, on the perceived strength of sexual selection revealed by correlating a male's ornament size (or other trait, such as body size or age) and some mate choice variable (such as reproductive success, latency to mating, female size/quality). In the field, experiments where females are given a choice of mates and observed to choose between them are often impossible to conduct. Instead, the presence or absence of mate choice is often inferred through correlation. This method is an intuitively appealing, and common, way of investigating mate choice. Significant correlation between the trait and the variable is deemed to indicate the presence of mate choice, and insignificant correlation, its absence.

However, this type of analysis implicitly assumes that any female could be associated with any male. In terms of mate choice, this means that any female could have chosen any male included in the analysis or, in other words, that females have perfect information about the males in the study population and are free to mate with any one of them. Having perfect information is extremely unlikely, as females are constrained in time and/or space and models of optimal mate choice predict that females should sample fewer males than the population total (Janetos 1980). However, to date, the impact of female subsampling of the male population on the population-level correlations that are commonly sought by behavioural ecologists has not been investigated. This is what this study aimed to do and, in particular, to ask the questions "do low correlations between male traits and mating variables really indicate that mate choice is not occurring?" and "under what circumstances are assumptions of perfect knowledge reasonable?"

This investigation uses simple simulation models. The basic simulation model consisted of females choosing between males. Each male possesses some attribute, such as age, size or tail length, which allows a rank to be assigned. Likewise, each female also has a rankable attribute – which could be any factor such as the arrival time at the breeding ground, size, number of eggs laid, dominance status or general "quality". In the model, each female samples males at random and selects the "best" male (using a "best-of-*n*" strategy: Janetos 1980). In some models ("non-pairing systems"), the female is assumed merely to mate with the chosen male, in which case each male can mate as many times as females choose him, and so the mate choice variable is male mating success. In other models ("pairing systems"), the female is assumed to pair with the best male, in which case his mating success is constrained, and the mate choice variable is female quality. We assume that there is assortative mating between males and females. Assortative mating is common (Crespi 1989; Ridley 1983): for example, there is assortative mating for tail length and parasite load in barn swallows (Møller 1994), and for body condition in American kestrels (Bortollotti and Iko 1992), and assortative mating for size is common in many invertebrates, such as insects (e.g. Brown 1990), spiders (e.g. Rubenstein 1987), crustacea (e.g. Ridley and Thompson 1979). Such assortative mating could arise though one of three mechanisms. (1) If males choose to pair with the best female from amongst those selecting them (e.g. American kestrel: Bortollotti and Iko 1992). (2) If higher-ranking females choose males before lower-ranking females (as might occur if they return to the nesting areas first; e.g. barn swallows: Møller 1994). (3) If there is competition between females such that higher-ranking females can displace lower-ranking females (e.g. some primates: Keddy-Hector 1992). At the end of each simulation, the population-level rank correlation was calculated, i.e. the correlation between male rank and the mate choice variable (mating success, or female quality) across the whole population. Given that females are choosing between males, we were interested in investigating the impacts of varying the females' sampling behaviour on these population-level correlations. The main variable altered in each model is the number of males that each female assesses. If each female meets a single male, there will be no mate choice, as she pairs at random. If each female meets every single male in the population, females will have perfect knowledge on which to base their decision with whom to pair or mate. In this case, we would expect to see high correlations between male trait and mating success or, in pairing systems, if there is assortative mating, we expect to see high correlations between male and female ranks.

Methods

In each simulation, the number of males that females could sample (m) was varied from 1 to the population size (p, usually 100). For each value of m, all females in the population ($F_i ... F_p$) were allowed to choose a mate, and then the population-level Spearman rank correlation coefficient was calculated. This was replicated 99 times. Error bars (where shown) are ±1 SD about the mean correlation, where $n = 100$.

The basic routine for mate choice was programmed as follows. Each female was selected at random. A random sample of males was then selected. In non-pairing systems, the highest-ranking male was selected from this sample, and a mating was "scored". In pairing systems, the best male was again selected, but sometimes the best male was already paired. In these cases, the second female may displace the first female depending on two factors: the size of a quantity, ε, which is a random normal deviate, and their relative ranks. If a female is displaced, she may resample the males. This mechanism results in assortative mating. Three interpretations of this process are possible, and all are logically consistent. First, females could compete for males and better females could displace lower-ranking resident females, in which case ε can be thought of as a "resident's advantage" for the first female. Second, the male chooses the best female willing to pair with him, in which case ε can be thought of as a noise term in the mutual assessment of rank. Third, higher-ranking females may choose first, in which case ε is a term that introduces noise into the order such that it is not strictly a rank order.

In addition to the impact on the correlation of the number of males that females sample, the impact of a number of other factors was investigated. These were:

(1) Relationship between a female's quality and the number of males sampled. In some simulations, the number of males that a female sampled was independent of rank (in which case all females sample m males). In others, the number of males actually sampled at a given m depended on the quality (i.e. rank) of the female. The default relationship was a linear relationship between the proportional rank ($\text{Rank}_p = \text{Rank/population size}$) and number of males sampled: $m = \text{Rank}_p$).

(2) Clumping of males. A reasonable female sampling strategy is for females to choose an initial place to settle, and sample m males in that locality. If males are scattered at random in the habitat, she will be sampling the males at random. In many situations in the field, good nesting (or display) sites are clumped in space and, as males may compete for the best territories, this results in male clumping. In such situations, it is possible that the quality of males that a female may sample

might depend on the clump that she first encounters. We investigate this by allowing a female to choose the first male at random, thereafter restricting the subsequent males sampled. Subsequent males were chosen at random from a normal distribution with a mean of the rank of the first male, and a standard deviation of 20, 10 or 5 – representing increasing male clumping. Sampling of males was programmed as a two-stage process. Each female was allowed to "visit" a number of males, chosen at random. Many of these males would be visited more than once, due to the random nature of the choice, but each was counted once as a "sample". The amount of effort a female put into sampling the males within a clump – the number of visits made – was either 10 or 100. If *m* is large, then females may need to visit more than one "clump" to sample sufficiently as many as *m* males. Hence after visiting 10 or 100 times, the female jumped to another clump.

(3) Varying ε. ε is a term that introduces noise, or a resident's advantage (depending on the interpretation of the program). It either takes the value of 0, or it is a random normal deviate. If the latter, the mean value is either 0 (if it is a noise variable), +5, or proportional to the female's Rank_p (if it is a resident's advantage).

(4) The number of breeding attempts. In many biological systems, successful breeding may follow a failed attempt. We therefore investigated the impact of varying the number of breeding attempts that low-ranking females displaced by higher ranks could make. The number of attempts varied from only 1 attempt, to many (100), or a number which depended on the female's rank ($\text{Rank}_p \times 10$).

(5) Population size. The population size was varied: 25, 100, 250.

(6) Polygyny. In systems where females pair with males, males may not always be monogamous, so we investigated the impact of allowing polygyny (males being paired with up to two or three females).

Unless otherwise stated, the default conditions of these variables are: population size = 100; ε = female's $\text{Rank}_p \times 10$; number of breeding attempts proportional to $\text{Rank}_p \times 10$; relationship between females' rank and number of males sampled proportional to Rank_p; clumping – none; polygyny – none.

The programs were written in Fortran77, using standard routines from the NAG library (Numerical Algorithms Group, Oxford, UK).

Results

Under most conditions (see Figs. 1, 4, 5), similar results emerge from the models: as the number of males that females sample increases, the population-level correlation increases rapidly from 0 (when females mate with the first male they encounter). The relationship is a convex curve, increasing rapidly and then asymptotically approaching (usually) 1 as the proportion of males in the population sampled itself approaches 1.

The effect of mate choice variable

The mate choice variable used (mating success where there is no paternal investment beyond mating, or female "quality" in pairing systems) made little difference to the overall shape of the relationship between the strength of the correlation and the number of males sampled (Fig. 1). In non-pairing systems, the relationship is slightly less steep than in pairing systems. If the number of males that a female samples depends on her quality, it has little impact on the correlation between male and female ranks, but does have an impact on the correlation between male rank and mating success. This is because in promiscuous mating systems, if all females sample all the males and make the same choice, then the best individual will get *all* the matings (so the number of males observed to mate will decrease towards 1). However, if the number of males sampled by each female depends on her rank, then the lowest-ranking females will be mating more or less randomly, which ensures that the correlations do not asymptote to 1.

The effect of male clumping

If the best territories, or display sites, are clumped together and males compete for territories, then males will be clumped according to some measure of competitive ability. If females sample males by locating a patch and searching for males *within* the patch then they will obviously not be sampling the male population at random. In such clumped populations, the relationship between the number of males a female samples and the population-level correlation is much less steep than where males are sampled randomly (Figs. 2, 3). Figure 2, using mating success as the mate choice variable, shows that whether or not the number of males a female samples depends on her rank makes a large difference (correlations asymptoting to 1 or ca 0.6), as does the "effort" with which she samples within a clump. As she puts more effort into finding more males within a single clump, she then samples fewer clumps to sample the same total number of males, and so does not get to sample as wide a range of the male population. Hence the more effort going into searching single clumps, the lower the correlations. Figure 3, using female quality as the mate choice variable, indicates that the "size" of the clumps is important for the same reasons.

Pairing systems: varying ε and the effects on the correlations

If, in pairing systems, the first female to select a male pairs with him for that season, and females are selected in a random order to sample the males, then the correlations remain zero, independent of the number of males sampled, i.e. there is no assortative pairing (Fig. 4a). If, however, females chose males in an order that depends on the female's rank, or higher-ranking females can displace lower-ranking females, or males choose the best female from those selecting them, then the relationship between the correlation and the number of males sampled rises steeply and asymptotes towards 1 (Fig. 4a,b). In Fig. 4a, ε is interpreted as noise (in mutual assessment of potential mate's ranks, or in the order that females come into breeding condition). ε is a random deviate whose mean is zero, but with a standard deviation in-

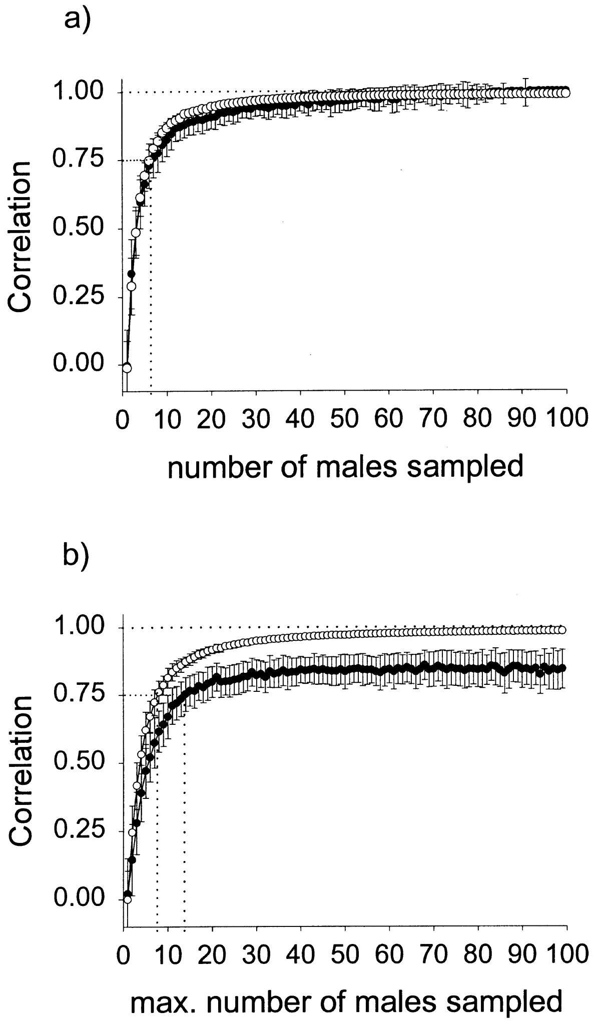

Fig. 1 The relationship between the number of males sampled and the correlations between male rank and a mate choice variable: mating success (*filled circles*) or female rank (*open circles*). *Dotted lines* are guidelines to allow better comparison between curves. Other variables were set at "defaults" described in Methods (*error bars* are ± 1 SD). **a** If the number of males that a female samples is independent of her rank (and constant across all females) then correlating a male trait with either his mating success (in non-pairing systems) or female quality (in pairing systems) produces very similar results, though in correlating the former the results are somewhat more variable. **b** If, however, the number of males sampled increases with female rank, then larger differences result. Note that here, for a given value on the x-axis, the number of males sampled will vary between females from 1 (lowest ranks) to that value (highest ranks)

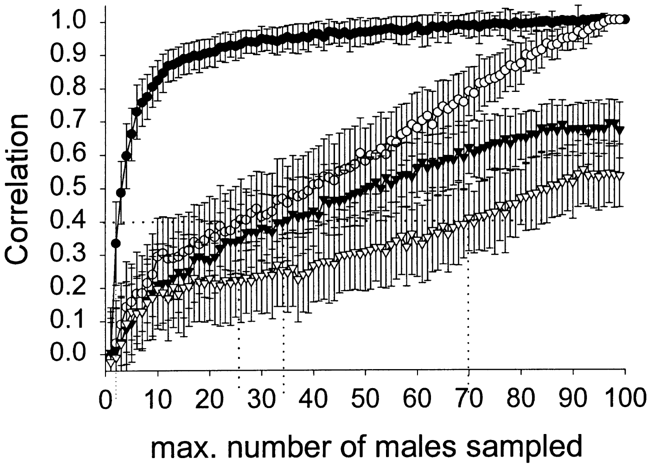

Fig. 2 The relationship between the number of males sampled by females and the correlation between male trait and mating success is markedly affected by whether males are randomly spread and by how females sample the "clumps". Females choose their first male at random and thereafter inspect males within that clump [males are ±(SD) 10 ranks on either side of the first male selected]. After either 10 or 100 attempts to sample different males (many attempts will "pick" the same males), the female leaves the clump and samples another. *Filled circles* no clumping; *open circles* number of males sampled independent of female rank, female moves to another clump after sampling 10 times; *filled triangles* number of males sampled depends on female rank, female moves to another clump after sampling 10 times; *open triangles* number of males sampled depends on female rank, female moves to another clump after sampling 100 times. *Error bars* are ± 1 SD

creasing from zero to 30. In this case, the addition of noise decreases the asymptote of the curve, but has little affect on the first part, where the curve rises steeply. This change, although weak, is significant (for sampling 1–10 males, $F_{2,2994} = 38.72$, $P < 0.0001$). In Fig. 4b, ε is interpreted as a resident's advantage (where females compete for males) and is either independent of rank (ε = 5 ± 1.7) for all females, or depends on rank in a linear or non-linear way. The type of relationship between ε and rank makes a marginal difference to the middle of the curve relating correlation to male sample size, but not the asymptote. Again, this difference, although weak, is significant (for sampling 1–10 males, $F_{3,2993} = 13.84$, $P < 0.0001$).

Pairing systems: the effects of other factors

There is little effect of population size on the relationship between sample size and correlation – the relationships of smaller populations rise slightly less steeply than those of larger populations (Fig. 5a). There is a negligible effect of the number of breeding attempts a female gets (following displacement by higher-ranking females; Fig. 5b). There is a moderately marked effect of male polygyny: the more mates that a male is allowed, the more shallow the relationship between sample size and correlation (Fig. 5c).

Discussion

The results obtained from a correlational analysis of a male trait (such as tail length) with a mate choice variable (such as reproductive success) across a population are markedly affected by the manner in which females sample the males. Most of the time, if females are sampling a reasonably large number of males, high values of the correlation coefficient reveal the underlying

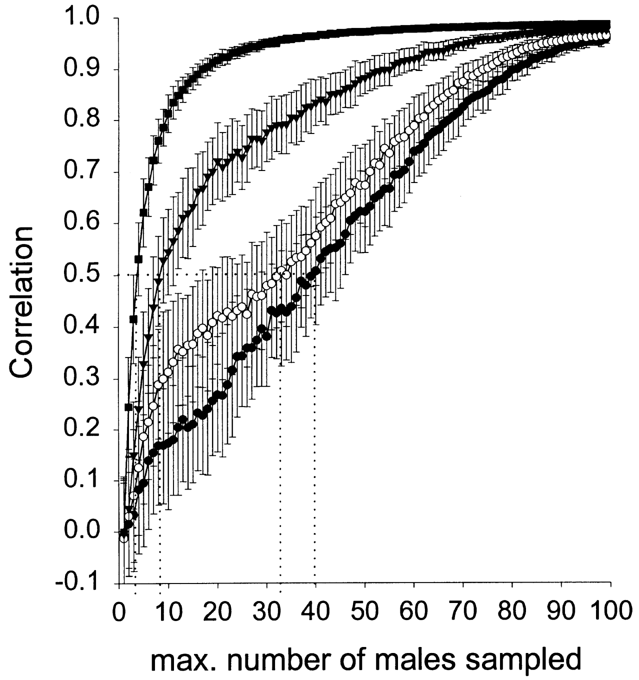

Fig. 3 The relationship between the number of males sampled by females and the correlation between male trait and female quality is markedly affected by the size of male clumps. Larger clumps (containing more males) produce higher correlations for a given number of males sampled. The SD of sampling distribution from which the females samples males "around" the first male chosen describes clump size. After attempting to sample 100 different males within a clump, the females select a new clump to sample additional males. *Filled squares* no clumping; *filled circles* "small clumps": SD = ± 5 males; *open circles* "medium clumps": SD = ±10 males; *filled triangles* "large clumps": SD = ±20 males. *Error bars* are ±1 SD

mate choice. However, if females are sampling a smaller number of males (under ten, certainly under five), a small correlation coefficient cannot be used as evidence either for weak mate choice or for a lack of mate choice.

In the field, obtaining information on the number of males that are sampled by females is obviously often impossible. Gibson and Langen (1996) review the published literature on the number of males that are sampled (their Table 1). Eleven studies are listed: eight birds, one toad, one crab and one beetle. In addition, we can add to these data from wrens, *Troglodytes troglodytes*, where females sampled 2.36 ± 1.39 ($n = 23$) males in 1995 and 2.21 ± 0.97 ($n = 14$) males in 1996 (M.R. Evans, unpublished data). The mean of the 13 studies gives an average of 3.8 ± 1.6 (SD) males visited, with a minimum of 1.7 (in the natterjack toad: Arak 1988) and a maximum of 7.5 (in the fiddler crab: Backwell and Passmore 1996). By pooling the data, we can calculate the standard deviation for all the data, which is 3.10 males per female ($n = 470$ females). What is noticeable is how similar these estimates are, given the range of species from which they are obtained. It seems that the majority of females, both within, and between, species, sample well under ten males when they choose a mate.

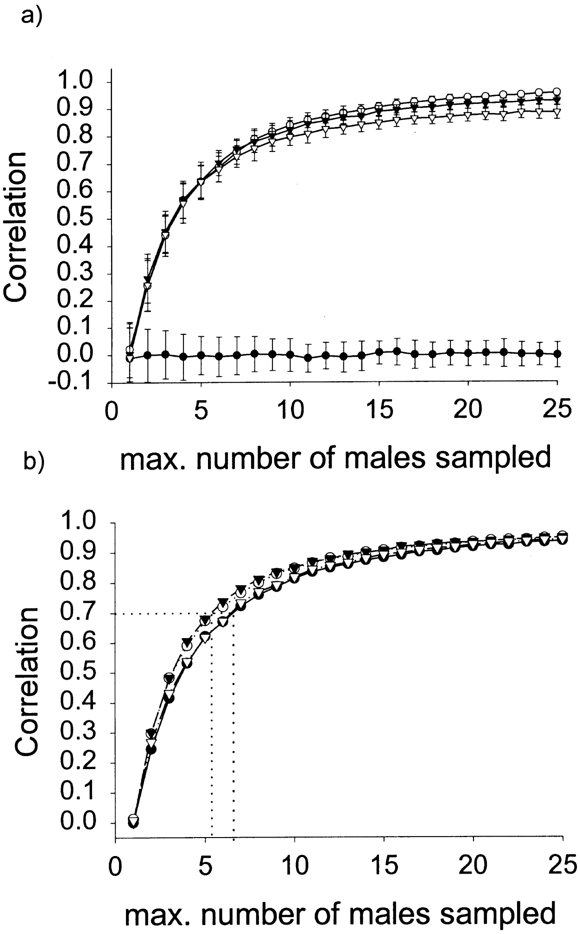

Fig. 4. The effects of varying ε on the correlation between the number of males sampled by females and the correlation between male trait and female quality. **a** ε as a noise variable in situations where males choose between all females selecting them, or where higher-ranking females come into breeding condition first (i.e. no "resident's advantage"). If females do not compete, or if the order of choosing is not related to rank, or if males do not choose between females, there is no assortative pairing (*filled circles*). Otherwise, the more noise in assessing rank, the lower the asymptotic correlation (*open circles* no noise; *filled triangles* SD = 10; *open triangles* SD = 30) (*error bars* ±1 SD). **b** Varying the relationship between rank and ε has little impact on the correlations: *open triangles* resident's advantage averages 5 ranks; *filled circles* average resident's advantage proportional to Rank_p; *open circles* average resident's advantage proportional to $\text{Rank}_p^{1/2}$; *open triangles* average resident's advantage proportional to $\text{Rank}_p^{1/3}$. Error bars not shown to aid clarity, though they are similar in magnitude to those shown in **a**

From the data given here, the maximum correlation one could expect if females are choosing amongst this number of males is about 0.5–0.6 (Figs, 1, 4, 5). However, if males are clumped according to their rank, the correlation could be as low as 0.1, *even though the females are selecting the males.*

The general conclusion espoused here – that female sampling behaviour is important – is not new. Many recent studies have shown that this is the case (Gibson and Langen 1996; Janetos 1980; Johnstone 1997; Real 1990). Previous studies have investigated the evolution of female sampling behaviour, by relating the number of

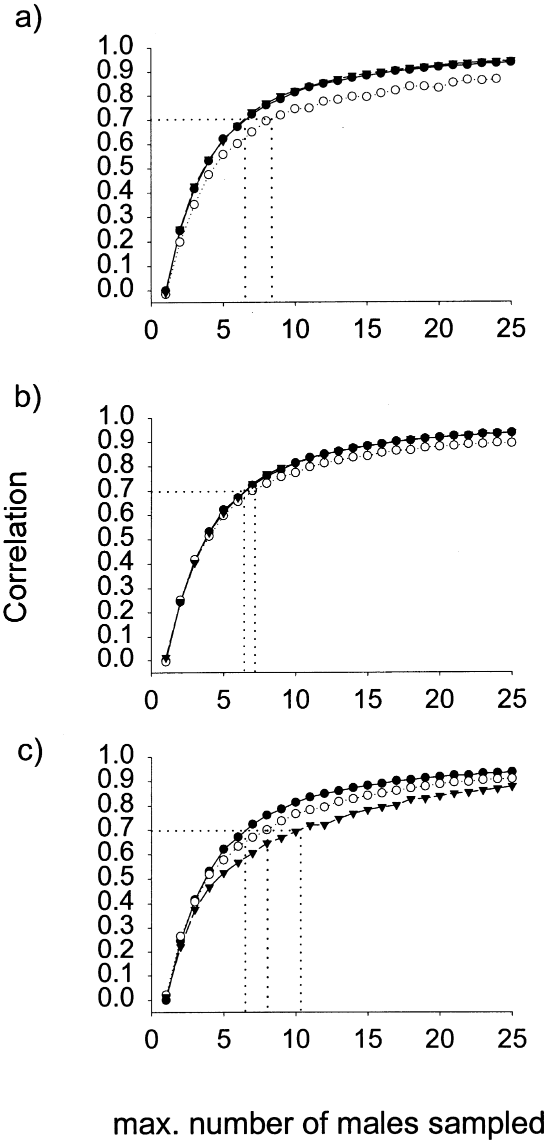

Fig. 5 a The effect of varying population size on the relationship between the number of males sampled by females and the correlation between male trait and female quality: smaller populations lead to lower correlations (*open circles* population size = 25; *filled circles* population size = 100; *filled triangles* population size = 250). **b** The effect of varying the number of breeding attempts that displaced females are allowed on the relationship between the number of males sampled by females and the correlation between male trait and female quality [*open circles* females allowed only one attempt; *filled triangles* females allowed 100 attempts; *filled circles* number of breeding attempts depends on rank ($\text{Rank}_p \times 10$)]. **c** The effect of polygyny on the relationship between the number of males sampled by females and the correlation between male trait and female quality: the more mates a male has, the smaller the correlations (*filled circles* monogamy; *open circles* polygyny: males allowed up to two mates; *filled triangles* polygyny: males allowed up to three mates)

males sampled to fitness. In this study, we assume that females have a best-of-*n* strategy, and we investigate the impact this has on the population-level correlation between a trait and a mate choice variable. We illustrate that a common method of identifying mate choice in the field, population-level correlations between traits and mate choice variables, can lead to misleading conclusions about the strength of mate choice unless care is taken to incorporate information about the number of males that a female assesses.

That population-level correlational analyses are a common method of analysis is shown by an overview of three journals – *Animal Behaviour*, *Behavioral Ecology* and *Behavioural Ecology and Sociobiology* – over the years 1991–1995. This review produced 42 studies of mate choice in the field where correlation was used. Thirty-seven of these studies assumed that there were no restrictions on the males available to mate with females. Thirteen of these combined data from several populations, 14 papers combined data from more than one breeding season. Four studies placed realistic constraints on the pool of available males, but only spatial *or* temporal constraints. Only one study placed both spatial and temporal restrictions on the males available to females. This study radio-tracked females involved in mate selection and compared the male chosen with the males known to be visited by the female under consideration (Bensch and Hasselquist 1992). Therefore, it appears that only a single study in our sample of 42 may have assessed the scope for mate choice correctly.

Including in an analysis all the data, irrespective of the number of males that females sample, is likely to reduce, sometimes markedly, the maximum correlation coefficient that can be found. This may lead to the conclusion that mate choice is weaker than it actually may be. For example, Palokangas et al. (1992), studying kestrels, found that in some years there is a strong correlation between male trait (tail length) and mate choice variable (latency to mating) but not in others (related to the density of voles, and so to the density of birds). They conclude that "females can be choosy. . . only if kestrel density is high" (p. 663). Our results would indicate that perhaps females *do* continue to choose males at low densitites, but because they are sampling fewer males, this choice does not show up in population-level correlations. On the other hand, if strong correlation is found it would indicate that mate choice is very strong, and/or that females are sampling many males.

The most important factor affecting the correlation between male trait and the mate choice variable was found to be whether or not males clump in space (or time) according to quality/trait size. This may occur generally: habitat is not uniform, better habitats supporting better territories may encourage better males to hold territories close together. Variability in the weather may promote clumping of males in time for females that are temporally constrained; for example, a good spell of weather early in the season may allow the best males to come into breeding condition early. If clumping does occur, it can have a marked effect on the population-level correlation. Even if large numbers of males are sampled, the correlation could be very low (Fig. 2). The fewer clumps that a female can access, the lower the potential correlation. Likewise, the smaller the clumps, the lower the correlation (Fig. 3).

If a female puts a "high" effort into sampling within a given clump (perhaps she is constrained to search a single clump), she will sample some of the males multiple times in an attempt to sample all the males. Perhaps this is an alternative (essentially non-adaptive) explanation for the often observed multiple visits females make to the same male (recent adaptive suggestions, based on females reducing their uncertainty of assessment of male quality, have been put forward by Luttbeg 1996).

Many studies of mate choice indicate assortative mating between males and females, though how this may arise is often unclear (Brown 1993; Crespi 1989; Ridley 1983). In our models of pairing systems, we assume that there is some mechanism to produce this. This mechanism could be that higher-quality females displace lower-quality females after competition for particular males, and this is how the model was explicitly constructed. However, identical results arise if, instead of females competing, the male assesses the female and chooses the best [so there is mutual mate choice, as documented in, for example, crested auklets (Jones and Hunter 1993), American kestrels (Bortolotti and Iko 1992), the beetle *Lytta magister* (Brown 1990) and the bug *Acrosternum hilare* (Capone 1995)]. In this case, what we have termed ε is equivalent to introducing a noise term into the mutual assessment of quality. Equally, identical results arise if the higher-quality females get to choose first, which may be the most general mechanism. For example, in barn swallows, females that arrive at nesting sites tend to have longer tails and choose males according to tail length, therefore producing a correlation between male and female tail lengths (Møller 1993). Again, ε should be interpreted as a noise term, such as would arise if females do not get to choose first in strict rank order.

We found that the exact size of ε, whether it was proportional to rank and whether it had an associated noise term (as would occur if females made errors in assessing competitor's ranks) made little difference to the overall correlations. Thus, however ε is interpreted (as a resident's advantage in female competition, as a noise term in male choice, or as a noise term in the order that females choose), our results seem robust. There *is* a significant impact of these different factors, but it is weak. For example, with ε set at zero, but varying the standard deviation, and so changing the amount of noise in the assessment of a potential mate's quality – or in the order that females choose – there is a small, but significant, impact reducing the correlations. Noise reducing the correlations is a result also found by Johnstone (1997) and implicitly by Luttbeg (1996).

The impact of population size could be important, especially if an animal is living in a very patchy environment where the maximum pool of potential mates is small. In such cases, the correlation can be quite low, which is essentially due to the overall smaller sample size from which the correlation is calculated. Likewise, in pairing-systems, polygyny tends to lower the correlations, because there are more opportunities for females to pair with the male of their choice, and so lower-ranking females are more likely to be able to pair with a higher-ranking male, thus lowering the correlation.

For those working in the field, we offer the following advice: it is likely that correlations will underestimate the strength of sexual selection if there is no information on female sampling strategies – females may well be exhibiting preferences, and choosing between males, but the statistical power of correlational analysis is insufficient to demonstrate this. If data are available on the males that each female samples, it is possible to incorporate this in an analysis (M.R. Evans, unpublished data). Each male a female visits can be scored as successful (if the female chooses him) or unsuccessful. A General(ised) Linear Model can then be conducted using the male trait as the dependent variable, and his score (0 or 1) as the independent variable, blocking by the female who chose. In this way, one is asking the statistical question: is the size of the male trait different between the group of chosen males and rejected males, when controlling for the female choosing?

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Communicated by J. Höglund