Animal Conservation (1998) **1**, 173–177 © 1998 The Zoological Society of London Printed in the United Kingdom

Female preferences and effective population size

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(Received 17 November 1997; accepted 23 February 1998)

Abstract

As effective population size (N_e) decreases, genetic factors may become relatively important to a population's or species' persistence. Conservation biologists should be aware of anything that can potentially cause a sudden reduction in N_e. I used simple models to illustrate how certain types of female mating preferences combined with certain types of male traits may lead to a sudden and substantial decrease in N_e. Specifically, if and when there is a sudden 'downward' shift in the expression of condition-dependent male traits, females using fixed-threshold mate choice criteria might find fewer acceptable males. While mechanisms of female choice remain elusive, a variety of sexually selected traits may be condition dependent. Because the expression of condition-dependent traits is likely to be impacted by natural or human-induced environmental changes, behavioral and conservation biologists should pay special attention to them around the mating season. Armed with knowledge of condition-dependent male traits, it may be possible to minimize the impact on condition-dependent traits while planning translocations or reintroductions.

INTRODUCTION

There are many causes of endangerment and extinction (Primack, 1993). Habitat destruction and other mechanisms that directly reduce the numbers of individuals can have a profound influence on how long a population or species persists. In addition to these direct causes of extinction, less-direct pathways may also influence persistence time. Awareness of less-direct pathways to extinction allows us to evaluate their importance in a given situation and may suggest novel, yet potentially important, remediation. One such pathway concerns the mechanisms by which females choose their mates and how this may influence the effective population size (N_e).

Females rarely chose their mates randomly and often base their decisions on one or more identifiable male traits (e.g. Bateson, 1983; Andersson, 1994). To choose among multiple males, females can either use a relative or an absolute assessment rule (Lande, 1981; Zuk *et al.*, 1990). Relative assessment is inferred when a female's choice is based on a sample of available males; females using this mechanism should immediately change their preferences if offered a different selection of males (Zuk *et al.*, 1990). While there is some empirical support for relative assessment mechanisms (e.g. Brown, 1981; Brown & Downhower, 1983; Ryan, 1985), if there are substantial assessment costs born by the female (e.g. time, energy, predation risk), females may have absolute threshold assessment mechanisms to minimize assessment time (Janetos, 1980; Wittenberger, 1983; Real, 1990). Thresholds may be fixed or adjustable (Reid & Stamps, 1997). When fixed, females prefer particular expressions of male traits regardless of the distribution of those traits in the population (Lande, 1981; Zuk *et al.*, 1990). When adjustable, thresholds may change based on sampling males in the population (Luttbeg, 1996; Reid & Stamps, 1997).

Mechanisms of threshold assessment may be visualized using preference curves that plot the distribution of a male trait on the abscissa and the probability of a female mating with a male with that trait expression (or a measurable correlate such as 'interest') on the ordinate (e.g. Fig. 1; Houde, 1987; Houde & Endler, 1990; Milinski & Bakker, 1990; Wagner, Murray & Cade, 1995; Ritchie, 1996). Female preference curves may have different shapes. Females may have asymptotic preferences where they prefer no males below a critical value and all males above another critical value. Between the critical values, the probability of mating increases with male trait expression. Females may have roughly parabolic preferences where they increase and then decrease their probability of mating as male trait expression increases. Parabolic-like preferences might be expected if female preferences co-vary with normally distributed male traits and each female has an 'ideal' mate (e.g. Jennions, Bacwell & Passmore, 1995).

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Parabolic preference functions would lead to stabilizing selection for male traits. Finally, although somewhat unlikely, females may have a fixed-range preference and mate only with males within a given range of trait expressions where the probability of mating increases with male trait expression. While fixed-range preferences are unlikely given that females seem to prefer exaggerated traits (Ryan & Keddy-Hector, 1992), they could potentially be found depending on the exact distribution of male traits (i.e. preferences could be asymptotic but there are no highly desirable males present).

Female preferences are only half the story. Many of the traits that females prefer vary according to male condition (Andersson, 1994). Males in good condition have longer tails (e.g. Møller, 1989), brighter colors (e.g. Endler, 1983), and vocalize more (e.g. Clutton-Brock & Albon, 1979). Andersson (1994: table 6A) provides a comprehensive review of sexually selected traits in both vertebrates and invertebrates. Of 232 reviewed studies on 186 species, 167 of the studies reported female choice for a trait. Many of the listed traits are likely to be condition dependent and condition-dependent traits used for mate choice are routinely being reported in the behavioral ecology literature.

Expression of a condition-dependent trait may be influenced by access to important resources (e.g. Endler, 1983), the presence of pathogens (e.g. Zuk *et al.*, 1990), or even the ability to properly display a trait (e.g. Endler & Théry, 1996). Thus, changes in resource distribution, the introduction of an otherwise non-lethal pathogen, or habitat alterations may influence trait expression.

What happens if females have fixed threshold preferences and a large number of males are suddenly unable to acquire enough resources to grow long tails, be bright, or vocalize a lot? Or, what happens if females have a flexible threshold that requires some sampling but they are unable to sample? A long winter, the sudden introduction of new parasites or pathogens, human impacts, or natural disasters may all reduce food availability or condition prior to a mating season and may result in uniform downward shift in the expression of condition-dependent traits or may increase the cost of sampling. I will use a simple simulation model to illustrate some ramifications of this scenario.

THE MODEL

Intuitively, the proportion of acceptable males will be a function of male trait distribution and the female preference function for that trait. To simulate these distributions I assumed a normally distributed male trait, varied the distribution's mean and standard deviation, and approximated three possible female preference functions (Fig. 1). The proportion of acceptable males given an asymptotic female preference was modeled as:

$$\varphi(z)=\begin{cases} 0 & z<-T, \\ zm & -T<z<T, \\ 1 & z>T, \end{cases} \qquad (1)$$

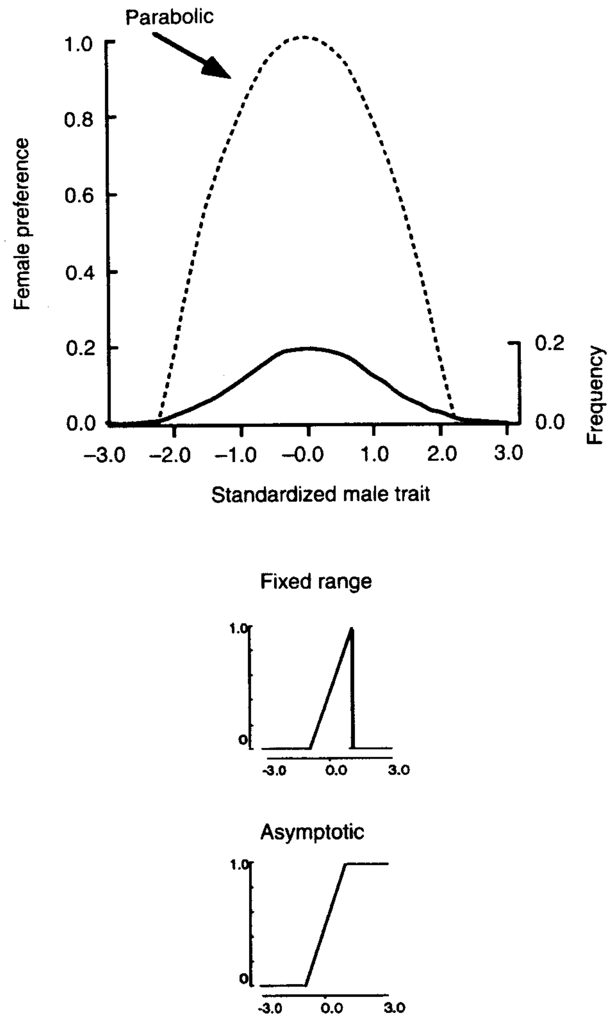

Fig. 1. A parabolic female preference function (female preference axis) superimposed over a hypothetical male trait distribution (frequency axis). Female preference functions plot the probability of mating with a male exhibiting a particular trait expression (e.g. tail size). Females with parabolic preferences increase and then decrease their probability of mating with a male as male trait expression increases. Females with fixed-range preference functions (below) mate only with males within a given range of trait expressions where the probability of mating increases with male trait expression. Females with asymptotic preference functions (below) mate with no males below a critical value and all males above a critical value. Between the critical values the probability of mating increases with trait expression.

where $\varphi(z)$ is the probability that a male with trait expression z will be mated given m, the steepness of the ascending part of the female preference, $-T$ is the threshold below which no males would be acceptable and T is the threshold above which all males would be acceptable. The proportion of acceptable males given a parabolic female preference was modeled as:

$$\varphi(z)=\begin{cases} z\left[\left(\frac{m^2}{4}\right) z^2\right]+zm & -T<z<T \\ 0 & \textit{otherwise.} \end{cases} \qquad (2)$$

In this case m describes the steepness of the parabola. The proportion of acceptable males given a linear and fixed-range female preference was modeled as in Eqn. (1), with the following constraints to make it a fixed-range preference function,

$$\varphi(z) = \begin{cases} 0 & z < -T, \\ zm & -T < z < T, \\ 0 & z > T. \end{cases} \tag{3}$$

For both the asymptotic and parabolic preference functions, the proportion of acceptable males declined quickly as the male distribution was shifted below the range of female preferences; for the fixed range preferences, results were less predictable although fixed range preferences uniformly resulted in fewer acceptable males (Fig. 2). As the variance in male trait distribution increased, the proportion of acceptable males decreased under an asymptotic female preference function, generally decreased under a parabolic function, and again remained somewhat location specific under a fixed-range preference function. As the slope of the female preference increased, more males generally became acceptable under asymptotic and parabolic preferences; fixed-range preferences, once again, produced location-specific responses.

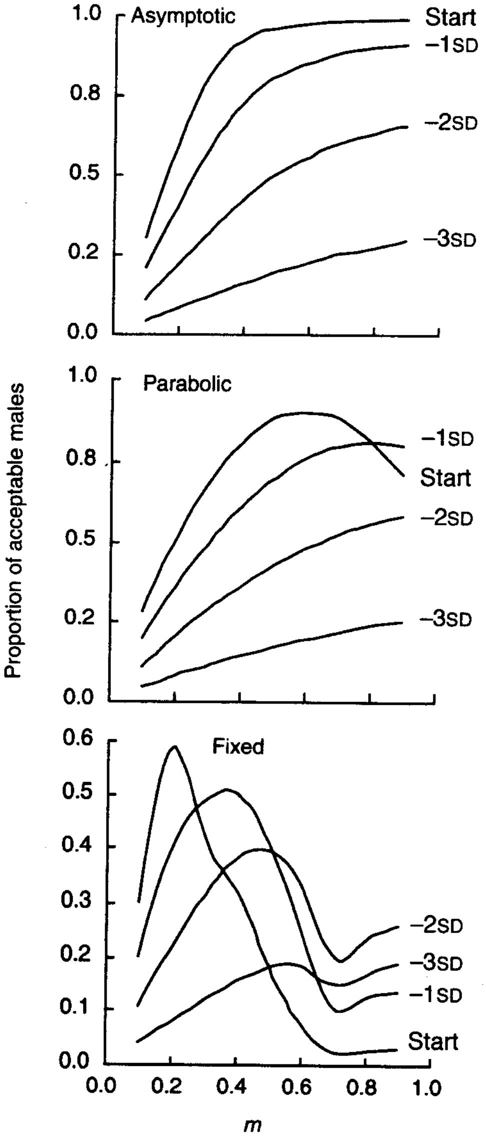

Fig. 2. Proportion of acceptable males as a function of the 'steepness' of the preference, m, for each of three different preference functions after shifting the distribution of male traits one SD, two SD, and three SD 'downward'. With asymptotic and parabolic preferences, there is almost always a substantial decline in the proportion of acceptable males.

To emphasize the importance of the number of acceptable males on effective population size, I have used a standard equation to calculate the effective population size for a non-age-structured population (Wright, 1938),

$$N_e = \frac{1}{\frac{1}{4N_m} + \frac{1}{4N_f}}, \tag{4}$$

where N_e is the effective population size, N_m is the number of breeding males in the population and N_f is the number of breeding females in the population. Calculations of N_e explicitly acknowledge that all individuals do not breed (e.g. Nunney 1993; Parker & Waite, 1997). The implicit assumption is that most breeding-age females breed but only a fraction of breeding-age males breed. I use these calculations to emphasize that certain mate choice criteria may further reduce the number of acceptable males because all females may not mate.

Assuming that female preferences will not change if and when females fail to encounter acceptable males, and assuming that all acceptable males mate, then as the number of acceptable males declines, the effective population size declines (Fig. 3). For instance, if females found only 40% of a population's males acceptable, a non-age-structured population is only 55% as large as it appears. Modeling the effect of a decline in acceptable males in a single breeding season in an age-structured population requires more parameters and assumptions, and while more complex (Charlesworth, 1994: 88–91), must nevertheless lead to a decline in N_e.

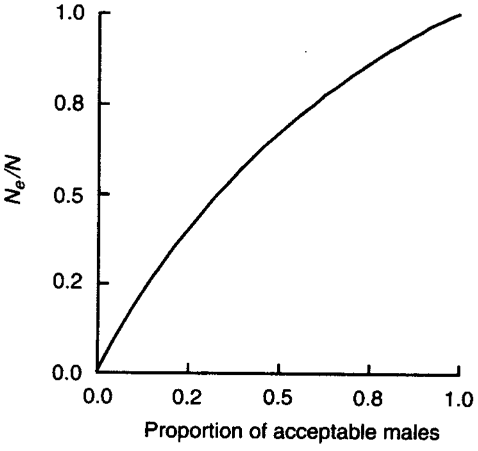

Fig. 3. The relationship between the proportion of acceptable males and Ne/N in a non–age-structured population. As fewer males are acceptable, Ne/N decreases rapidly.

DISCUSSION

There has been a recent emphasis in the importance of understanding behavior, particularly sexual behavior, for more population biology oriented conservation biologists (Berger, 1996; Höglund, 1996; Parker & Waite, 1997; Waite & Parker, 1997). Conservation biologists should be concerned about the mechanisms of mate choice for several reasons. While we have long realized that sexual selection may reduce the mean population fitness (Fisher, 1958), demonstrating its effects on extinction and the maintenance of biodiversity has taken more time.

Recent studies found that introduced bird species with plumage dimorphism (a correlate of sexual selection) were more likely to go extinct on an island than introduced non-dimorphic species (McLain, Moulton & Redfearn, 1995). These authors suggested that maintaining dimorphic traits may have a cost in terms of a reduced ability to compete with other species.

Female preferences also may create or maintain species diversity. The number of species of African cichlid fish living in Lake Victoria have been declining for some years. Seehausen, van Alphen & Witte (1997) provide compelling evidence that the loss of diversity is related to increased turbulence, a consequence of farming practices, which decreases female visual acuity, and prevents females from expressing preferences for certain colors. In the cichlids' case, females hybridize with other species leading to a loss of species diversity. If hybrids were not fertile, it would lead to an immediate reduction in the number of fish as well. Neither the importance of direct impacts by humans on cichlids, nor less-direct effects via mate choice should be ignored. Expressing sexually selected traits may reduce a species' competitive ability or make it particularly vulnerable to human impacts that modify the expression of those traits.

More specifically, for those species where females have fixed threshold preferences for male condition-dependent traits, a sudden change in the phenotypic distribution of those male traits may cause a decline in the number of acceptable males and a concomitant decline in N_e. The effects of small population sizes are well known (Franklin, 1980; Gilpin & Soulé, 1986; Chepko-Sade *et al.*, 1987; Nunney, 1993; Frankham, 1995*a,b*; Parker & Waite, 1997). As N_e decreases, genetic variation is lost, the likelihood of inbreeding and its potentially deleterious effects increases, and the likelihood of random demographic effects leading to local extinction increases. Recent reviews of N_e/N ratios (Frankham, 1995*a,b*) suggest that N_e in wildlife populations may already be very small. Thus, anything that can cause a further decline in N_e is worthy of attention, particularly if the effects of a declining N_e are not predictable (Frankham, 1995*c*).

We know that the expression of a variety of male traits may be influenced by the male's condition (Andersson, 1994). Unfortunately, we know relatively little about the heritability of female preferences (but see Ryan & Wilczynski, 1988; Bakker, 1993; Butlin, 1993; Godin & Dugatkin, 1995; Ritchie, 1996), neither do we know whether females who appear to have fixed thresholds can or will change their preferences when faced with an array of formerly unacceptable males (*sensu* Forsgren, 1992; Berglund, 1993). Thornhill (1984) provides evidence of some preference flexibility in ecological time for a species with threshold assessment mechanisms, and Reid & Stamps (1997) illustrate an example of an adjustable threshold, but more data are required to generalize about responsiveness. However, especially for species with brief fertile periods, it is possible that females may not have enough time to respond to a sudden decline in male 'quality'. If so, there will be an immediate drop in N_e in three ways: (1) there will be fewer acceptable males, (2) females may be unable to find a suitable mate while she is fertile, and (3) some females may choose not to breed; failure to breed in a given year is not unheard of in natural populations (e.g. Boag & Grant, 1981). Moreover, female condition and fertility is also likely to co-vary with the same environmental resources that influence male condition; females in poor condition may need to spend more time foraging and less time assessing male quality. If females are unable to breed, the effect of a decline in acceptable males would be magnified and N_e would decline even more.

Perhaps this scenario is an argument against having a fixed threshold assessment mechanism for species who base mate choice on variation in condition-dependent traits. Nevertheless, in lieu of more information about mechanisms of female choice, we should consider fixed thresholds a possibility.

There are important ramifications for the management of threatened or endangered species if female mating preferences can contribute to a rapid decline in N_e. First, more must be known about female assessment mechanisms. Behavioral ecologists can make an important contribution to conservation biology by studying the mechanisms of female mate choice in more detail. With this knowledge, traits may be manipulated (e.g. lengthen tail, change color, etc) to increase mating probability. Second, care should be taken to avoid situations where condition-dependent male traits will not be fully expressed during breeding seasons. For instance, translocations (Griffith *et al.*, 1989) may be timed to avoid stressing males in ways that may influence the expression of condition-dependent traits.

Acknowledgements

I thank numerous people at UC Davis for feedback about the idea, Amos Bouskila, Richard Gomulkiewicz, Mike Maxwell and Paul Switzer for help with the model, and John Endler, Richard Gomulkiewicz, Michael Hellberg, Mike Maxwell Maria Orieve, Mary Reid, Marlene Zuk and two anonymous reviewers for comments on previous versions of the manuscript. Support during the initial development of this paper was through UC Davis graduate student fellowships; final manuscript preparation was supported by NIH NRSA F32 MH10793.

REFERENCES

Andersson, M. (1994). *Sexual selection.* Princeton: Princeton University Press.

Bakker, T. C. M. (1993). Positive genetic correlation between female preference and preferred male ornament in sticklebacks. *Nature, Lond.* **363**: 255–257.

Bateson, P. (Ed.) (1983). *Mate choice.* Cambridge: Cambridge University Press.

Berger, J. (1996). Animal behaviour and plundered mammals: is the study of mating systems a scientific luxury or a conservation necessity? *Oikos* **77**: 207–216.

Berglund, A. (1993). Risky sex: male pipefishes mate at random in the presence of a predator. *Anim. Behav.* **46**: 169–175.

Boag, P. T. & Grant, P. R. (1981). Intense natural selection in a population of Darwin's finches (Geospizinae) in the Galápagos. *Science* **214**: 82–85.

Brown, L. (1981). Patterns of female choice in mottled sculpins (Cottidae, Teleostei). *Anim. Behav.* **29**: 375–382.

Brown, L. & Downhower, J. F. (1983). Constraints on female choice in the mottled sculpin. In *Social behavior of female vertebrates:* 39–54. Wasser, S. K. (Ed.). New York: Academic Press.

Butlin, R. K. (1993). The variability of mating signals and preferences in the brown planthopper, *Nilaparvata lugens* (Homoptera: Delphacidae). *J. Insect Behav.* **6**: 125–140.

Charlesworth, B. (1994). *Evolution in age-structured populations.* 2nd edn. Cambridge: Cambridge University Press.

Chepko–Sade, B. D., Shields, W. M., Berger, J., Halpin, Z. T., Jones, W. T., Rogers, L. L., Rood, P. P. & Smith, A. T. (1987). The effects of dispersal and social structure on effective population size. In *Mammalian dispersal patterns: the effects of social structure on population genetics:* 287–321. Chepko-Sade, B. D. & Halpin, Z. T. (Eds). Chicago: University of Chicago Press.

Clutton-Brock, T. H. & Albon, S. D. (1979). The roaring of red deer and the evolution of honest advertisement. *Behaviour* **69**: 145–169.

Endler, J. A. (1983). Natural and sexual selection on color patterns in poeciliid fishes. *Environ. Biol. Fishes* **9**: 173–190.

Endler, J. A. & Théry, M. (1996). Interacting effects of lek placement, display behavior, ambient light, and color pattern in three neotropical forest-dwelling birds. *Am. Nat.* **148**: 421–452.

Fisher, R. A. (1958). *The genetical theory of natural selection.* 2nd edn. New York: Dover Publications, Inc.

Forsgren, E. (1992). Predation risk affects mate choice in a gobiid fish. *Am. Nat.* **140**: 1041–1049.

Frankham, R. (1995*a*). Effective population size/adult population size ratios in wildlife: a review. *Genet. Res. Camb.* **66**: 95–107.

Frankham, R. (1995*b*). Conservation genetics. *Annu. Rev. Gen.* **29**: 205–327.

Frankham, R. (1995*c*). Inbreeding and extinction: a threshold effect. *Conserv. Biol.* **9**: 792–799.

Franklin, I. R. (1980). Evolutionary change in small populations. In *Conservation biology: an evolutionary-ecological perspective:* 135–149. Soulé, M. E. & Wilcox, B. A. (Eds). Sunderland, MA: Sinauer.

Gilpin, M. E. & Soulé, M. E. (1986). Minimum viable populations: processes of species extinction. In *Conservation biology the science of scarcity and diversity:* 19–34. Soulé, M. E. (Ed.). Sunderland, MA: Sinauer Associates, Inc.

Godin, J. J.–G. & Dugatkin, L. A. (1995). Variability and repeatability of female mating preferences in the guppy. *Anim. Behav.* **49**: 1427–1433.

Griffith, B., Scott, J. M., Carpenter, J. W. & Reed, C. (1989). Translocation as a species conservation tool: status and strategy. *Science* **245**: 477–480.

Höglund, J. (1996). Can mating systems affect local extinction risks? Two examples of lek-breeding waders. *Oikos* **77**: 184–188.

Houde, A. E. (1987). Mate choice based upon naturally occurring color-pattern variation in a guppy population. *Evolution* **41**: 1–10.

Houde, A. E. & Endler, J. A. (1990). Correlated evolution of female mating preferences and male color patterns in the guppy *Poecilia reticulata. Science* **248**: 1405–1408.

Janetos, A. A. (1980). Strategies of female mate choice: a theoretical analysis. *Behav. Ecol. Sociobiol.* **7**: 107–112.

Jennions, M. D., Bacwell, P. R. Y. & Passmore, N. I. (1995). Repeatability of mate choice: the effect of size in the African painted reed frog, *Hyperolius mamoratus. Anim. Behav.* **49**: 181–186.

Lande, R. (1981). Models of speciation by sexual selection on polygenic traits. *Proc. Natl. Acad. Sci. USA* **78**: 3721–3725.

Luttbeg, B. (1996). A comparative Bayes tactic for mate assessment and choice. *Behav. Ecol.* **7**: 451–460.

McLain, D. K., Moulton, M. P. & Redfearn, T. P. (1995). Sexual selection and the risk of extinction of introduced birds on oceanic islands. *Oikos* **74**: 27–34.

Milinski, M. & Bakker, T. C. M. (1990). Female sticklebacks use male coloration in mate choice and hence avoid parasitized males. *Nature, Lond.* **344**: 330–333.

Møller, A. P. (1989). Viability costs of male tail ornaments in a swallow. *Nature, Lond.* **339**: 132–135.

Nunney, L. (1993). The influence of mating system and overlapping generations on effective population size. *Evolution* **47**: 1329–1341.

Parker, P. G. & Waite, T. A. (1997). Mating systems, effective population size, and conservation of natural populations. In *Behavioral approaches to conservation in the wild:* 243–261. Clemmons, J. R. & Buchholz, R. (Eds). Cambridge: Cambridge University Press.

Primack, R. B. (1993). *Essentials of conservation biology.* Sunderland, MA: Sinauer.

Real, L. (1990). Sequential search theory and mate choice I. Models of single-sex discrimination. *Am. Nat.* **136**: 376–404.

Reid, M. L. & Stamps, J. A. (1997). Female mate choice tactics in a resource-based mating system: field tests of alternative models. *Am. Nat.* **150**: 98–121.

Ritchie, M. G. (1996). The shape of female mating preferences. *Proc. Natl. Acad. Sci. USA.* **93**: 14628–14631.

Ryan, M. J. (1985). *The túngara frog.* Chicago: University of Chicago Press.

Ryan, M. J. & Keddy-Hector, A. (1992). Directional patterns of female mate choice and the role of sensory biases. *Am. Nat.* **139**: S4–S35.

Ryan, M. J. & Wilczynski, W. (1988). Coevolution of sender and receiver: effect on local mate preference in cricket frogs. *Science* **240**: 1786–1788.

Seehausen, O., van Alphen, J. M. & Witte, F. (1997). Cichlid fish diversity threatened by eutrophication that curbs sexual selection. *Science* **277**: 1808–1811.

Thornhill, R. (1984). Alternative female choice tactics in the scorpionfly *Hylobittacus apicalis* (Mecoptera) and their implications. *Am. Zool.* **24**: 367–383.

Wagner, W. E. Jr, Murray, A.-M. & Cade, W. H. (1995). Phenotypic variation in the mating preferences of female field crickets, *Gryllus integer. Anim. Behav.* **49**: 1269–1281.

Waite, T. A. & Parker, P. G. (1997). Extra-pair paternity and the effective size of socially monogamous populations. *Evolution* **51**: 620–621.

Wittenberger, J. F. (1983). Tactics of mate choice. In *Mate choice:* 435–447. Bateson, P. (Ed.). Cambridge: Cambridge University Press.

Wright, S. (1938). Size of population and breeding structure in relation to evolution. *Science* **87**: 430–431.

Zuk, M., Johnson, K., Thornhill, R. & Ligon, J. D. (1990). Mechanisms of female choice in red jungle fowl. *Evolution* **44**: 477–485.