



Do males matter? The role of males in population dynamics

Daniel J. Rankin and Hanna Kokko

D. J. Rankin (daniel.rankin@helsinki.fi) and H. Kokko, Dept of Biological and Environmental Science, Univ. of Helsinki, PO Box 65 (Viikinkaari 1), FI-00014 Helsinki, Finland.

Models of population dynamics generally neglect the presence of males. While this assumption holds under many circumstances, behavioural ecology increasingly tells us that the presence (or absence) of males may have an impact on female fitness, and hence population sizes. Here we ask the question of whether males matter to population dynamics, operationally defined as a dependency of population growth on the relative density of males. We provide simple models, and evaluate the current empirical evidence for them, that illustrate various mechanisms of such male influence: mate searching behavior, male resource use (including effects of sexual dimorphism), sexual harassment and sexual segregation. In each case, theory predicts that males can have an effect on population densities, and in some extreme cases a positive feedback between an increasingly male-biased sex ratio and female harassment may theoretically even bring about population extinction. The results of this study, and the literature reviewed, show that the males can have a substantial effect on population dynamics, particularly so when human influences result in biased sex ratios.

The majority of population dynamical models only view the population from the female point of view (Caswell 2001). This assumption makes life rather simple, and allows for mathematical tractability in more complicated models of populations (May 1976). The logic behind the assumption is that males will be born and die at the same rate as females. This means that the sex ratio is always even, and the female density therefore constitutes half of the total population density.

The assumptions used in single-sex models hold under limited conditions, where models assume that male availability does not limit female reproduction, the sex-ratio is even, and male life history does not differ from that of females (Caswell and Weeks 1986, Lindström and Kokko 1998, Engen et al. 2003). If such assumptions are fulfilled, a model incorporating two sexes will always produce a total population that is twice the number of females, rendering the explicit incorporation of males unnecessary. If the presence and behaviour of males does have a discernible influence on population equilibria or stability, one-sex population models should be abandoned in favour of two-sex models, particularly when thinking about conservation

(Sæther et al. 2004) or biological control programmes (Ferguson et al. 2005, Schliekelman et al. 2005).

It is now increasingly recognised that the presence and behaviour of males may matter to population processes. Even in a 'null model' in which males do not impact female fitness directly, if male and female numbers contribute equally to density-dependence removing males will increase the population density as there will be more room for females (Clutton-Brock et al. 2002). Table 1 details other ways in which males may have a positive or negative effect on population densities. This can occur, for example, through sexual harassment of females, males having a larger influence on resource availability than females, and a lack of males being a limiting factor in female fertilisation (Mysterud et al. 2002, Møller 2003, Bessa-Gomes et al. 2004). Behaviour related to mate choice has been shown to have an influence on population processes (Doherty et al. 2003, Kokko and Brooks 2003, Møller 2003, Morrow and Pitcher 2003) and recent studies have examined whether different mating systems can play a role in the extinction risk of a population (Milner-Gulland et al. 2003, Bessa-Gomes et al. 2004, Le Galliard et al. 2005).

Table 1. Generalised effects of removing males on overall population density.

The effect of removing males on population density	
Density increases	Density decreases
Density dependence	Sperm limitation
Higher male resource requirement	Parental care
Sexual segregation	Sexual segregation
Sexual harassment	Male nuptial gifts
Disease transmission	Infanticide

Here our aim is to provide an overview of various mechanisms of how males may “matter” to the growth of populations. As an operational definition, males “matter” if population growth at a given female density depends on the relative density of males. We will present simple two-sex models of population growth, using equilibrium population densities to illustrate the point that male effects on dynamics are not transient but will impact carrying capacities. We review empirical studies, in each case assessing how likely it is to encounter scenarios where ‘males matter’ in natural populations, and whether there is a sense in which we can state these effects to be ‘positive’ or ‘negative’.

Mate finding and sperm limitation

When considering whether or not males matter we must first think about various factors which influence their presence in natural populations. There are many biological and anthropogenic factors which can influence the sex ratio. Local mate competition (Hamilton 1967), temperature in poikilotherms (Janzen and Paukstis 1991), and male killers such as *Wolbachia* (Dyson and Hurst 2004) can influence the number of males born, and therefore the adult sex ratio. Perhaps much more commonly, the adult sex ratio will also be biased if males follow different life history schedules than females (e.g. due to lack or presence of paternal investment, or mortality due to male-male contests and costly sexually-dimorphic ornaments). While these natural causes can influence population dynamics, understanding the dynamics becomes especially important if humans influence the sex ratio, for example through selective hunting of males.

In many models in both sexual selection and population ecology, it is frequently assumed that female reproduction is not limited by the number of males (Andersson 1994, Caswell 2001). In models of sexual selection, for example, it is often females who are limiting and the assumption that a female will always find a mate is widespread throughout the literature (but see Kokko and Mappes 2005). However, examples are accumulating that male ejaculates are not always cost-

free to produce, and females can consequently become sperm limited (Wedell et al. 2002).

How likely is it that this limitation also has population-level consequences? Models that consider strictly monogamous populations suggest that population dynamics will be very sensitive to alterations in the sex ratio (Bessa-Gomes et al. 2004), and any process that removes males under monogamy could thus have disastrous effects on populations. Strict monogamy is, however, rare across taxa, and it is therefore important to examine how strong sperm limitation has to be before it has considerable population-level consequences. We illustrate the logic with a simple model of the dynamics of a sexual population, with densities of both males and females specified as M and F , respectively. For simplicity, we consider a continuous-time setting. The density dependent death rates of males and females are written as g_M and g_F , respectively. Birth will depend on the primary sex ratio r , the maximum birth rate of a fully fertilised female b , weighted by the probability that a given female will be fertilised. The general dynamics of males and females is therefore

$$\begin{aligned} \frac{dM}{dt} &= f(F, M)brF - g_M(F, M)M \\ \frac{dF}{dt} &= f(F, M)b(1 - r)F - g_F(F, M)F \end{aligned} \quad (1)$$

where birth depends, most importantly, on the number of females and the fertilisation probability $f(F, M)$, but will also be affected by the number of males M and thus by the primary sex ratio r . Density dependent death is given by the function $g_i(F, M)$ where i represents the mortality of either males (M) or females (F), and will depend on the total number of individuals in the population, i.e. both F and M .

Assuming that males and females consume identical amounts of resources, we can write the death rate as a function of the sum $M + F$. The simplest function is of the form $g_i(F, M) = (M + F)\delta_i$, where the death rate δ_i can be sex-specific and the overall death rate increases linearly with the addition of each male and female in the population.

Fertilization success depends on how efficiently individuals search for mates. Here we opt for a simple function, which describes the probability of a given female being fertilised as a function of sex ratio as $f(F, M) = x/(x + c)$ (Fig. 1a), where x is the adult sex ratio (ASR, the proportion of adult males in the population). As the relative density of males decreases, so does the per capita fecundity. Such a function has been found when males are severely limiting (Milner-Gulland et al. 2003). The shape of the function is determined by c . Very low values of c are likely to be more realistic, as we can assume that sperm limitation

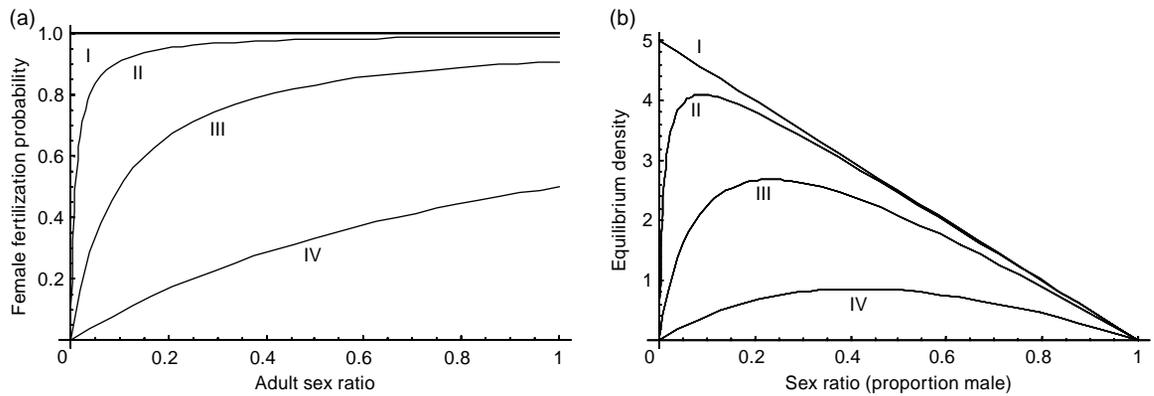


Fig. 1. (a) The fertilization probability of a female as a function of the adult sex ratio (ASR, proportion of adult males). (b) The influence of male mortality on the equilibrium population density (i.e. the total number of males and females) for different sensitivities to ASR (I–IV). The different lines represent different sensitivities of fertilization probability to changes in the ASR: $c = 0$ (I), $c = 0.01$ (II), $c = 0.1$ (III), $c = 1.0$ (IV). The adult sex ratio is manipulated by changing the primary sex-ratio r . Other parameters are $b = 50$, $\delta_F = 10$ and $\delta_M = 10$.

only comes in to play when there are very few males (Milner-Gulland et al. 2003), but we also consider other shapes of this function.

Figure 1b shows how the primary sex ratio (proportion of males) affects the carrying capacity. It can be seen that male-biased sex-ratios result in lower population densities. However, under high sperm limitation, female-biased sex ratios can also reduce population density as fewer females are fertilised. This depends on the efficiency with which males can fertilize females. Even if sperm limitation does not limit populations at all (i.e. $c = 0$), a male-biased sex-ratio will still result in a linear decline in density, due to there being less “space” for females (Clutton-Brock et al. 2002).

Unsurprisingly, the efficiency with which the two sexes find each other (parameter c) has a strong effect on population performance. An assessment of how often sperm limitation truly influences population growth therefore requires estimating functions depicted in Fig. 1a. In many instances, population growth appears to be sustained despite very low relative male densities, suggestive of a very low c . Extreme sex-ratio biases due to factors such as male killers provide clear examples: in the butterfly *Hypolimna bolina*, male-killing *Wolbachia* has been found to dramatically decrease the number of males by manipulating females into only producing other females. As a result of this, the population of butterflies in western Samoa has been found to have 1.1% males in the population (Dyson and Hurst 2004). As the population still remains viable, such an extreme sex-ratio bias suggests that a very small number of males can fertilise a large number of females.

Still, the butterfly study documented significant declines (averaging 57%) in female fecundity when persisting with *Wolbachia* (Dyson and Hurst 2004).

Less extreme polygynous examples have also yielded evidence for sensitivities to sperm limitation. The problem is perhaps best studied in ungulates, and here the conclusions vary: despite the lack of male parental care, per capita female reproduction suffers in some species when the sex ratio becomes female-biased (Kokko et al. 2001, Myrsterud et al. 2002). It is noteworthy that management options usually include targeting males, both because of their larger size and potential for trophy hunting, and for the sake of sparing females to produce young. However, such a management strategy is based on the ability of males to fertilize many females, and this may push the sex ratio at which maximal offspring production occurs very close to the threshold under which sperm limitation has a sudden and severe impact on population growth (Kokko et al. 2001). A spectacular example has occurred in the Saiga antelope, where selective hunting of males has led to a reduction in male density to the point where many females have become unable to find a mate, reducing the population density to dangerously low levels (Milner-Gulland et al. 2003).

Since female fitness is strongly determined by her own offspring production, any problems related to sperm limitation should provoke an evolutionary response in females. To alleviate problems of sperm limitation, we may expect females to evolve adaptations ranging from appropriately reduced choosiness (Kokko and Mappes 2005) to pheromone production (Svensson 1996). However, as the Saiga antelope example shows, the efficiency of such mechanisms can be seriously compromised when novel environmental scenarios are encountered, and such cases may be common if populations currently exist at lower densities than they have typically encountered during their evolutionary history (Kokko and Mappes 2005). At

present, it is perhaps therefore best concluded that sperm limitation is a possible mechanism through which “males matter”, although the conclusion from the model and empirical evidence would suggest that the effect will be weak in the absence of highly skewed ratios (Milner-Gulland et al. 2003). The abruptness of the relationship between fecundity and relative male density (Fig. 1a) makes it a difficult but important function to estimate empirically.

Male mating strategies

As well as the problems of finding a mate, female fitness itself may be directly and negatively affected by the behaviour of males in the population. Sexual conflict, loosely defined as occurring when males and females do not share a common interest (Chapman et al. 2003, Arnqvist and Rowe 2005, Tregenza et al. 2006), can reduce female fitness through factors such as male harassment (Réale et al. 1996). A consequence of anisogamy is that it is often more advantageous for males to mate multiply than for females (reviewed by Kokko et al. 2006). Increased mating rates may cause a reduction in female fitness through male harm, but whether this has population consequences is debated (Kokko and Brooks 2003, Rowe and Day 2006).

The extent of male harassment will depend on the mating rate (Arnqvist et al. 2005), which in turn may be profoundly influenced by both the sex ratio (Le Galliard et al. 2005) and the density of individuals (Kokko and Rankin 2006). Altering the sex ratio or density of males in the population could increase the extent to which harassment affects population processes, and thus bears examination in the context of this paper. If there are costs of mating, these will depend not only on the sex ratio and density of individuals, but will be inextricably linked to the mating system; if matings impose costs on females, those mating with only one male should suffer less than multiply mating females.

We therefore extend the simple model above to account for male harassment. The same assumptions about both males and females apply as above. However, now we introduce the function h to describe additional female mortality due to male harassment. The dynamics are now described by the following equations:

$$\frac{dM}{dt} = rbF - g_M(F, M)M \quad (2a)$$

$$\frac{dF}{dt} = b(1-r)F - g_F(F, M)F - h(F, M)F \quad (2b)$$

Equation 2a and 2b describe the dynamics of both males and females, respectively. The first expressions deal with birth, and the latter deal with death, in a manner similar to Eq. 1. In this model we are interested

in how the mating rate affects female survival, and so we must take into account the fact that an increasing mating rate has a negative impact on survival. The per capita mortality h due to harassment of females is determined by the density of males and females, and we provide an example that makes use of the following function:

$$h(F, M) = k \left(\frac{M}{(1-\alpha)F + \alpha} \right)^\gamma \quad (3)$$

Here k scales the intensity of harassment. One could envisage that the harassment experienced by females depends either on the sex ratio or, alternatively, more directly on male density irrespective of the number of males per female. To be able to model either extreme as well as intermediate cases, we include the parameter α that measures the extent to which the mating system depends on either sex ratio or male density ($\alpha=0$ denotes a sex-ratio determined mating system, and $\alpha=1$ denotes a mating system determined by male density). The parameter γ determines how strongly harassment depends on either of the factors mentioned above. When $\gamma=0$, then harassment occurs independently of either the proportion or number of males in the population.

The model can be investigated for varying levels of male mortality δ_M (Fig. 2). As male mortality decreases, the population becomes more male-biased, and there is an increase in female mortality which causes the overall population size to decline (Fig. 2a). The model described here incorporates a positive feedback between male density and population density (Crespi 2004); the more males there are in the population, the more females will suffer from harassment females. This reduces the number of females in the population relative to males, which increases the level of harassment, and the process may continue until population persistence is threatened. The final outcome depends on the mating system (Fig. 2a). Catastrophic outcomes can occur if the mating system is influenced more strongly by the proportion of males in the population, rather than absolute density. This results in the complete extinction of the population, where harassment drives disproportionate levels where the population can no longer be sustained (Fig. 2a, III). This is in stark contrast to the somewhat unrealistic case where the level of harassment is independent of the proportion or density of males ($\gamma=0$, Fig. 2a, I). In this case the population density remains unchanged regardless of the density of males; in such a case an asexual approximation would be appropriate.

As discussed above, our model shows that the results of harassment should depend very much on the extent to which the mating rate depends on the sex ratio or population density. This has long been realised in

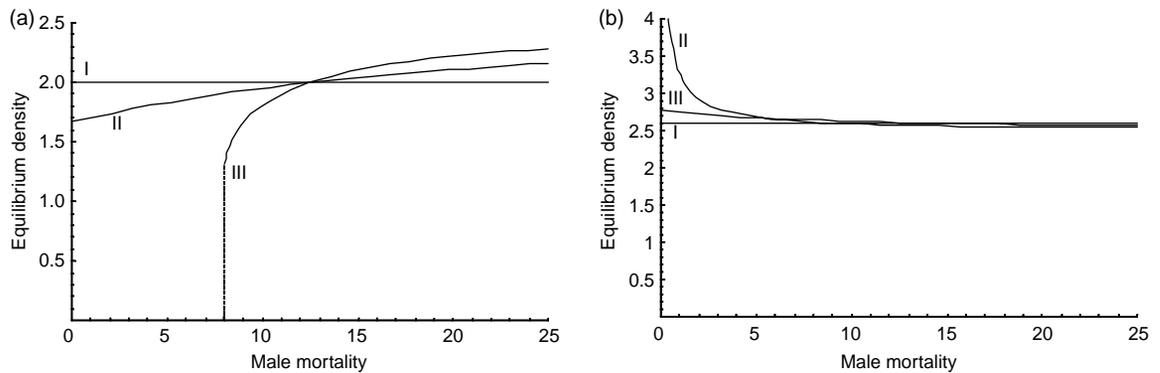


Fig. 2. The equilibrium population density (total number of males and females) as a function of male mortality, where males inflict direct costs on females (Fig. 2a, $k = 1$) or provide direct benefits (Fig. 2b, $k = -1$). Three scenarios are represented by the lines: I male harassment of females not influenced by male density ($\gamma = 0$), II male harassment of females influenced by male density ($\gamma = 1$, $\alpha = 1$) and III male harassment of females influenced by the sex ratio ($\gamma = 1$, $\alpha = 0$). Other parameters are $b = 50$, $\delta_F = 10$ and $r = 0.5$. The dotted line represents the point where the population is driven to extinction; zero is the only stable equilibrium in this case. Only stable equilibrium points are shown. Note the difference in scale between Fig. 2a and 2b.

behavioural ecology, and several studies of sexual conflict have manipulated male harassment by simply altering the sex ratio (Holland and Rice 1999, Wigby and Chapman 2004). Obviously, manipulating the mating rate is one way in which females can reduce the impact of male harassment (Arnqvist and Nilsson 2000), and in systems in which sexual conflict is prevalent, an increase in the mating rate will impose more costs on the females, subsequently reducing population density. If costs increase with mating rate, females are predicted to mate at an intermediate rate in order to maximise their fitness (Arnqvist and Nilsson 2000).

A similar result to that shown in Fig. 2a has been studied in the common lizard *Lacerta vivipara*. By simply manipulating the adult sex ratio, Le Galliard and colleagues found that male-biased populations were much more prone to sexual conflict than were female-biased populations (Le Galliard et al. 2005). Comparing female and male biased populations, the authors found a severe decline in both female survival and fecundity under male bias (Le Galliard et al. 2005). A greater rate of injury to females, revealed by a higher number of mating scars, gave strong support to the prediction that more males would lead to more harassment. If a higher relative density of males in a population increases female mortality, then the sex-ratio should become more male-biased in the future, perpetuating a high level of harassment in the population. A model revealed that if such harassment continued, the positive feedback between male density and declining female densities could ultimately result in the population being driven extinct within 40 years (Le Galliard et al. 2005).

The resulting extinction may be seen as something analogous to the tragedy of the commons (Hardin

1968, Rankin and Kokko 2006), as it is to the male's advantage to compete for females, even if this reduces female survival. While there have been a number of studies examining the influence of sexual selection in general on population density and extinction risk (reviewed by Kokko and Brooks 2003), to our knowledge this is the first looking at the population-level consequences of sexual conflict as a result of sex-ratio manipulations.

The extent to which sexual conflict affects population processes is still in its infancy. The study of Le Galliard and colleagues (Le Galliard et al. 2005) remains unique, in that it explicitly considers the population consequences of male harassment. However, the capacity for such consequences is large, as there are many examples in the literature of how males can affect female fitness through various mating strategies. Males of red-sided garter snakes *Thamnophis sirtalis parietalis* which are too eager to mate can end up strangling the females, a factor which no-doubt increases female mortality (Shine et al. 2001). In feral sheep, sexual harassment by males has also been shown to increase female mortality during the mating season (Réale et al. 1996).

One of the most curious examples of sexual conflict is the spiked penis of the been weevil *Callosobruchus maculatus* (Crudgington and Siva-Jothy 2000). It is known that these spines puncture the female reproductive tract during mating, and it has been suggested that females kick males to reduce the cost of mating (Crudgington and Siva-Jothy 2000). One study found that the spines may have evolved as a side-adaptation, rather than to aid males in sperm competition, demonstrated by the fact that preventing females from kicking during their second copulation did not make the second mates more successful in sperm competition

(Edvardsson and Tregenza 2005). The role of female counteradaptations is clearly underexplored. Female resistance may itself incur fecundity or survival costs through investment in avoidance strategies (Croft et al. 2006), and thus it may not be sufficient enough to buffer the effect of male harm on population densities.

The prevalence of sexual conflict in the animal kingdom leads to the inevitable question of how male harassment can persist, given that it has the potential to impose extreme costs on the population. Population ecology itself may offer one explanation. If males can have a negative effect on population density, then they effectively change the environment under which selection operates (Kokko and Rankin 2006). The reduction in the absolute numbers of males and females may make it less advantageous for males to attempt to monopolise females, resulting in less overall sexual harassment, and a lesser impact on population processes. However, empirical evidence is so far both limited and conflicting (Kokko and Rankin 2006). There is also the question whether males can exhibit sufficiently fast evolutionary responses to counteract a process that occurs over ecological time (Fig. 2a). The feedback between population processes and behaviour may be an important factor influencing the behaviour, and further study is much needed.

Mating with many partners inevitably increases the risk of contracting sexually transmitted diseases (STDs), a factor which can be seen as having the same effect as male harassment when it reduces female lifespan or fecundity. The model presented above can also be interpreted in terms of the risk to a female of contracting a sexually transmitted disease, where a higher mating rate will lead to more individuals becoming infected with STDs, and thus a lower population density. Sexually transmitted diseases are often expected to be more prevalent in females than in males, mainly due to the variance in male reproductive success that leaves some males without a chance to mate (Thrall et al. 2000). The sex of a host can also make a difference to the transmission of parasites, thus male behaviour can also matter in the spread of disease in general and not just in the context of STDs (Skorping and Jensen 2004).

Infanticide

Another way in which male behaviour may negatively affect female fitness is infanticide. In the above examples we have seen that removing males can, under some circumstances, lead to higher population densities through freeing resources and reducing the level of harassment of females. Even though infanticide when performed by males is a 'negative' behaviour in terms of population performance, it differs from the earlier

examples in that it can increase when males are removed. Killing males can result in male replacement, and the replacing male may kill the offspring of any previously present males in order to increase his reproductive success (Swenson et al. 1997, Møller 2004, Whitman et al. 2004). Selective hunting of males has been shown to result in infanticide in both brown bears (*Ursus arctos*) and African lions (*Panthera leo*). In lions, removing a male typically makes a coalition more vulnerable to a takeover by an outside male (Whitman et al. 2004). When this happens, the incoming male will typically evict all older male lions, and kill all cubs under 9 months old (Whitman et al. 2004).

Modelling the impact of infanticide on population density suggests that an increase in infanticide caused by removing males from the population can increase the risk of population extinction (Whitman et al. 2004). However, this result depends on the age of the males that are hunted, and reducing the hunting of younger males should allow them to rear a cohort of young, reducing the prevalence of infanticide (Whitman et al. 2004). In brown bears, infanticide caused by selective hunting can lead to a dramatic decline in cub survival (Swenson et al. 1997). Comparing populations with and without selective hunting of males revealed that infanticide was responsible for reduced cub survival, which led the authors to predict that removing one adult male from the population was equivalent to killing between 0.5 and 1 female (Swenson et al. 1997). Hunted populations of bears are predicted to be highly susceptible to population extinction (Wiegand et al. 2001), and infanticide may be one important factor of this. Finally, there is experimental support for the importance of infanticide in shaping population dynamics: a field experiment in which male root voles (*Microtus oeconomus*) were removed nearly halved population growth (Andreassen and Gundersen 2006).

Infanticide, in combination with the possibility of sperm limitation, could exacerbate the effects of selectively hunting males, as fecundity is reduced both by decreasing the probability that a female is fertilized and an increased likelihood of infanticide. In the barn swallow, *Hirundo rustica*, for example, male quality was negatively associated with the degree of infanticide in the population due to the ability of males to defend nests against infanticidal males (Møller 2004). However, the same study also found that, at lower population densities, infanticide was less prevalent, most likely due to a relatively higher proportion of males that are able to find a mate (Møller 2004). Such a density-dependent effect could potentially reduce the risk that infanticide poses to the population by reducing its prevalence as the population approaches low density (see also Kokko and Rankin 2006).

Not all males are nasty

As a caveat, it should be noted that males can also influence female fitness in a positive way, by providing direct benefits for females they mate with (Møller and Jennions 2001). In this paper we have contrasted the fundamental reason why females require males, i.e. their fertilization ability, with several potential negative effects that males can have on female fitness.

In species with biparental care (Trivers 1972), removing the social mate can have particularly negative impacts, as the social mate is probably the only male willing to provide paternal care, and he may also defend the female against other male intruders (Sergio and Bogliani 2001). It has been shown that male parental care can increase the survival and number of offspring (Johnson et al. 1993, Reid et al. 2002, Wright 2006).

Consider a case where a single-parent brood has lower survival than a brood biparentally cared for. Despite a tradeoff between abandoning a nest and offspring survival, females may benefit by abandoning a brood to nest elsewhere if this allows them to found a new nest (Székely and Cuthill 2000). Thus, if females use male parental care efforts in this way, the reproductive output of the population could significantly increase: such a solution is possible if two parents caring each for their own brood (as, for example, in some shorebirds) result in more surviving offspring than two parents caring for the same brood. In general, removing males can have a significant influence on population recruitment in species with paternal or biparental care.

Males can also provide direct benefits to females through substances transferred in seminal fluids (Møller and Jennions 2001). Because of this, females mating at intermediate mating rates may have lower fitness than those with higher mating rates, as they miss out on the beneficial nuptial gifts provided by males (Arnqvist et al. 2005). For such situations, we look at the case when $k = -1$, in the model presented by Eq. 2, to look at how increased mating may increase female fecundity through direct benefits provided by males (Fig. 2b). In such a case, we find that density increases with the proportion of males, and again this depends on whether the mating rate is based on the sex ratio or the absolute density of males. Interestingly, after a certain amount of male mortality, male deaths no longer have a discernable influence on the absolute density, suggesting that the effects of direct benefits are mostly important when there are very many males in the population (Fig. 2b).

Sexual dimorphism and resource use

In Figs. 1 and 2, we assumed a simple form of density dependence in which males and females had equal

effects on the carrying capacity: adding one individual of either sex diminishes resource availability equally between both sexes. However, sexual selection often leads to size dimorphism (Fairbairn 1997). In birds and mammals, males are often larger than females, while female-biased sexual size dimorphism (hereafter SSD) predominates among invertebrates and poikilothermic vertebrates (Fairbairn 1997). Assuming that males and females use the same niche, resource use increases with body size, and the resource in question plays a central role in density dependence, we can expect that sex ratios will have an effect on resource availability and hence the growth rate of a population, with obvious management implications (Langvatn and Loison 1999, Matsuda et al. 1999, Clutton-Brock et al. 2002).

We can illustrate this phenomenon using the model above (Eq. 1). For simplicity, we shall now assume that sperm is not limiting, and that therefore $f(F,M) = 1$. Equation 1 can still be used to describe the dynamics, but $g_i(F,M)$ is now written as $g_i(FM) = (\theta_M M + \theta_F F)\delta_i$, where θ represents the effect of males and females on the carrying capacity. We can scale θ_M and θ_F so that they are relative to each other: $\theta = \theta_M/\theta_F$, so the function becomes $g_i(F,M) = (\theta M + F)\delta_i$. This allows us to re-write Eq. 1 as:

$$\begin{aligned}\frac{dM}{dt} &= brF - (\theta M + F)\delta_M M \\ \frac{dF}{dt} &= b(1-r)F - (\theta M + F)\delta_F F\end{aligned}\quad (4)$$

If sexes do not differ in their mortalities, we predict that high values of θ diminish equilibrium population sizes: male-biased sexual size dimorphism has a negative effect on populations (Fig. 3a). However, large body size often also means higher mortality under resource limitation. Males that allocate disproportionately to ornaments or weapons, are larger, or behave more aggressively than females put themselves at risk (Kodric-Brown et al. 2006, Møller and Nielsen 2006). There is indeed evidence for greater sensitivity of males to poor conditions, that often correspond to high density (Gaskin et al. 2002, Kokko and Rankin 2006). Hence any effect of a difference in resource consumption may be buffered by males dying off at a greater rate than females at higher densities (Fig. 3b).

Kokko and Brooks (2003) showed in a similar model that increased male vulnerability can increase population sizes when males consume a larger proportion of resources than females. This will compensate for their negative effect on population growth, and may even mean that strong male-biased SSD increases equilibrium population sizes compared with a one-sex model (Fig. 3b). The equivalent effects happen with female-biased SSD, but as a mirror image: if large females die at high density due to

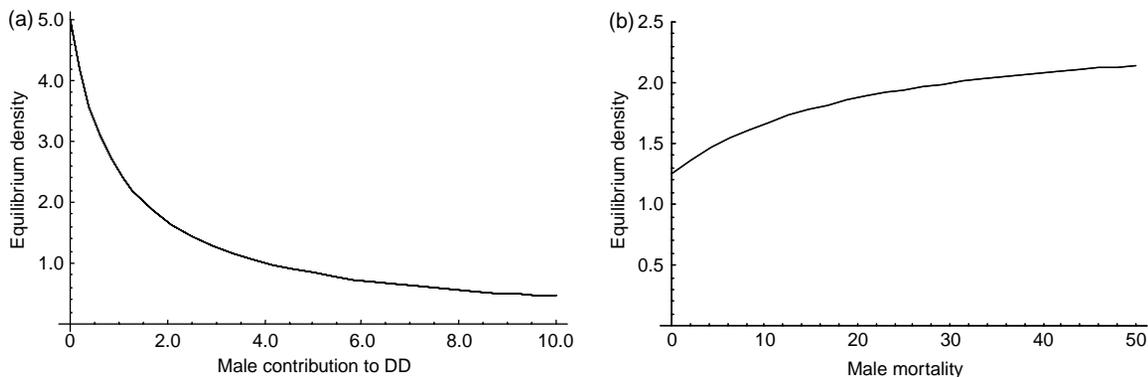


Fig. 3. The equilibrium population density (i.e. the total number of males and females) as a function of (a) male contribution to density-dependence (the amount that males consume relative to females, which is given by θ) and (b) male mortality (δ_M) under higher male resource competition. Mortality is given by the function $g_i = (\theta + F) \delta_i$, where i denotes the respective sex. In (a) $\delta_M = 10$, while in (b) $\theta = 2$. Other parameters are $b = 50$, $\delta_F = 10$, and $r = 0.5$.

their high energy requirements, the resulting male-biased populations do not allow high population growth, and the population will equilibrate sooner (i.e. at lower density).

How likely are strong effects of SSD on population growth? The question of male vs female resource use has been most extensively studied in ungulates (reviewed by Myerud 2000), where resource use differences can be strong and they also pose interesting management questions as hunters are mostly interested in males (Clutton-Brock et al. 2002). For example, in a study of moose *Alces alces*, a strong correlation between sex-ratio and population density was observed, and it was found that males were smaller when sex-ratios were more female biased (Solberg and Sæther 1994).

Other taxa appear to have attracted less interest in this respect, but given the ubiquity of SSD, resource use should provide ample opportunities for study. For example, an interesting case is provided by hermit crabs *Diogenes nitidimanus* that rely on sand snail shells (*Umbonium moniliferum*) for shelter (Asakura 1995). Male crabs are larger than females, and appear to be less discriminating in their shell use. Males also seem to be stronger intraspecific competitors for vacant shells than females, which may restrict female growth as shell-limited individuals restrain growth until a larger shell is available. Males, however, also have higher mortality, which may indicate greater sensitivity to shell-limitation stress, and the natural populations are consequently female-biased (Asakura 1995).

However, the situations depicted by Fig. 3a and 3b do not form an exhaustive list of the possible effects of resource use of males and females. Below, we review prospects and evidence for population effects of two further factors that can influence resource use: correlated responses to selection, and sexual segregation.

Female traits as correlated responses to selection on males

Sexually selected traits are characteristics that improve the access to reproductive partners. Unless both sexes suffer from limited access to mates (e.g. due to low mobility), such selective pressures should be felt by one sex only. However, perfect sex-limited expression of traits does not evolve easily in an instant. Many traits, body size included, are influenced by multiple loci, and selection pressure in one sex often produces a correlated response in the other, leading to a deviation from the optimal trait size in both sexes (Chippindale et al. 2001). Such correlations can break down over time, but significant evolutionary lags are often expected (Rhen 2000). Consequently, females can exhibit traits that are suboptimal regarding female reproductive performance. This can be hypothesized to have a negative impact on population growth, but we are not aware of any studies explicitly testing the idea.

There is evidence, however, for some of the components of the hypothesis: in the case of body size with male-biased SSD, females can evolve to be larger as a correlated response (Fairbairn 1997, Andersson and Wallander 2004). Large body size typically implies small growth rates (“slow-fast” life history continuum, e.g. lizards: Clobert et al. 1998, birds: Sæther and Engen 2002, Sæther et al. 2002), and this remains true even in fishes despite the fact that largest-bodied females often have the highest fecundity (Goodwin et al. 2005, Reynolds et al. 2005). Large body size also correlates with low population densities across many taxa (Colinvaux 1978, Blackburn and Gaston 1999, Sæther and Engen 2002). In principle, negative effects of other sexually selected traits could have similar effects on population performance, but we are not aware of any studies showing this, and

moreover, it often requires careful experimentation to test whether the expression of a sexually selected trait in a female is a correlated response to selection on males, or an independently adaptive trait (Emlen et al. 2005).

Sexual segregation

For simplicity, our models (Figs. 1–3) ignore the possibility of sexual segregation in niche use. Given the often markedly different body sizes of females and males, it is perhaps surprising that their feeding niches are so often identical: for example, in a study of shorebird sexual dimorphism, this fact allowed Székely et al. (2004) to use bill length as a variable that is subject to functional selection pressure rather than sexual selection. The Huia bird (*Heteralocha acutirostris*) is an example of a species where bill shape and length differ widely between the sexes, the female's bill being long and curved, the male's strong and short. This does not necessarily mean that the feeding niches evolved to be separate, however: it has been hypothesized that the bird foraged in pairs, the male breaking up rotting tree trunks and the female gaining access to insect prey using the thin curved bill.

Sadly, empirical tests can no longer be performed as the species only persisted in New Zealand until the early 20th century (<http://www.terranature.org/huia.htm>). Still, the uniqueness of Huia type bill dimorphism does pose the question why vertebrate species do not more often opt for wholly divergent foraging options for males and females. Extreme sexual size dimorphism in some fishes form perhaps the best examples (in extreme cases, dwarf males merge with females, Pietsch 2005). In general, invertebrates show perhaps better examples of drastic resource partitioning between the sexes than vertebrates. Males and females of the Mediterranean hermit crabs *Calcinus tubularis* differ dramatically in their shelter use. Males use loose shells, and females inhabit attached tubes (Gherardi 2004), and this resource partitioning reduces competition between the sexes. In insects, adult stages often differ in their feeding habits. For example, females of most mosquito species need vertebrate blood to form eggs, while both sexes feed on nectar (Foster 1995). Whether this has population dynamic consequences is unclear, however, as the dynamics of many insect populations is largely determined in the larval stage.

Milder forms of differentiated resource use (ecological segregation) between the sexes appears common in vertebrates, however (Mysterud 2000). For example, both sexes of southern giant petrels (*Macronectes giganteus*) feed mainly on penguin and seal carrion, but the smaller females also feed extensively on fish, squid and crustaceans (Forero et al. 2005). Sexual segregation refers to situations where males and females

can in principle utilize the same resource, but the sexes differ behaviourally such that their resource utilization patterns become different. This has implications for population growth as well as correct estimation of vital rates and resighting probabilities (Härkönen et al. 1999). There is an ongoing debate on the reasons behind segregation, particularly in ungulates (Ruckstuhl and Neuhaus 2006), but possibilities across taxa are likely to extend beyond the 'social selection' and 'activity budget' hypotheses mostly discussed in the ungulate literature.

A likely determinant of sexual segregation is that males (particularly when they are the larger sex) are also behaviourally dominant, and drive females into using poorer microhabitats. Good evidence for this exists e.g. in wintering migratory birds: stable isotope studies have revealed that male American redstarts *Setophaga ruticilla* occupy the best (mangrove) habitat, forcing females and juveniles to over-winter in sites (inland scrub) that do not allow for good performance (Marra 2000). An experiment that removed old, dominant males led to females and juveniles upgrading to mangrove. These birds maintained body mass from winter to spring, departed earlier on spring migration, and returned at a higher rate in the following winter (Studds and Marra 2005). On a larger spatial scale, the wintering areas of many birds are segregated, so that the distances migrated can differ significantly between the sexes (Myers 1981, Cristol et al. 1999, Nebel et al. 2002). This can occur over oceans too: Black-browed albatross *Thalassarche melanophrys* females over-winter several degrees further north and west than males (Phillips et al. 2005), as do female giant petrels (Gonzalez-Solis et al. 2000). Whether this relates to site quality is unclear, but in the case of female giant petrels, their longer trips and foraging further west forced them into areas with more long-line fishing (a significant human-induced mortality risk, Gonzalez-Solis et al. 2000).

A mammalian study also shows a counterexample where males are forced into poorer habitats despite male-biased sexual size dimorphism: most males of Galapagos sea lions (*Zalophus californianus wollebaeki*) have to use suboptimal inland habitats, due to a combination of strong intrasexual selection and female avoidance of male harassment (Wolf et al. 2005). Avoidance of sexual harassment probably deserves much more attention as a factor influencing the spatial distribution of individuals (Agrillo et al. 2006), yet unlike the sea lion example, in general it does not guarantee that females have access to superior habitats. In guppies, sexual harassment has been shown to drive females into areas of high predation risk (Croft et al. 2006). Males, being the more vulnerable sex in the presence of predators, avoid these dangerous areas,

which highlights the complexity of ways in which sexual dimorphism can impact female fitness.

Sexual segregation may diminish the effect of males on population densities, as resource partitioning means that males and females will not be in direct competition for resources. However, this conclusion is reversed if segregation occurs as a result of dominant males who prevent females from using preferred resources. Ours is not meant to be an exhaustive list of sexual segregation and the associated differences in habitat or resource use, but it highlights the various possibilities how intraspecific competition can alter the resources available to female reproduction. Insofar this means poorer resources for females, the effect of males is likely to be negative; if this leads to higher mortality of females too, the effect might be amplified, as females then have to compete for resources in a male-biased population.

Discussion

We have shown that males can have a diverse range of effects on models of population density: resource use alone predicts that the relative density of males will often influence population growth, and there are several other mechanisms that imply that “males matter”. The direction of the change depends on the behaviour of the sexes, and the extent to which each sex contributes to density-dependent processes. There are many instances where the removal of males appears to have little effect on population persistence, indicated by examples such as extreme sex ratio bias in the face of male killing *Wolbachia* (Dyson and Hurst 2004), or the simple observation that populations subjected to selective harvesting of males can be sustainable if it is not excessive (Milner-Gulland and Lhagvasuren 1998). However, persistence does not mean that population growth has not been impacted: in the example of butterfly system subject to *Wolbachia*, a dearth of males caused a 57% reduction in average female fecundity (Dyson and Hurst 2004).

The importance of males in population dynamics is not limited to conservation action. Malarial pest control programmes have mostly focused on the biology of the female, and taking male biology into account can bring valuable information to help control the disease (Ferguson et al. 2005). As such, functions should be considered as plausible examples representing biological control programmes have benefited by factoring males into population dynamics, and the realisation of the role males may play in population dynamics obviously has potential benefits in both pest control (Ferguson et al. 2005, Schliekelman et al. 2005) and conservation biology. Males have also been an important factor in recent demographic studies on humans (Löfstedt et al. 2004). The one-child family policy in China, for

example, has resulted in a higher number of abortions of female foetuses relative to male foetuses, a factor which has resulted in strong male-bias in some areas (Löfstedt et al. 2004, Hesketh et al. 2005). The results of this may be just as severe for human populations as they are for animal populations, especially with regard to male harassment of females and the socio-economic problems that male populations bring to society (Hesketh and Xing 2006).

One-sex models of population dynamics are highly competent at describing population dynamics. Yet, based on our simple models and the view from the literature, we can expect surprising deviations from those predicted if male dependence of population dynamics has not been incorporated in the dynamical explanation. Empirically derived graphs depicting changes in population growth (or more explicitly still, changes in the numbers of females and males separately) at various male and female densities would be a welcome sight in the literature.

Future directions

Very few studies have actively looked at how the adult sex ratio has had an impact on population size, and the examples covered in this paper show that removing males can range from having no effect (Dyson and Hurst 2004), to a positive effect (e.g. Le Galliard et al. 2005) or a negative effect (Milner-Gulland et al. 2003). Mathematically, the best population growth is expected in female-biased populations (Ovidiu Vlad 1989), thus it is remarkable how we lack studies that relate population-wide sex ratios and population densities to reproductive output (most such studies are concerned with detecting sperm limitation, Danthanarayana and Gu 1991, Hines et al. 2003, Milner-Gulland et al. 2003, Levitan 2004). But then, there are surprisingly few studies that have ever attempted the far simpler task of graphing population growth against population density: Sibly and Hone (2002) found only 25.

There are therefore still many gaps in our knowledge of how males affect population dynamics. It is important to note that the processes given in Table 1 can be divided into either “evolutionary” or “ecological” problems, according to the attention they have attracted, even though we have shown here that all processes listed are capable of altering population densities and are thus being ecologically important. For example, sexual conflict has remained in the realm of evolutionary biology, where researchers are interested in questions such as why females mate multiply (Arnqvist and Rowe 2005), while very little remains on how such behaviours can influence density (but see Kokko and Brooks 2003, Le Galliard et al. 2005). Similarly, parental care and nuptial gifts have been

primarily studied from an evolutionary angle, and the potential effects of their absence on population dynamics remain unexplored. In contrast, infanticide has been studied from a population and conservation perspective (Swenson et al. 1997, Møller 2004, Whitman et al. 2004) in addition to its evolutionary roots (O'Connor 1978, Young and Clutton-Brock 2006). Meanwhile, there have been a number of studies on how differential resource use might influence density, or how the sex ratio could affect female fertilisation rate, but studies on the latter are rather conflicting, with some systems appearing almost immune to the effects of sperm limitation.

What should be clear from our paper is that, with the exception of studies on ungulates, the vast majority of situations in which males might “matter” have been studied by their influence on individual female fitness rather than population-wide reproductive output. The strength of density-dependence in birth and death rates is likely to affect the extent to which higher female productivity will increase population density. As a result, rather than just looking at per female productivity, we strongly advocate investigating the role of males on population dynamics in a population setting.

Model limitations

The models presented in the chapters are illustrative, but certainly simplistic. This reflects the lack of two-sex models describing how different aspects of male behaviour can influence population densities. There have been a number of two-sex models of population dynamics, but these have generally focused on the specific problems of Allee effects (Berec et al. 2001, Engen et al. 2003, Bessa-Gomes et al. 2004) and stability (Caswell and Weeks 1986, Doebeli and Koella 1994, Lindström and Kokko 1998, Ranta et al. 1999, Flatt et al. 2001), rather than aiming at solid predictions of population densities despite the importance of such a measure for population management. Our functions should be considered as plausible examples representing first steps of the required modelling effort. For example, our density-dependent mortality g is rather simplistic, but allows us to spell the intuitive reasoning behind the relative contributions of males and females to density dependence. Similarly, the function f , which describes females fecundity as a function of male and female density, is based on evidence from one study, showing that males only become limiting at highly female-biased sex-ratios (Milner-Gulland et al. 2003). Other functions could be used to incorporate different mating systems (Bessa-Gomes et al. 2004). Similarly, male harassment could be modelled in a different way, incorporating both juvenile and adult age classes (Le Galliard et al. 2005)

or being more explicit about the exact mating system. There is clearly much room for further theoretical advances in this field too.

Other effects

In this review we have mainly concentrated on effects of males on equilibrium population densities, but the presence of males may also have an influence on the stability of the equilibrium (Doebeli and Koella 1994, Flatt et al. 2001). While some studies have found that sex does not necessarily affect population dynamics (Castillo-Chavez and Huang 1995), others have found that a small amount of sexual reproduction can stabilize population dynamics (Doebeli and Koella 1994, Flatt et al. 2001). However, the stabilising effect of sex often depends on the details of the mating system: deviations from monogamy often mean that sexual reproduction can destabilize dynamics rather than stabilize it (Caswell and Weeks 1986, Lindström and Kokko 1998, Ranta et al. 1999). Unstable dynamics generally occur at high growth rates, and the mixed results on stability make sense in the light of our current results: we generally find that various aspects of male behaviour can either promote or hinder population growth, thus future models should be explicit about considering a wide enough range of processes if they are to make general conclusions.

Our study concentrated on direct costs and benefits provided by males. Recombination is known to have many benefits for the population, and has been used as a major argument for why sex is so prevalent (Hadany and Feldman 2005), and the type of males present as well as female mate choice may affect the effective population size (Wedekind 2002). We have ignored the question of whether the presence of males can provide genetic benefits to females (recently reviewed by Andersson and Simmons 2006, Kokko et al. 2006), and whether competition between males can decrease the mutational load of sexual populations (Radwan 2004). How immediately such effects would show up in a study of population dynamics is currently unknown.

Conclusion

All models are always approximations (Levins 1966) and ecology and evolution has certainly progressed substantially with single-sex models. However, with our increasing understanding of the effects that individual behaviour has on population dynamics (Sutherland 1996) and the pressing need to be able to adequately predict how populations will respond to anthropogenic change, it is increasingly necessary to consider that males may also have an important role in population

processes. This is particularly important if populations exist at sex ratios or densities that have not been frequently encountered in the evolutionary past. Whether planning actions of conservation management or pest control, one should not forget the potential of males in influencing the dynamics of those populations. We thus encourage more systematic study to the effects that males have on population dynamics.

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References

- Agrillo, C. et al. 2006. Sexual harassment influences group choice in female mosquitofish. – *Ethology* 112: 592–598.
- Andersson, M. 1994. Sexual selection. – Princeton Univ. Press.
- Andersson, M. and Wallander, J. 2004. Relative size in the mating game. – *Nature* 431: 139–141.
- Andersson, M. and Simmons, L. W. 2006. Sexual selection and mate choice. – *Trends Ecol. Evol.* 21: 296–302.
- Andreassen, H. P. and Gundersen, G. 2006. Male turnover reduces population growth: an enclosure experiment on voles. – *Ecology* 87: 88–94.
- Arnqvist, G. and Nilsson, T. 2000. The evolution of polyandry: multiple mating and female fitness in insects. – *Anim. Behav.* 60: 145–164.
- Arnqvist, G. and Rowe, L. 2005. Sexual conflict. – Princeton Univ. Press.
- Arnqvist, G. et al. 2005. Mating rate and fitness in female bean weevils. – *Behav. Ecol.* 16: 123–127.
- Asakura, A. 1995. Sexual differences in life history and resource utilization by the hermit crab. – *Ecology* 76: 2295–2313.
- Berec, L. et al. 2001. Linking the allee effect, sexual reproduction, and temperature-dependent sex determination via spatial dynamics. – *Am. Nat.* 157: 217–230.
- Bessa-Gomes, C. et al. 2004. Allee effects, mating systems and the extinction risk in populations with two sexes. – *Ecol. Lett.* 7: 802–812.
- Blackburn, T. M. and Gaston, K. J. 1999. The relationship between animal abundance and body size: a review of the mechanisms. – *Adv. Ecol. Res.* 28: 181–210.
- Castillo-Chavez, C. and Huang, W. 1995. The logistic equation revisited: the two-sex case. – *Math. Biosci.* 128: 299–316.
- Caswell, H. 2001. Matrix population models. – Sinauer.
- Caswell, H. and Weeks, D. E. 1986. Two-sex models: chaos, extinction, and other dynamic consequences of sex. – *Am. Nat.* 128: 707–735.
- Chapman, T. et al. 2003. Sexual conflict. – *Trends Ecol. Evol.* 18: 41–47.
- Chippindale, A. K. et al. 2001. Negative genetic correlation for adult fitness between sexes reveals ontogenetic conflict in *Drosophila*. – *Proc. Natl Acad. Sci.* 98: 1671–1675.
- Clobert, J. et al. 1998. The evolution of demographic tactics in lizards: a test of some hypotheses concerning life history evolution. – *J. Evol. Biol.* 11: 329–364.
- Clutton-Brock, T. H. et al. 2002. Sex differences in emigration and mortality affect optimal management of deer populations. – *Nature* 415: 633–637.
- Colinvaux, P. A. 1978. Why big fierce animals are rare: an ecologist's perspective. – Princeton Univ. Press.
- Crespi, B. J. 2004. Vicious circles: positive feedback in major evolutionary and ecological transitions. – *Trends Ecol. Evol.* 19: 627–633.
- Cristol, D. A. et al. 1999. Differential migration revisited: latitudinal segregation by age and sex class. – *Curr. Ornithol.* 15: 33–88.
- Croft, D. P. et al. 2006. Predation risk as a driving force for sexual segregation: a cross-population comparison. – *Am. Nat.* 167: 867–878.
- Crudgington, H. S. and Siva-Jothy, M. T. 2000. Genital damage, kicking and early death. – *Nature* 407: 855–856.
- Danthanarayana, W. and Gu, H. 1991. Multiple mating and its effect on the reproductive success of female *Epiphyas postvittana* (Lepidoptera, Tortricidae). – *Ecol. Entomol.* 16: 169–175.
- Doebeli, M. and Koella, J. C. 1994. Sex and population dynamics. – *Proc. R. Soc. Lond. B* 257: 17–23.
- Doherty, P. F. et al. 2003. Sexual selection affects local extinction and turnover in bird communities. – *Proc. Natl Acad. Sci.* 100: 5858–5862.
- Dyson, E. A. and Hurst, G. D. D. 2004. Persistence of an extreme sex-ratio bias in a natural population. – *Proc. Natl Acad. Sci.* 101: 6520–6523.
- Edvardsson, M. and Tregenza, T. 2005. Why do male *Callosobruchus maculatus* harm their mates? – *Behav. Ecol.* 16: 788–793.
- Emlen, D. J. et al. 2005. Evolution of sexual dimorphism and male dimorphism in the expression of beetle horns: phylogenetic evidence for modularity, evolutionary lability, and constraint. – *Am. Nat.* 166: S42–S68.
- Engen, S. et al. 2003. Demographic stochasticity and allee effects in populations with two sexes. – *Ecology* 84: 2378–2386.
- Fairbairn, D. J. 1997. Allometry for sexual size dimorphism: pattern and process in the coevolution of body size in males and females. – *Annu. Rev. Ecol. Syst.* 28: 659–687.
- Ferguson, H. M. et al. 2005. Redressing the sex imbalance in knowledge of vector biology. – *Trends Ecol. Evol.* 20: 202.
- Flatt, T. et al. 2001. A bit of sex stabilizes host-parasite dynamics. – *J. Theor. Biol.* 212: 345–354.
- Forero, M. G. et al. 2005. Stable isotopes reveal trophic segregation by sex and age in the southern giant petrel in two different food webs. – *Mar. Ecol. Prog. Ser.* 296: 107–113.
- Foster, W. A. 1995. Mosquito sugar feeding and reproductive genetics. – *Annu. Rev. Entomol.* 40: 443–474.

- Gaskin, T. et al. 2002. Increased density and male-male interactions reduce male longevity in the medfly, *Ceratitis capitata*. – *Anim. Behav.* 63: 121–129.
- Gherardi, F. 2004. Resource partitioning between sexes in the “unconventional” hermit crab, *Calcinus tubularis*. – *Behav. Ecol.* 15: 742–747.
- Gonzalez-Solis, J. et al. 2000. Foraging partitioning between giant petrels *Macronectes* spp. and its relationship with breeding population changes at Bird Island, South Georgia. – *Mar. Ecol. Prog. Ser.* 204: 279–288.
- Goodwin, N. B. et al. 2005. Life history correlates of density-dependent recruitment and adult production in marine fishes. – *Can. J. Fish. Aquat. Sci.* 63: 494–509.
- Hadany, L. and Feldman, M. W. 2005. Evolutionary traction: the cost of adaptation and the evolution of sex. – *J. Evol. Biol.* 18: 309–314.
- Hamilton, W. D. 1967. Extraordinary sex ratios. – *Science* 156: 477–488.
- Hardin, G. 1968. The tragedy of the commons. – *Science* 162: 1243–1248.
- Härkönen, S. T. et al. 1999. Age- and sex-specific behaviour in harbour seals *Phoca vitulina* leads to biased estimates of vital population parameters. – *J. Appl. Ecol.* 36: 825–841.
- Hesketh, T. and Xing, Z. W. 2006. Abnormal sex ratios in human populations: causes and consequences. – *Proc. Natl Acad. Sci.* 103: 13271–13275.
- Hesketh, T. et al. 2005. The effect of China’s one-child family policy after 25 years. – *New Engl. J. Med.* 353: 1171–1176.
- Hines, A. H. et al. 2003. Evidence for sperm limitation in the blue crab, *Callinectes sapidus*. – *Bull. Mar. Sci.* 73: 287–310.
- Holland, B. and Rice, W. M. 1999. Experimental removal of sexual selection reverses intersexual antagonistic coevolution and removes a reproductive load. – *Proc. Natl Acad. Sci.* 96: 5083–5088.
- Janzen, F. J. and Paukstis, G. L. 1991. Environmental sex determination in reptiles-ecology, evolution and experimental design. – *Q. Rev. Biol.* 66: 149–179.
- Johnson, L. S. et al. 1993. The cost of polygyny in the house wren *Troglodytes-Aedon*. – *J. Anim. Ecol.* 62: 669–682.
- Kodric-Brown, A. et al. 2006. The allometry of ornaments and weapons. – *Proc. Natl Acad. Sci.* 103: 8733–8738.
- Kokko, H. and Brooks, R. 2003. Sexy to die for? Sexual selection and the risk of extinction. – *Ann. Zool. Fenn.* 40: 207–219.
- Kokko, H. and Mappes, J. 2005. Sexual selection when fertilization is not guaranteed. – *Evolution* 59: 1876–1885.
- Kokko, H. and Rankin, D. J. 2006. Lonely hearts or sex in the city? Density-dependent effects in mating systems. – *Philos. Trans. R. Soc. Lond. B* 361: 319–334.
- Kokko, H. et al. 2001. Life histories and sustainable harvesting. – In: Reynolds, J. D. et al. (eds), *Conservation of exploited species*. Cambridge Univ. Press, pp. 301–322.
- Kokko, H. et al. 2006. Unifying and testing models of sexual selection. – *Annu. Rev. Ecol. Syst.* 37: 43–66.
- Langvatn, R. and Loison, A. 1999. Consequences of harvesting on age structure, sex ratio and population dynamics of red deer *Cervus elaphus* in central Norway. – *Wildlife Biol.* 5: 213–223.
- Le Galliard, J. F. et al. 2005. Sex ratio bias, male aggression, and population collapse in lizards. – *Proc. Natl Acad. Sci.* 102: 18231–18236.
- Levins, R. 1966. The strategy of model building in population biology. – *Am. Sci.* 54: 421–431.
- Levitan, D. R. 2004. Density-dependent sexual selection in external fertilizers: variances in male and female fertilization success along the continuum from sperm limitation to sexual conflict in the sea urchin *Strongylocentrotus franciscanus*. – *Am. Nat.* 164: 298–309.
- Lindström, J. and Kokko, H. 1998. Sexual reproduction and population dynamics: the role of polygyny and demographic sex differences. – *Proc. R. Soc. Lond. B* 265: 483–488.
- Löfstedt, P. et al. 2004. Abortion patterns and reported sex ratios at birth in rural Yunnan, China. – *Reproductive Health Matters* 12: 86–95.
- Marra, P. P. 2000. The role of behavioral dominance in structuring patterns of habitat occupancy in a migrant bird during the nonbreeding season. – *Behav. Ecol.* 11: 299–308.
- Matsuda, H. et al. 1999. A management policy for sika deer based on sex-specific hunting. – *Res. Popul. Ecol.* 41: 139–149.
- May, R. M. 1976. Models for single populations. – In: May, R. M. (ed.), *Theoretical ecology. Principles and applications*. Blackwell Scientific Publications, pp. 4–25.
- Milner-Gulland, E. J. and Lhagvasuren, B. 1998. Population dynamics of the Mogolian gazelle *Procapra guturosa*: an historical analysis. – *J. Appl. Ecol.* 35: 240–251.
- Milner-Gulland, E. J. et al. 2003. Reproductive collapse in saiga antelope harems. – *Nature* 422: 135.
- Møller, A. P. 2003. Sexual selection and extinction: why sex matters and why asexual models are insufficient. – *Ann. Zool. Fenn.* 40: 221–230.
- Møller, A. P. 2004. Rapid temporal change in frequency of infanticide in a passerine bird associated with change in population density and body condition. – *Behav. Ecol.* 15: 462–468.
- Møller, A. P. and Jennions, M. 2001. How important are direct fitness benefits of sexual selection? – *Naturwissenschaften* 88: 401.
- Møller, A. P. and Nielsen, J. T. 2006. Prey vulnerability in relation to sexual coloration of prey. – *Behav. Ecol. Sociobiol.* 60: 227–233.
- Morrow, E. H. and Pitcher, T. E. 2003. Sexual selection and the risk of extinction in birds. – *Proc. R. Soc. Lond. B* 270: 1793–1799.
- Myers, J. P. 1981. A test of three hypotheses for latitudinal segregation of the sexes in wintering birds. – *Can. J. Zool.* 59: 1527–1534.
- Mysterud, A. 2000. The relationship between ecological segregation and sexual body size dimorphism in large herbivores. – *Oecologia* 124: 40–54.
- Mysterud, A. et al. 2002. The role of males in the dynamics of ungulate populations. – *J. Anim. Ecol.* 71: 907–915.
- Nebel, S. et al. 2002. Western sandpipers (*Calidris mauri*) during the non-breeding season: spatial segregation on a hemispheric scale. – *Auk* 119: 922–928.

- O'Connor, R. J. 1978. Brood reduction in birds—selection for fratricide, infanticide and suicide. — *Anim. Behav.* 26: 79–96.
- Ovidiu Vlad, M. 1989. The optimal sex ratio for age-structured populations. — *Math. Biosci.* 93: 181–190.
- Phillips, R. A. et al. 2005. Summer distribution and migration of nonbreeding albatrosses: individual consistencies and implications for conservation. — *Ecology* 86: 2386–2396.
- Pietsch, T. W. 2005. Dimorphism, parasitism, and sex revisited: modes of reproduction among deep-sea ceratioid anglerfishes (Teleostei: Lophiiformes). — *Ichthyol. Res.* 52: 207–236.
- Radwan, J. 2004. Effectiveness of sexual selection in removing mutations induced with ionizing radiation. — *Ecol. Lett.* 7: 1149–1154.
- Rankin, D. J. and Kokko, H. 2006. Sex, death and tragedy. — *Trends Ecol. Evol.* 21: 225–226.
- Ranta, E. et al. 1999. Sex in space: population dynamic consequences. — *Proc. R. Soc. Lond. B* 266: 1155–1160.
- Réale, D. et al. 1996. Female-biased mortality induced by male sexual harassment in a feral sheep population. — *Can. J. Zool.* 74: 1812–1818.
- Reid, J. M. et al. 2002. Males matter: the occurrence and consequences of male incubation in starlings (*Sturnus vulgaris*). — *Behav. Ecol. Sociobiol.* 51: 255–261.
- Reynolds, J. D. et al. 2005. Biology of extinction risk in marine fishes. — *Proc. R. Soc. Lond. B* 272: 2337–2344.
- Rhen, T. 2000. Sex-limited mutations and the evolution of sexual dimorphism. — *Evolution* 54: 37–43.
- Rowe, L. and Day, T. 2006. Detecting sexual conflict and sexually antagonistic coevolution. — *Philos. Trans. R. Soc. Lond. B* 361: 277–285.
- Ruckstuhl, K. E. and Neuhaus, P. (eds). 2006. Sexual segregation in vertebrates. — Cambridge Univ. Press.
- Sæther, B. E. and Engen, S. 2002. Pattern of variation in avian population growth rates. — *Philos. Trans. R. Soc. Lond. B* 357: 1185–1195.
- Sæther, B. E. et al. 2002. Demographic characteristics and population dynamical patterns of solitary birds. — *Science* 295: 2070–2073.
- Sæther, B. E. et al. 2004. Time to extinction in relation to mating system and type of density regulation in populations with two sexes. — *J. Anim. Ecol.* 73: 925–934.
- Schliekelman, P. et al. 2005. Pest control by genetic manipulation of sex ratio. — *J. Econ. Entomol.* 98: 18–34.
- Sergio, F. and Bogliani, G. R. 2001. Nest defense as parental care in the northern hobby (*Falco subbuteo*). — *Auk* 118: 1047–1052.
- Shine, R. et al. 2001. Bumpus in the snake den: effects of sex, size, and body condition on mortality of red-sided garter snakes. — *Evolution* 55: 598–604.
- Sibly, R. M. and Hone, J. 2002. Population growth rate and its determinants: an overview. — *Philos. Trans. R. Soc. Lond. B* 357: 1153–1170.
- Skorping, A. and Jensen, K. H. 2004. Disease dynamics: all caused by males? — *Trends Ecol. Evol.* 19: 219–220.
- Solberg, E. J. and Sæther, B. E. 1994. Male traits as life-history variables—annual variation in body-mass and antler size in moose (*Alces alces*). — *J. Mammal.* 75: 1069–1079.
- Studds, C. E. and Marra, P. P. 2005. Nonbreeding habitat occupancy and population processes: an upgrade experiment with a migratory bird. — *Ecology* 86: 2380–2385.
- Sutherland, W. J. 1996. From individual behaviour to population ecology. — Oxford Univ. Press.
- Svensson, M. 1996. Sexual selection in moths: the role of chemical communication. — *Biol. Rev.* 71: 113–135.
- Swenson, J. E. et al. 1997. Infanticide caused by hunting of male bears. — *Nature* 386: 450–451.
- Székely, T. and Cuthill, I. C. 2000. Tradeoff between mating opportunities and parental care: brood desertion by female Kentish plovers. — *Proc. R. Soc. Lond. Ser. B* 267: 2087–2092.
- Székely, T. et al. 2004. Sexual selection explains Rensch's rule of size dimorphism in shorebirds. — *Proc. Natl Acad. Sci.* 101: 12224–12227.
- Thrall, P. H. et al. 2000. Sexually transmitted diseases in polygynous mating systems: prevalence and impact on reproductive success. — *Proc. R. Soc. Lond. B* 267: 1555–1563.
- Tregenza, T. et al. 2006. Introduction. Sexual conflict: a new paradigm? — *Philos. Trans. R. Soc. Lond. B* 361: 229–234.
- Trivers, R. L. 1972. Parental investment and sexual selection. — In: Campbell, B. (ed.), *Sexual selection and the descent of man*. Aldine Publishing Co, pp. 136–179.
- Wedekind, C. 2002. Sexual selection and life-history decisions: implications for supportive breeding and the management of captive populations. — *Conserv. Biol.* 16: 1204–1211.
- Wedell, N. et al. 2002. Sperm competition, male prudence and sperm-limited females. — *Trends Ecol. Evol.* 17: 313–320.
- Whitman, K. et al. 2004. Sustainable trophy hunting of African lions. — *Nature* 428: 175–178.
- Wiegus, R. B. et al. 2001. Estimating effects of adult male mortality on grizzly bear population growth and persistence using matrix models. — *Biol. Conserv.* 98: 293–303.
- Wigby, S. and Chapman, T. 2004. Female resistance to male harm evolves in response to manipulation of sexual conflict. — *Evolution* 58: 1028–1037.
- Wolf, J. B. W. et al. 2005. Males in the shade: habitat use and sexual segregation in the Galápagos sea lion (*Zalophus californianus wollebaeki*). — *Behav. Ecol. Sociobiol.* 59: 293–302.
- Wright, H. W. Y. 2006. Paternal den attendance is the best predictor of offspring survival in the socially monogamous bat-eared fox. — *Anim. Behav.* 71: 503–510.
- Young, A. J. and Clutton-Brock, T. 2006. Infanticide by subordinates influences reproductive sharing in cooperatively breeding meerkats. — *Biol. Lett.* 2: 385–387.