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REPORT

Predicting the direction of sexual selection

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Abstract

Our current understanding of the operation of sexual selection is predicated on a sex difference in parental investment, which favours one sex becoming limiting and choosy over mates, the other competitive and nonchoosy. This difference is reflected in the operational sex ratio (OSR), the ratio of sexually receptive males to females, considered to be of fundamental importance in predicting the direction of sexual selection. Difficulties in measuring OSR directly have led to the use of the potential reproductive rates (PRR) as a measure of the level of investment in offspring of males and females. Several recent studies have emphasized that other factors, such as variation in mate quality and sex differences in mortality patterns, also influence the direction of sexual selection. However, as yet there has been no attempt to form a comprehensive theory of sex roles. Here we show that neither OSR nor PRR is the most fundamentally important determinant of sex roles, and that they are not interchangeable. Instead, the cost of a single breeding attempt has a strong direct effect on competition and choosiness as well as consistent relationships to both OSR and PRR. Our life history based approach to mate choice also yields simple, testable predictions on lack of choice in either sex and on mutual mate choice.

Keywords
Cost of breeding, mate acquisition, mutual mate choice, operational sex ratio, parental investment, sex roles.

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INTRODUCTION

Understanding how the forces of sexual selection shape the morphology and behaviour of organisms has developed into a key area of evolutionary biology over the past 30 years (Andersson 1994). Trivers (1972) provided the basis for our current understanding of the operation of sexual selection by his argument that differences in parental investment will cause the higher investing sex to become limiting and favour the evolution of choosiness in that sex with respect to potential mates; the other nonlimiting sex will compete for access to the limiting sex and be comparatively unselective in its mating behaviour. Investment differences between the sexes are reflected in the ratio of sexually receptive males to females (the operational sex ratio (OSR); Emlen & Oring 1977). Established theory therefore currently holds that the OSR is the fundamental variable that determines the level of competition for mates and hence the direction and strength of sexual selection.

The OSR is difficult to measure directly, resulting in the need for indirect, presumed proxy, measurements. Clutton-Brock & Vincent (1991) suggested the use of the potential reproductive rates (PRR) of males and females as a more easily measurable predictor of mating competition. Recent work has expanded on this idea, noting that the time that individuals are unreceptive to further mating opportunities, the so-called "time out", is the basic variable that determines the PRR and hence OSR (Clutton-Brock & Parker 1992; Parker & Simmons 1996). However, other factors also influence the direction of sexual selection, such as the relative advantages of obtaining a high-quality mate (Clutton-Brock & Parker 1992; Owens & Thompson 1994; Johnstone *et al.* 1996; Kvarnemo & Simmons 1999). Furthermore, it has recently been pointed out that sex-differences in mortality patterns can have an important effect on sex roles (Okuda 1999; Tershy & Croll 2000), overriding small biases in OSR, and that only individuals "qualified to mate" should be included in the calculations (Ahnesjö *et al.*, in press). Also, it has been pointed out that choosiness and competition are not opposite alternatives; the balance of costs and benefits of choice may, in some cases, make the more competitive sex also more choosy (Johnstone *et al.* 1996; Kvarnemo & Simmons 1999).

Despite these deviations from simple OSR-based predictions, there has as yet been no attempt to develop a more comprehensive theory to predict the direction of sexual selection. Here, we show that that the OSR is not as fundamental as a summarizing index of differential parental investment as hitherto thought. By developing a life-history-based model of mating systems, we show that OSR and PRR are not in fact interchangeable, and that neither of them is the most fundamentally important determinant of the direction of sexual selection. Instead, the cost of a single breeding attempt, which in iteroparous organisms can be measured as the probability of death as a consequence of the current breeding attempt, has a strong, direct effect on choosiness as well as consistent relationships to both OSR and PRR. This highlights the importance of Trivers's (1972) original definition of parental investment. Unlike models based on OSR or PRR only, our life history model of competition and mate choice also yields simple, testable predictions relating to the circumstances that favour lack of choice in either sex, or choosiness in both sexes.

A LIFE-HISTORY-BASED MODEL OF SEX ROLES

Following recent demonstrations of the importance of life-history theory in sexual selection (Kokko 1997; Qvarnström 1997; Höglund & Sheldon 1998; Kokko *et al.* 1999; Griffith 2000), we use lifetime reproductive success as the appropriate fitness measure in a population regulated by lifetime offspring production (Brommer 2000). The sex ratio (males:females) of individuals that reach maturation is α. This parameter encapsulates any differences in primary sex ratio and juvenile mortality rates. Breeding occurs continuously, and mature males and females can be in one of two states: receptive (searching for mates, i.e. in "time in") or nonreceptive (dealing with the result of previous matings, i.e. in "time out"). The "times out" of females and males are T_F and T_M, respectively, and they specify the rates ($T_F{}^{-1}$ and $T_M{}^{-1}$) at which individuals re-enter the receptive state. These rates also equal the potential reproductive rates of females, $\mathrm{PRR}_F = T_F{}^{-1}$, and of males, $\mathrm{PRR}_M = T_M{}^{-1}$.

The rate at which an individual meets receptive mates equals M in a population of unbiased OSR. If the OSR equals β males:females, it follows that individual females encounter males at a rate $M\sqrt{\beta}$, and males encounter females at a rate $M/\sqrt{\beta}$. Mortality rates may differ between time out (μ_{OF}, μ_{OM}) and time in (μ_{IF}, μ_{IM}); these may also differ between females (F) and males (M) as indicated. We first consider a scenario in which neither sex spends time discriminating amongst the receptive mates available, so that the encounter rate equals the mating rate, and then investigate the conditions under which choosiness can spread. Each completed breeding attempt brings about a fitness increment, which we set to unity for randomly mating individuals.

The probability that a female, entering the breeding population at $t_0 = 0$, is gaining fitness by completing a breeding attempt at time t, equals $P_{OF}(t)T_F{}^{-1}$, where the probability $P_{OF}(t)$ is the probability that she is alive and in "time out" state at time t. This probability is derived from the relative time spent "in" and "out" and the associated mortality rates:

$$\left\{\begin{aligned} &\frac{dP_{OF}}{dt} = P_{OF}(t)(-\mu_{OF} - T_F^{-1}) + P_{IF}(t)M\sqrt{\beta} \\ &\frac{dP_{IF}}{dt} = P_{OF}(t)T_F^{-1} + P_{IF}(t)(-\mu_{IF} - M\sqrt{\beta}) \\ &P_{OF}(0) = 0 \\ &P_{IF}(0) = 1 \end{aligned}\right. \tag{1}$$

Solving for $P_{OF}(t)$ and integrating leads to female lifetime fitness

$$W_F = \int_0^{\infty} P_{OF}(t)T_F^{-1}dt = \frac{M\sqrt{\beta}}{\mu_{IF} + \mu_{IF}\mu_{OF}T_F + \mu_{OF}T_F M\sqrt{\beta}} \tag{2a}$$

Using a similar derivation, male lifetime fitness equals

$$W_M = \frac{M/\sqrt{\beta}}{\mu_{IM} + \mu_{IM}\mu_{OM}T_M + \mu_{OM}T_M M/\sqrt{\beta}} \tag{2b}$$

The operational sex ratio, β, depends on the sex ratio at maturation, α, and the probabilities of finding an individual in "time in":

$$\beta = \alpha \int_{t=0}^{\infty} P_{IM}(t)dt \bigg/ \int_{t=0}^{\infty} P_{IF}(t)dt$$

When we define the cost of breeding as $C_F = \mu_{OF}T_F/(1 + \mu_{OF}T_F)$ for females and $C_M = \mu_{OM}T_M/(1 + \mu_{OM}T_M)$ for males, evaluating the integrals leads to the OSR equation

$$\beta = \alpha\frac{\mu_{IF} + C_F M\sqrt{\beta}}{\mu_{IM} + C_M M/\sqrt{\beta}} \tag{3}$$

The closed form solution for the OSR is

$$\beta = \frac{1}{2\mu_{IM}^2}\Big[M^2(\alpha C_F - C_M)^2 + 2\alpha\mu_{IF}\mu_{IM} + M(\alpha C_F - C_M)\sqrt{M^2(\alpha C_F - C_M)^2 + 4\alpha\mu_{IF}\mu_{IM}}\Big]$$

That C reflects the cost of breeding is easily seen as it equals the probability that the individual dies as a result of the current breeding attempt: during breeding, the rate of dying is a constant μ_O, and the rate of finishing breeding T^{-1}, hence the probability of death equals $C = \mu_O/(T^{-1} + \mu_O) = \mu_O T/(1 + \mu_O T)$. Since the right-hand side of equation 3 increases with C_F and μ_{OF}, the OSR always increases (becomes more male-biased) with increasing female breeding cost and nonbreeding mortality, and decreases with male breeding cost and nonbreeding mortality.

RESULTS: SOLVING THE MODEL

We can now ask which sex will benefit more from an increase in the mating rate. This sex is expected to compete for mates more strongly. All previous models make the *a priori* assumption that males compete more if the operational sex ratio is male-biased ($\beta > 1$). We do not make this assumption; instead we define the competitive benefit ratio (CBR) as the relative increase of fitness of males *versus* females when the mating rate increases: CBR = $[(\partial W_M/\partial M)/W_M]/[(\partial W_F/\partial M)/W_F]$. Using the equations for lifetime fitness (equations 2a and 2b) we obtain

$$\mathrm{CBR} = \frac{\beta M C_F \mu_{IM} + \sqrt{\beta}\mu_{IF}\mu_{IM}}{M C_M \mu_{IF} + \sqrt{\beta}\mu_{IF}\mu_{IM}}$$

Males are more competitive than females if CBR > 1, which simplifies to

$$\beta > \frac{\mu_{IF} C_M}{\mu_{IM} C_F} \qquad (4)$$

According to equation 4, a male-biased sex ratio (large β) tends to make males more competitive. However, the threshold value of the operational sex ratio at which males turn more competitive than females is not generally equal to 1. If breeding is costlier for females than for males, males may remain more competitive even if they are the limiting sex, e.g. due to high juvenile mortality of males (Fig. 1). This illustrates that the difference in the cost of breeding is more important than the operational sex ratio in determining the direction of sexual selection.

Intense competition in one sex does not translate to choosiness in the other (Johnstone *et al.* 1996; Van Dongen *et al.* 1998; Kvarnemo & Simmons 1999), and conditions for the spread of choosiness have to be addressed separately. Choosiness increases the average quality of accepted mates, at the expense of a reduction in the mating rate M. Here, "quality" refers to any benefit, direct or indirect (Andersson 1994), that increases the fitness gain from a single breeding attempt. We assume that females can improve the expected quality of their mates by a factor $q_M > 1$, by accepting a fraction $p_M < 1$ of males; the corresponding parameters for males choosing females are q_F and p_F.

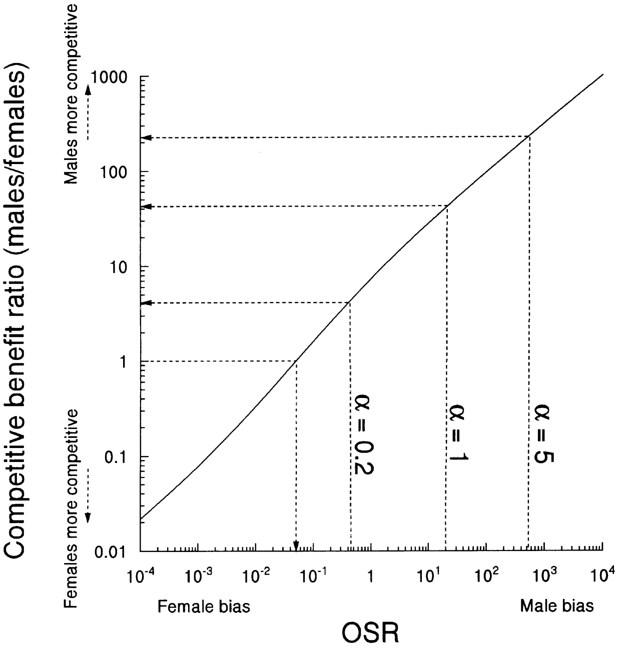

Figure 1 The CBR as a function of the OSR, when females suffer a much higher cost of breeding than males ($C_F = 0.1$, $C_M = 0.01$), but males suffer higher mortality during mate searching ($\mu_{IM} = 0.2$, $\mu_{IF} = 0.1$). Mate encounter rate $M = 10$. The OSR is determined by these parameters and by sex ratio at maturation, α. Males are more competitive than females (CBR > 1) when juvenile mortality leads to a male-biased sex ratio at maturation ($\alpha = 5$), but also when sex ratio at maturation is even ($\alpha = 1$) or heavily female-biased ($\alpha = 0.2$). With $\alpha = 0.2$, the operational sex ratio becomes female-biased ($\beta = 0.43$ from equation 3), but males remain more competitive than females. Males are expected to be more competitive than females whenever CBR > 1; this translates to OSR > 0.05 (leftmost arrow), as shown by equation 4.

Choosiness can invade the female population if fitness (equation 2a) of choosy females is greater than that of nonchoosy females,

$$\frac{q_M p_M M\sqrt{\beta}}{\mu_{IF} + \mu_{IF}\mu_{OF} T_F + \mu_{OF} T_F p_M M\sqrt{\beta}} > \frac{M\sqrt{\beta}}{\mu_{IF} + \mu_{IF}\mu_{OF} T_F + \mu_{OF} T_F M\sqrt{\beta}}$$

$$\leftrightarrow C_F M\sqrt{\beta} > \mu_{IF}\frac{1 - p_M q_M}{p_M(q_M - 1)} \qquad (5a)$$

Likewise, choosiness can invade the male population, if

$$\frac{q_{\mathrm{F}}p_{\mathrm{F}}M/\sqrt{\beta}}{\mu_{\mathrm{IM}}+\mu_{\mathrm{IM}}\mu_{\mathrm{OM}}T_{\mathrm{M}}+\mu_{\mathrm{OM}}T_{\mathrm{M}}p_{\mathrm{F}}M/\sqrt{\beta}} > \frac{M/\sqrt{\beta}}{\mu_{\mathrm{IM}}+\mu_{\mathrm{IM}}\mu_{\mathrm{OM}}T_{\mathrm{M}}+\mu_{\mathrm{OM}}T_{\mathrm{M}}M/\sqrt{\beta}}$$

$$\leftrightarrow C_{\mathrm{M}}\frac{M}{\sqrt{\beta}} > \mu_{\mathrm{IM}}\frac{1-q_{\mathrm{F}}p_{\mathrm{F}}}{p_{\mathrm{F}}(q_{\mathrm{F}}-1)} \qquad (5b)$$

Thus, whether a sex is choosy depends on the following factors:

1 The sex-specific mortality cost of breeding $C = \mu_{\mathrm{O}}T/(1+\mu_{\mathrm{O}}T)$; high cost C favours choosiness. The cost C increases with breeding-induced mortality, μ_{O}, as well as with "time out", T (and hence decreases with increasing potential reproductive rate PRR $= T^{-1}$).

2 Rate of encountering mates, $M\sqrt{\beta}$ for females and $M/\sqrt{\beta}$ for males. A high rate of encounter between potential mates increases choosiness in both sexes since mates can be readily compared. Biases in operational sex ratio, β, cause sex differences in encounter rates. A male-biased operational sex ratio (large β) will make males less likely to be choosy since evaluating females requires more of costly time, and vice versa.

3 Sex-specific mortality during the time in state, μ_{I}. High mortality during mate searching reduces choosiness.

4 Variation in mate quality, expressed as a trade-off between the degree of improvement in mate quality, q, and rate of encountering high quality mates, p. If mate quality is highly variable, significant increases in mate quality q can be achieved without reducing the mating rate too much. The resulting combination of high q and high p then favours choosiness (see also Owens & Thompson 1994; Petrie & Lipsitch 1994). If $qp > 1$ (increase in quality more than compensates for reduction in mating rate, e.g. halving the mating rate more than doubles quality), choosiness is always favoured, regardless of mortality rates, times out, and mate encounter rates.

The choosiness equations (5a and 5b) predict the range of OSR values in which females, males, both, or neither should be choosy. Figure 2 shows an example where neither sex is choosy if the cost of breeding is low. In this example, females again have a longer "time out", but male "time in" mortality is higher than that of females. Males are more competitive even where the OSR is female-biased. Females become choosy when the cost of breeding increases; choosiness spreads in females if $C > 0.048$. This is mainly due to the direct effect of high breeding cost C – the area of female choice widens quickly as C increases – and only to a small degree due to increasing OSR: at $C = 0.048$ in Fig. 2(a), the OSR is still female-biased (0.7 males:females) and changes only slowly with C, yet here females choose and males are competitive. At still higher cost of breeding, both sexes benefit from being choosy.

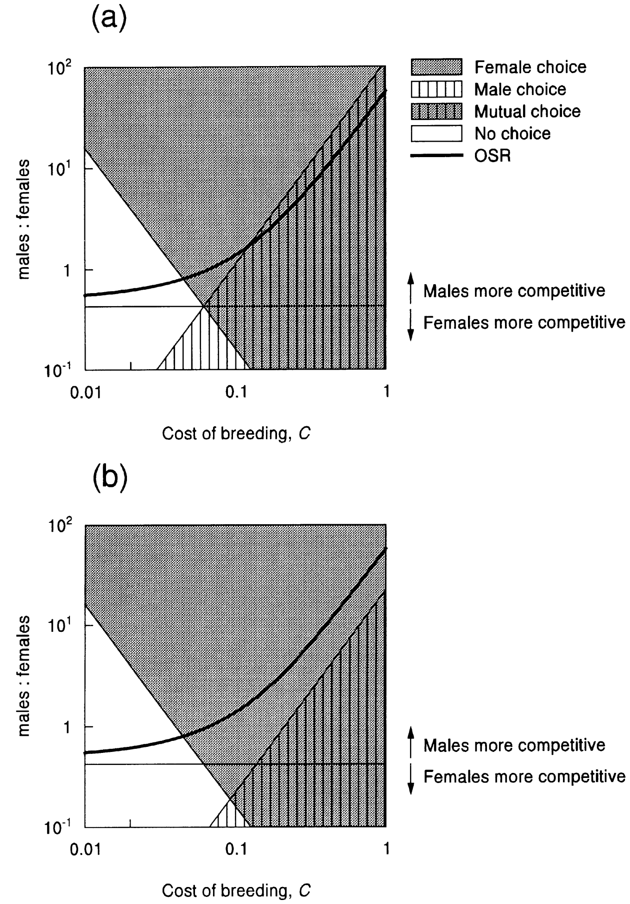

Figure 2 Influence of cost of breeding, C, on the direction of sexual selection. Areas indicate the range of values of operational sex ratio, β, for which male and/or female choosiness can spread. The solid line describes the actual OSR predicted by the mating dynamics, and solutions are read along this curve. Male cost of breeding is 15% lower than the cost for females: $C_{\mathrm{M}} = 0.85C$, $C_{\mathrm{F}} = C$; males have higher mortality during "time in", $\mu_{\mathrm{IM}} = 2$, $\mu_{\mathrm{IF}} = 1$. Males are more competitive than females above the horizontal line ($\mu_{\mathrm{IF}}C_{\mathrm{M}}/\mu_{\mathrm{IM}}C_{\mathrm{F}} = 0.425$, equation 4), while the opposite is true below. As cost of breeding C increases, the operational sex ratio turns from female-to male-biased. In (a), both sexes vary equally in quality ($p_{\mathrm{F}} = p_{\mathrm{M}} = 0.5$, $q_{\mathrm{F}} = q_{\mathrm{M}} = 1.2$), and the more competitive sex is always less choosy. At high cost of breeding, both sexes are choosy. In (b), females vary less in quality than males ($q_{\mathrm{F}} = 1.1$, $q_{\mathrm{M}} = 1.2$, p as before), which shifts the male choosiness threshold to the right, and choosiness will evolve only in females. Mating rate is $M = 100$ in both examples.

In Fig. 2(a), both sexes vary equally in quality, and the more competitive sex is always less choosy. In Fig. 2(b), female quality is assumed to vary less than male quality. This makes males less likely to be choosy, and indeed mutual mate choice does not evolve even at very high cost of breeding in both sexes.

DISCUSSION

We have developed a comprehensive theory of the direction of sexual selection, which combines the effect of parental investment, mortality, sex ratio at maturation, and the quality variation of the two sexes. Instead of assuming an *a priori* relationship between the operational sex ratio and the direction of sexual selection, we derive explicitly the sex-specific fitness gain from an increase in the mating rate or in the quality of mates. The model suggests a more fundamental role for Triversian parental investment (Trivers 1972) than is captured by its effect on operational sex ratio. It shows that the OSR does not alone determine the direction of sexual selection, nor should potential reproductive rates be viewed as a mere proxy for the OSR. Instead, both have their independent effects on sex roles, and they interact with sex-specific mortalities to produce the mating system. Also, the model predicts OSR by taking into account differential mortalities of the sexes and the sex-specific cost of breeding, and thus quantifies the effect of PRR on OSR under various mortality schemes and adult sex ratios, instead of assuming a direct relationship between these two.

Because of this complexity, we may explain cases that would remain puzzling under the standard theory of sexual selection. Firstly, our model identifies cases where a biased OSR will override differences in PRR. In the cardinalfish *Apogon notatus*, the potential reproductive rate of females is more than twice that of males, yet the fish is not sex role reversed (Okuda 1999). This is due to high female mortality, which may in part be explained in females breeding more often than males. Consider a case with male-biased time out ($T_M = 0.5$, $T_F = 0.25$), high mortality of breeding females ($\mu_{OF} = 6$, $\mu_{OM} = 2$), and equal mortality in the two sexes during time in ($\mu_{OF} = \mu_{OM} = 1$). The operational sex ratio remains male-biased (e.g. $\alpha = 1$, $M = 20$, $P = 0.5$ and $q = 1.2$ produces OSR = 0.1886), and females remain choosy. The choosy sex has a higher cost of breeding despite its shorter time out ($C_F = 0.6$, $C_M = 0.5$).

Likewise, differences in the cost of breeding may override the effect of OSR. The OSR is not solely determined by "time out" differences: demographic differences between the sexes have an effect on the OSR (Partridge & Endler 1987; Clutton-Brock & Parker 1992). Investment in mating competition is often costly and causes high mortality in the competitive sex (Clutton-Brock *et al.* 1985; Promislow 1992; Promislow *et al.* 1992). This reduces the bias in operational sex ratio that is caused by the mortality cost of the sex that provides parental care (Owens & Bennett 1994). The resulting direction of the OSR bias depends on the relative mortalities caused by competition for mates *versus* parental care (equation 3; see also Promislow *et al.* 1994), but given sufficient difference in the cost of breeding, we predict that the sex with the higher cost – longer time out or higher breeding mortality – should remain choosy, even if the OSR becomes biased towards this sex. Van Dongen *et al.* (1998) describe this situation in the winter moth *Operophtera brumata*, where the number of matings a male can achieve is limited because of costs of time and spermatophore production. Males, but not females, are choosy in this species, despite a heavily male-biased OSR (Van Dongen *et al.* 1998).

High mortality during mate searching (time in) reduces choosiness in both sexes. Excluding cases with $pq > 1$ (described above), neither sex will be choosy if mortality occurs solely as a consequence of mate-searching. This applies regardless of potential reproductive rates or operational sex ratios (cost $C = 0$ if $\mu_O = 0$, regardless of time out T). Generally, short-lived species (high μ_I) that are capable of breeding quickly (small C) are not likely to exert mate choice, neither are those that encounter mates rarely (small M). Conversely, mutual mate choice can evolve even under highly biased operational sex ratios, if breeding is costly for both sexes and rate of encountering mates is high – assuming that the cost of breeding and the quality variation are similar in both sexes.

We have derived our examples assuming that parental care decisions are fixed, as are sex-specific mortalities. A more comprehensive game-theoretic model of mutual mate choice, which takes into account that mortalities may depend on the mating strategies used (e.g. high mortality during "time in" may be a consequence of investment in competitiveness) and includes assortative mating and quality-dependent mating rates, supports the generality of these predictions (H. Kokko & R. A. Johnstone, submitted).

Even though we have argued that the OSR is not the primary determinant of the direction of sexual selection, variations in OSR tend to predict sexual competition well (Kvarnemo & Ahnesjö 1996). The reason for this is that many of our parameters covary: e.g. all other factors being equal, a difference in PRR biases the OSR, and both shift the mating system in the same direction. For example, in many mammals, the difference in the cost C is so great between the sexes that it automatically means a strongly biased OSR as well (equation 3). Disentangling the effect of these two factors is difficult in such species. The fact that the OSR and the cost of breeding have separable effects on the mating system becomes much more easily visible, and more amenable to experimentation, in biparentally caring species such as many birds or fishes. Empirical studies focusing on "borderline cases" with almost equal investment in males and females could thus provide more fruitful information than large-scale comparative data, which easily confound the effects of the OSR and the cost of breeding.

Our model tracks the effect of many parameters on the mating system, but if we were to simplify the complexity of sexual selection to a single parameter that best predicts the mating system, it would be the cost of breeding C. This variable has a consistent influence on OSR: the sex for which breeding is costly tends to be rare. In addition, the cost on future offspring production C has a direct strong effect on choosiness, which acts together with, but is stronger than, the influence of C on the OSR. C corresponds to Trivers' definition of the cost of parental investment as a reduced ability to invest in future offspring (Trivers 1972). The cost does not have to take the specific form of our iteroparous model, where it equals the probability of dying as a consequence of the current breeding attempts. One example of a small C is provided by butterflies, most of which are described as "capital breeders" (Wiklund *et al.* 1998). When protein for eggs is accumulated during larval feeding, which cannot be resumed during adult life, processing a mating (disposing of eggs) has little or no cost on future offspring production as new eggs could not be formed in any case. By contrast, due to short adult lifespans, waiting to mate is costly for virgin females. When μ_I is high and C is small, our model predicts no choosiness in either sex, thus providing a basis for the evolution of active mate acquisition strategies – including pheromone production – in both sexes of many butterflies.

C also captures the effects of potential reproductive rates (correctly diminishing their importance if breeding has little cost in life-history terms), and where it can be interpreted as the probability of dying as a consequence of the current breeding attempt, it shares the advantage of PRR that it is often empirically easier to measure than the OSR. Focusing on the cost of breeding in terms of the life-history of the individual also provides an intuitive ground for explaining variation in choosiness: a male mammal is much more likely to survive a single copulation than a female to survive the consequences of pregnancy and lactation. Hence the female should be choosy, even in cases where she has fewer potential mates to compare than the male.

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BIOSKETCH

Hanna Kokko is interested in interactions between individual behaviour, life-history theory and population dynamics. Her work focuses especially on conflicts that underlie sexual selection, social behaviour and space use strategies.

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