Costs of breeding and their effects on the direction of sexual selection

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A recent life-history model has challenged the importance of the operational sex ratio and the potential reproductive rates of males and females as the factors most important for the control of sexual selection, arguing that the cost of breeding, interpreted as the probability of dying as a consequence of the current breeding attempt, is the single most important factor that best predicts a mating system. In one species of bushcricket, the mating system can be reversed by resource manipulation. Here, we examine the costs of breeding in this system. Consistent with the model, increased costs of breeding can explain female competition and increased male choosiness under resource limitation. However, this is due to differences in the time required for a breeding attempt, rather than differences in breeding mortality which did not differ between the sexes. In general, males lived longer than females and we discuss the possible reasons behind this pattern of sex-biased non-breeding mortality.

Keywords: cost of breeding; direction of sexual competition; choosiness; sex roles; tettigoniids; sex-biased mortality

1. INTRODUCTION

Sexual selection is widely recognized as a pervasive force in evolution, favouring morphological and behavioural adaptations that promote success in reproductive competition (Darwin 1871; Andersson 1994). Typically, males exhibit secondary sexual traits that serve as weapons with which to monopolize females and/or as signals with which to attract females for mating. Nevertheless, there are examples in which both sexes appear subject to sexual selection (Jones & Hunter 1993), or in which it is females that exhibit secondary sexual traits (Amundsen 2000; Amundsen & Forsgren 2001; LeBas *et al.* 2003). Research on animal mating systems has thus focused on understanding the factors that control variation in the direction and intensity of sexual selection (Emlen & Oring 1977; Clutton-Brock & Parker 1992; Arnold & Duvall 1994).

The proximate determinant of the direction of sexual selection is currently thought to be the operational sex ratio (OSR), the ratio of sexually active males to receptive females (Emlen & Oring 1977). Sexual selection operates on individuals of the sex which is most abundant because they must compete for the limited supply of the opposite sex. In turn, the OSR is thought to be set by the relative parental investments of the sexes (Bateman 1948; Williams 1966; Trivers 1972). Specifically, the cost of reproduction in terms of the 'time out' required to undergo and recover from a breeding attempt should be a strong determinant of the potential reproductive rate (PRR) of the sexes and hence the OSR (Clutton-Brock & Parker 1992; Parker & Simmons 1996). Empirical studies show that even when parental expenditure is not predictive of the direction of sexual selection, the relative PRR of the

sexes is (Clutton-Brock & Vincent 1991; Wiklund *et al.* 1998).

In natural populations of mammals, mortality rates are, generally, higher for males than for females and it is typically males that are the predominantly competitive sex. The degree of male biased mortality seems to be positively associated with the intensity of sexual selection acting on males (Promislow 1992; Moore & Wilson 2002). In birds, mortality is generally female biased (Promislow *et al.* 1992; Liker & Székely 2005). Here, both increased sexual competition among males during 'time in' and increased paternal care by males during time out are associated with increased male biased mortality, while female mortality is independent of sexual competition among females or levels of maternal care (Liker & Székely 2005). These data suggest that mortality costs of reproduction might be important factors in predicting the direction and intensity of sexual competition, and indeed may mitigate biases in PRR (Okuda 1999; Tershy & Croll 2000). Moreover, while a bias in the OSR may generate competition between members of the sex in excess, it need not influence sexual selection via mate choice which depends not just on the availability of members of the opposite sex, but also on the variance in mate quality (Owens & Thompson 1994; Johnstone *et al.* 1996; Kvarnemo & Simmons 1999).

Thus, Kokko & Monaghan (2001) offered a life-history based model of mating systems. In their model, the OSR became more male-biased with increases in female breeding costs (probability of dying during time out) and non-breeding mortality (during time in) and became more female-biased with increases in male breeding costs and non-breeding mortality. They showed that if breeding is costlier for females than for males, males could remain the more competitive sex even when the OSR is biased toward

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an excess of males. Increasing the cost of breeding also increased choosiness. Kokko & Monaghan (2001) suggested that focusing on 'borderline cases' with almost equal parental investment by males and females offered the best empirical approach to testing their general model.

One of the most complete empirical tests of theoretical models for the control of sexual selection comes from studies of the Australian tettigoniid, *Kawanaphila nartee*. Both sexes invest in their offspring via nutrient provisions to the egg. The male's contribution comes from the spermatophylax, a large proteinaceous mass attached to the spermatophore and consumed by the female during insemination (Simmons 1990; Simmons & Gwynne 1993). This mating system represents a borderline case in which the relative values of male and female investments vary, depending on the availability of nutrient resources in the environment (Gwynne & Simmons 1990; Simmons & Bailey 1990). When resources are limited, male expenditure on the spermatophylax exceeds female expenditure on eggs (Simmons 1992, 1994). As resource availability increases female expenditure begins to exceed male expenditure. This reversal in the relative parental expenditures of males and females generates reversals in the PRRs of the sexes which in turn shift the OSR from a female bias at low resource availability to a male bias at high resource availability (Simmons 1995). In accord with traditional sexual selection theory, there is a concomitant reversal in the direction of sexual selection, with females competing for access to choosy males when resources are limited and males competing for females when resources are abundant (Gwynne & Simmons 1990; Simmons & Bailey 1990). Variation in male mate choice is not entirely dependent on the OSR however. Variance in female quality is greater under nutrient limitation (Simmons & Bailey 1990) and Kvarnemo & Simmons (1999) showed that it is this variation in female quality that predicts male mate choice, rather than variation in the OSR *per se*.

Here we use the *K. nartee* mating system to explore how the costs of breeding for males and females covary with the nutrient-mediated reversals in the direction of sexual selection. We estimated the cost of breeding by monitoring patterns of male and female mortality in populations experimentally manipulated to have either role reversed or conventional mating systems.

2. MATERIAL AND METHODS

Animals were collected as immatures from Kings Park, Perth, Western Australia and returned to a constant temperature laboratory set at average spring conditions (12 h light at 18 °C : 12 h dark at 10 °C). Sexes were separated and maintained in population cages with constant access to water, spring flowers, and pollen granules obtained from a health food store. Animals were allowed to feed and mature for one week.

A total of 80 mature males and 80 mature females were randomly selected from the population cages and marked on the pronotum with a small spot of yellow enamel paint. Eight populations of 10 marked males and 10 marked females were established in flyscreen cages measuring 25 × 25 × 25 cm, and containing grass tree fronds and acacia sprigs. The grass tree fronds were inserted into two 150 ml vials of moist sand, which served as an oviposition substrate, while acacia sprigs were set in a small vase of water. Manipulation of resource

availability within experimental populations has been shown to generate reversals in the direction of sexual selection (Gwynne & Simmons 1990). As in Gwynne & Simmons (1990), four populations were selected at random to receive high resource availability while the remaining populations received low resource availability. Two small Petri dishes (5 cm diameter) containing a teaspoon of ground pollen were placed onto the floor of each high resource cage while each low resource cage received two empty Petri dishes. In addition, both high and low resource populations received 10 cotton swabs that had been coated in ground pollen and inserted amongst the grass tree fronds. Thus, the high resource populations could feed *ad libitum* on the supplemental pollen supplies while the low resource populations depleted their supplies within 1–2 days. Two large (38 × 38 × 38 cm) reserve population cages, one high resource and one low resource, were established at the same time as the experimental populations. Each cage contained 50 unmarked males and 50 unmarked females. The number of pollen coated cotton buds was adjusted so that the per capita amounts were similar to the experimental populations, and the cages were provided with identical oviposition substrates so that the reserve animals could breed at the same rate as the experimental animals. All populations were sprayed daily with water.

The day after populations were first established, scan samples were made 3 h after the onset of the dark cycle and the number of mated females in each experimental population determined. The peak period of mating activity occurs during the first 3 h of darkness (Simmons & Bailey 1990) and mated females are readily apparent from the presence of a spermatophore. Populations were cleaned every seventh day during the light cycle. They were provided with fresh vegetation and pollen coated cotton buds, and on alternate weeks, a small piece of fresh apple. During cleaning the number of males and females that had died in the preceding week was noted. In order to maintain the population density and sex ratio within experimental populations, dead individuals were replaced with unmarked animals of the appropriate sex and resource treatment from the reserve populations. On the day following cleaning, populations were again scan sampled to determine the numbers of matings. This procedure was repeated each week for seven weeks or until all of the marked focal individuals within a population had died. Oviposition vials were then sieved and the number of eggs counted. The experiment was terminated at seven weeks, in mid November, because although animals can live longer in the laboratory, by this time natural populations have reached their maximum lifespan, dying with the onset of high summer temperatures (Gwynne & Bailey 1988; Gwynne *et al.* 1988).

Finally, we established a further eight single sexed populations in order to monitor the mortality of non-breeding animals. Unmated females will mature eggs (L. W. Simmons, unpublished observations). Therefore, in these cages grass tree fronds were placed in an empty vial so that there was no substrate available for females to lay any eggs that they may have developed.

3. RESULTS

Consistent with previous experimental manipulations of this species, variation in resource availability had a significant impact on the reproductive outputs of breeding

Figure 1. Survival curves for male (blue) and female (red) *Kawanaphila nartee* in experimental populations with either (a) high resource or (b) low resource availability (solid lines are for breeding animals, broken lines are for non-breeding animals).

males and females. There were significantly more matings, and thus spermatophores donated, in low resource populations than in high resource populations (cumulative mean ± 1 s.e. number of matings observed on the weekly census: low 7.3 ± 1.0 , high 2.5 ± 0.9 , $t_6 = 3.38$, $p = 0.015$) and the number of eggs laid was lower in the low resource populations than in the high resource populations (mean total number of eggs laid over the seven weeks: low 129 ± 15 , high 300 ± 26 , $t_6 = 5.70$, $p = 0.001$). Thus, as with previous manipulations, breeding males invested more in reproduction and breeding females less in low resource populations compared with high resource populations.

Survival data were analysed using the non-parametric Cox regression. We asked whether there was an effect of resource availability and sex on mortality in our breeding populations, and whether there was a reversal in any sex differences in mortality across our resource availability treatments which would be revealed by a significant resource by sex interaction. We also confirmed that there were no significant differences between cages nested within resource availability treatments. The whole model was significant ($\chi^2_9 = 76.3$, $p < 0.0001$). Mortality was significantly higher in low resource populations than in

Table 1. Lifespan (mean $\pm$ s.e. weeks) of breeding and non-breeding male and female *Kawanaphila nartee* in experimental populations with high and low resource availability.

	males		females	
resources	non-breeding	breeding	non-breeding	breeding
high	6.7 ± 0.2	6.3 ± 0.3	5.4 ± 0.3	5.2 ± 0.4
low	5.2 ± 0.4	2.7 ± 0.3	3.8 ± 0.4	2.1 ± 0.2

high resource populations ($\chi^2_1 = 67.7$, $p < 0.0001$) and females had a higher mortality than males ($\chi^2_1 = 11.2$, $p < 0.001$). There was no resource by sex interaction ($\chi^2_1 = 2.8$, $p = 0.100$; figure 1) and no differences in mortality between cages within the resource availability treatments ($\chi^2_6 = 5.5$, $p = 0.486$). The average lifespans of breeding males and females are shown in table 1. Note that although data were left censored, observations were stopped when animals could no longer be found in the field so that these are biologically real lifespans.

There was also a significant effect of sex and resource availability on mortality in non-breeding populations (whole model $\chi^2_7 = 43.8$, $p < 0.0001$; effect of sex $\chi^2_1 = 36.0$, $p < 0.0001$; resource availability $\chi^2_1 = 11.2$, $p = 0.0008$). Although, the interaction between resource availability and sex was not significant ($\chi^2_1 = 3.4$, $p = 0.07$) there was a strong trend for non-breeding males to be relatively less affected by low resource availability than non-breeding females (figure 1, table 1). There were no significant cage effects (cage nested within resource availability and sex, $\chi^2_4 = 1.8$, $p = 0.78$).

The data presented in figure 1 and table 1 suggest that breeding reduced lifespan for males and females. Because we could find no significant cage effects for either our breeding or non-breeding populations, we pooled data across cages to formally test for a cost of breeding. The whole model was again significant ($\chi^2_1 = 143.7$, $p < 0.0001$). Resource availability ($\chi^2_1 = 71.1$, $p < 0.0001$) sex ($\chi^2_1 = 22.2$, $p < 0.0001$) and breeding ($\chi^2_1 = 31.6$, $p < 0.0001$) all had significant effects on the patterns of mortality. The interaction between these three factors was not significant ($\chi^2_1 = 0.1$, $p = 0.71$) and was therefore removed from the model. There was a significant interaction between resource availability and sex ($\chi^2_1 = 4.3$, $p = 0.037$), a strong trend between resource availability and breeding ($\chi^2_1 = 3.6$, $p = 0.057$), but no interaction between sex and breeding ($\chi^2_1 = 0.56$, $p = 0.455$). Thus, females suffered a, generally, higher mortality under resource limitation, both males and females suffered an equal cost of breeding, and the cost of breeding tended to be elevated by resource limitation (figure 1).

4. DISCUSSION

In their life-history model, Kokko & Monaghan (2001) calculated the cost of breeding as the probability of dying during a breeding attempt, $\mu_0/T(1 + \mu_0)$, where μ_0 is the rate of dying while breeding and T is the time out required to complete a breeding attempt. Their model predicted that males would become the more competitive sex when the cost of breeding for males exceeded that for females and/or when the non-breeding mortality for females

exceeded that for males (eqn (4) in Kokko & Monaghan 2001). That is, breeding and non-breeding mortality have opposite effects on the direction of sexual competition.

Our data show that non-breeding mortality is greater for females than it is for males which should have the effect of biasing the OSR toward an excess of males. However, our data also show breeding mortality to be considerably higher than non-breeding mortality and that males and females suffer the same rate of mortality due to breeding, irrespective of resource abundance, $\mu_{0\text{males}} = \mu_{0\text{females}}$. We know that time out due to breeding varies greatly with resource abundance; when resources are abundant female time out is an order of magnitude higher than male time out but when resources are limited male time out can exceed female time out (Simmons 1995). Thus, consistent with Kokko & Monaghan's (2001) model, under resource abundance male competition will be associated with a higher cost of breeding for females (probability of dying as a result of a single breeding attempt) because $T_{\text{females}} > T_{\text{males}}$. Conversely, under resource limitation female competition will be associated with a higher cost of breeding for males because $T_{\text{females}} < T_{\text{males}}$. These changes in time out will result in corresponding changes in the OSR, from a male bias under resource abundance to a female bias under resource limitation.

Kokko & Monaghan (2001) stated that if they were to simplify the complexity of sexual selection to a single parameter that best predicted a mating system, it would be the mortality cost of breeding. Our data for *K. nartee* show that this is true only to the extent that males and females vary in the time out (T) required for a breeding attempt so that traditional models based on PRR (Clutton-Brock & Parker 1992; Parker & Simmons 1996) are perfectly adequate to explain the mating system. We doubt whether the complexity of sexual selection could ever be reduced to a single parameter. Nevertheless, we feel that time out is likely to be a more reliable predictor of a mating system than breeding mortality. In many animals, mating competition is found to vary substantially within species, both in space and time (Kvarnemo and Ahnesjö 1996, 2002; Forsgren *et al.* 2004). This is also true for *K. nartee*, which can shift from one sex-role to another almost over night (Gwynne *et al.* 1998). Hence, it seems unlikely that long term changes in breeding mortality would be able to govern such highly flexible and dynamic shifts in mating competition as are found in *K. nartee* and many other species. Rather, it may be that sexual equality in breeding mortality, as found here for *K. nartee*, characterize these borderline cases and environmental fluctuations that influence the PRR and thus the OSR (Simmons 1995) generate dynamic shifts in the direction of sexual competition in such systems.

Kokko and Monaghan's (2001) model also suggested that the cost of breeding can have a direct effect on mate choosiness. Increased costs of breeding were predicted to result in an increase in choosiness. Our data for *K. nartee* show that resource limitation resulted in a substantial increase in mortality for non-breeding males and females and that mortality due to breeding tended to be further elevated. In both natural (Simmons & Bailey 1990) and experimental populations (Gwynne & Simmons 1990) resource limitation is associated with an increase in male choosiness but a decrease in female choosiness. An important parameter to consider in predicting choosiness

is variance in mate quality (Johnstone *et al.* 1996; Kvarnemo & Simmons 1999). Female variance in fecundity, and thus mate quality, depends on resource abundance, being greater under resource limitation (Simmons & Bailey 1990). However, male mate quality, in terms of the amount of resources provided in the spermatophylax, does not depend on resource abundance (Simmons & Bailey 1990; Simmons 1994). In Kokko & Monaghan's model, high variance in female quality is associated with a large parameter space in which male choice is expected while low variance in male quality is associated with a small parameter space in which female choice is expected (see fig. 2 in Kokko & Monaghan 2001). Thus, the observation that increased costs of breeding under resource limitation is associated with elevated male choice but not female choice is consistent with Kokko & Monaghan's (2001) life-history model.

Why do male *K. nartee* live longer than females? Sex-biased patterns of mortality are a widespread feature of animal life-histories (Promislow 2003). In mammals females tend to be the longer lived sex (Promislow 1992) while in birds it is males (Promislow *et al.* 1992). Among insects the patterns are mixed; in *Drosophila* spp. there are cases of both male and female biased mortality (Promislow & Haselkorn 2002), while in bean weevils, *Collosobruchus maculatus*, there is male biased mortality (Tatar & Carey 1994; Fox *et al.* 1999) and in butterflies mortality can be male biased or unbiased (Gotthard *et al.* 2000; Wiklund *et al.* 2003). Evolutionary life-history theories of ageing argue that patterns of mortality are adaptive (Williams 1957; Kirkwood & Rose 1991; Stearns 1992). Consistent with these theories, there is genetic variation in longevity (e.g. Zwaan *et al.* 1995; Fox *et al.* 1999) and patterns of sex specific mortality seem to reflect differences in selection pressures operating on males and females. Thus, in birds (Promislow *et al.* 1992; Liker & Székely 2005) and mammals (Promislow 1992; Moore & Wilson 2002), male mortality seems to be associated with the costs of secondary sexual trait development and male contest competition, as predicted by Trivers (1972). In birds, male biased mortality also increases with the degree of paternal care (Liker and Székely 2005) so that Kokko and Monaghan's (2001) models predict a general reduction in sexual competition amongst male birds as the levels of paternal care increase. In butterflies, the degree of male biased mortality appears to be associated with the temporal availability of mates; in the monandrous peacock butterfly, *Inachus io*, there is a short mating period at the beginning of the breeding season which should not favour males with long lifespans, and consistently, male *I. io* do have a shorter lifespan than females (Wiklund *et al.* 2003). In contrast, the polyandrous comma butterfly, *Polygonia c-album*, has a long mating season which is predicted to favour longer lifespans in both sexes, and consistently there is no sex-bias in mortality in this species (Wiklund *et al.* 2003). Likewise in the monandrous speckled wood butterfly, *Pararge aegeria*, mortality is male biased in northern latitudes where the breeding season is short but is unbiased in tropical latitudes where the breeding season is continuous (Gotthard *et al.* 2000).

In *K. nartee*, there is a relatively short breeding season and the majority of matings occur early, when resources are limited (Simmons & Bailey 1990). For males then, we might expect selection to favour early reproduction at the

expense of prolonged lifespan. This temporal pattern would predict shorter male than female lifespans, a pattern opposite to that observed. Thus, unlike butterflies (Wiklund *et al.* 2003), the observed mortality bias in *K. nartee* cannot be explained by temporal variation in mating opportunities. An alternative explanation put forward for sex-biased mortality is that mutations on the X-chromosome are unguarded in the heterogametic sex resulting in mortality biased toward that sex (Trivers 1985). The difference between mammals and birds is in the direction expected under this hypothesis because male mammals are XY and female birds are ZW. However, *K. nartee* males are XO (Rentz 1993) so that they would be predicted to have the higher mortality, which was not the case. Thus, sex-biased mortality in *K. nartee* cannot be explained by mutations on the unguarded X chromosome. Although, we are unable to make firm conclusions, we suggest that the prolonged period of sexual competition between females during the early spring, when resources are limited, may have favoured traits that enhance early performance in female contest competition (Simmons & Bailey 1990; Gwynne & Bailey 1999) at a cost to lifespan (*sensu* Williams 1957).

In conclusion, our data for *K. nartee* provide support for a recently proposed life-history based model in which the relative costs of breeding (defined as the probability of dying during a single breeding attempt) are predicted to generate variation in the direction of sexual competition and mate choosiness. Nevertheless, our data suggest that the relative costs of breeding are only important insofar as they incorporate the time costs associated with a single breeding attempt. Mortality due to breeding is equal for male and female *K. nartee* and shifts in the direction of sexual competition are determined directly by the PRRs of males and females which determine the OSR.

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