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2 **Do males matter? The role of males in population dynamics**

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Abstract

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 the effects on 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.

Key words: Population density, sexual selection, sexual conflict, mate finding, male resource use, sexual harassment, density dependence

1 Introduction

2 The majority of population dynamical models only view the population from the

3 female point of view (Caswell 2001). This assumption makes life rather simple, and

4 allows for mathematical tractability in more complicated models of populations (May

5 1976). The logic behind the assumption is that males will be born and die at the same

6 rate as females. This means that the sex ratio is always even, and the female density

7 therefore constitutes half of the total population density.

8 The assumptions used in single-sex models hold under limited conditions, where

9 models assume that male availability does not limit female reproduction, the sex-ratio

10 is even, and male life history does not differ from that of females (Caswell and Weeks

11 1986, Lindström and Kokko 1998, Engen et al. 2003). If such assumptions are

12 fulfilled, a model incorporating two sexes will always produce a total population that

13 is twice the number of females, rendering the explicit incorporation of males

14 unnecessary. If the presence and behaviour of males does have a discernible influence

15 on population equilibria or stability, one-sex population models should be abandoned

16 in favour of two-sex models, particularly when thinking about conservation (Saether

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

18 al. 2005).

19 It is now increasing recognised that the presence and behaviour of males may matter

20 to population processes. Even in a 'null model' in which males do not impact female

21 fitness directly, if male and female numbers contribute equally to density-dependence

22 removing males will increase the population density as there will be more room for

23 females (e.g. Clutton-Brock et al. 2002). Table 1 details other ways in which males

3

1 may have a positive or negative effect on population densities. This can occur, for

2 example, through sexual harassment of females, males having a larger influence on

3 resource availability than females, and a lack of males being a limiting factor in

4 female fertilisation (Mysterud et al. 2002, Møller 2003, Bessa-Gomes et al. 2004).

5 Behaviour related to mate choice has been shown to have an influence on population

6 processes (Doherty et al. 2003, Kokko and Brooks 2003, Møller 2003, Morrow and

7 Pitcher 2003) and recent studies have examined whether different mating systems can

8 play a role in the extinction risk of a population (Milner-Gulland et al. 2003, Bessa-

9 Gomes et al. 2004, Le Galliard et al. 2005).

10 Here our aim is to provide an overview of various mechanisms of how males may

11 "matter" to the growth of populations. As an operational definition, males "matter" if

12 population growth at a given female density depends on the relative density of males.

13 We will present simple two-sex models of population growth, using equilibrium

14 population densities to illustrate the point that male effects on dynamics are not

15 transient but will impact carrying capacities. We review empirical studies, in each

16 case assessing how likely it is to encounter scenarios where 'males matter' in natural

17 populations, and whether there is a sense in which we can state these effects to be

18 'positive' or 'negative'.

19 Mate finding and sperm limitation

20 When considering whether or not males matter we must first think about various

21 factors which influence their presence in natural populations. There are many

22 biological and anthropogenic factors which can influence the sex ratio. Local mate

23 competition (Hamilton 1967), temperature in poikilotherms (Janzen and Paukstis

4

1 1991), and male killers such as *Wolbachia* (Dyson and Hurst 2004) can influence the

2 number of males born, and therefore the adult sex ratio. Perhaps much more

3 commonly, the adult sex ratio will also be biased if males follow different life history

4 schedules than females (e.g. due to lack or presence of paternal investment, or

5 mortality due to male-male contests and costly sexually-dimorphic ornaments). While

6 these natural causes can influence population dynamics, understanding the dynamics

7 becomes especially important if humans influence the sex ratio, for example through

8 selective hunting of males.

9 In many models in both sexual selection and population ecology, it is frequently

10 assumed that female reproduction is not limited by the number of males (e.g.

11 Andersson 1994, Caswell 2001). In models of sexual selection, for example, it is often

12 females who are limiting and the assumption that a female will always find a mate is

13 widespread throughout the literature (but see Kokko and Mappes 2005). However,

14 examples are accumulating that male ejaculates are not always cost-free to produce,

15 and females can consequently become sperm limited (Wedell et al. 2002).

16 How likely is it that this limitation also has population-level consequences? Models

17 that consider strictly monogamous populations suggest that population dynamics will

18 be very sensitive to alterations in the sex ratio (Bessa-Gomes et al. 2004), and any

19 process that removes males under monogamy could thus have disastrous effects on

20 populations. Strict monogamy is, however, rare across taxa, and it is therefore

21 important to examine how strong sperm limitation has to be before it has considerable

22 population-level consequences. We illustrate the logic with a simple model of the

23 dynamics of a sexual population, with densities of both males and females specified

24 as M and F, respectively. For simplicity, we consider a continuous-time setting. The

1 density dependent death rates of males and females are written as g_M and g_F,

2 respectively. Birth will depend on the primary sex ratio r, the maximum birth rate of a

3 fully fertilised female b, weighted by the probability that a given female will be

4 fertilised. The general dynamics of males and females is therefore

5
$$\frac{dM}{dt} = f(F,M)brF - g_M(F,M)M$$
$$\frac{dF}{dt} = f(F,M)b(1-r)F - g_F(F,M)F$$
(1)

6 where birth depends, most importantly, on the number of females and the fertilisation

7 probability $f(F,M)$, but will also be affected by the number of males M and thus by the

8 primary sex ratio r. Density dependent death is given by the function $g_i(F,M)$

9 where i represents the mortality of either males (M) or females (F), and will depend

10 on the total number of individuals in the population, i.e. both F and M.

11 Assuming that males and females consume identical amounts of resources, we can

12 write the death rate as a function of the sum $M+F$. The simplest function is of the

13 form $g_i(F,M) = (M+F)\delta_i$, where the death rate δ_i can be sex-specific and the

14 overall death rate increases linearly with the addition of each male and female in the

15 population.

16 Fertilization success depends on how efficiently individuals search for mates. Here we

17 opt for a simple function, which describes the probability of a given female being

18 fertilised as a function of sex ratio as $f(F,M) = x/(x+c)$ (Figure 1a), where x is the

19 adult sex ratio (ASR, the proportion of adult males in the population). As the relative

20 density of males decreases, so does the per capita fecundity. Such a function has been

1 found when males are severely limiting (Milner-Gulland et al. 2003). The shape of the

2 function is determined by c. Very low values of c are likely to be more realistic, as we

3 can assume that sperm limitation only comes in to play when there are very few males

4 (Milner-Gulland et al. 2003), but we also consider other shapes of this function.

5 Figure 1b shows the how the primary sex ratio (proportion of males) affects the

6 carrying capacity. It can be seen that male-biased sex-ratios result in lower population

7 densities. However, under high sperm limitation, female-biased sex ratios can also

8 reduce population density as fewer females are fertilised. This depends on the

9 efficiency with which males can fertilize females. Even if sperm limitation does not

10 limit populations at all (i.e. $c = 0$), a male-biased sex-ratio will still result in a linear

11 decline in density, due to there being less "space" for females (Clutton-Brock et al.

12 2002).

13 Unsurprisingly, the efficiency with which the two sexes find each other (parameter c)

14 has a strong effect on population performance. An assessment of how often sperm

15 limitation truly influences population growth therefore requires estimating functions

16 depicted in Figure 1a. In many instances, population growth appears to be sustained

17 despite very low relative male densities, suggestive of a very low c. Extreme sex-ratio

18 biases due to factors such as male killers provide clear examples: in the butterfly

19 *Hypolimna bolina*, male-killing *Wolbachia* has been found to dramatically decrease

20 the number of males by manipulating females into only producing other females. As a

21 result of this, the population of butterflies in western Samoa has been found to have

22 1.1% males in the population (Dyson and Hurst 2004). As the population still remains

23 viable, such an extreme sex-ratio bias suggests that a very small number of males can

1   fertilise a large number of females.

2   Still, the butterfly study documented significant declines (averaging 57%) in female

3   fecundity when persisting with *Wolbachia* (Dyson and Hurst 2004). Less extreme

4   polygynous examples have also yielded evidence for sensitivities to sperm limitation.

5   The problem is perhaps best studied in ungulates, and here the conclusions vary:

6   despite the lack of male parental care, per *capita* female reproduction suffers in some

7   species when the sex ratio becomes female-biased (Kokko et al. 2001, Mysterud et al.

8   2002). It is noteworthy that management options usually include targeting males, both

9   because of their larger size and potential for trophy hunting, and for the sake of

10   sparing females to produce young. However, such a management strategy is based on

11   the ability of males to fertilize many females, and this may push the sex ratio at which

12   maximal offspring production occurs very close to the threshold under which sperm

13   limitation has a sudden and severe impact on population growth (Kokko et al. 2001).

14   A spectacular example has occurred in the Saiga antelope, where selective hunting of

15   males has led to a reduction in male density to the point where many females have

16   become unable to find a mate, reducing the population density to dangerously low

17   levels (Milner-Gulland et al. 2003).

18   Since female fitness is strongly determined by her own offspring production, any

19   problems related to sperm limitation should provoke an evolutionary response in

20   females. To alleviate problems of sperm limitation, we may expect females to evolve

21   adaptations ranging from appropriately reduced choosiness (Kokko and Mappes 2005)

22   to pheromone production (Svensson 1996). However, as the Saiga antelope example

23   shows, the efficiency of such mechanisms can be seriously compromised when novel

24   environmental scenarios are encountered, and such cases may be common if

1 populations currently exist at lower densities than they have typically encountered

2 during their evolutionary history (Kokko and Mappes 2005). At present, it is perhaps

3 therefore best concluded that sperm limitation is a possible mechanism through which

4 "males matter", although the conclusion from the model and empirical evidence

5 would suggest that the effect will be weak in the absence of highly skewed ratios (e.g.

6 Milner-Gulland et al. 2003). The abruptness of the relationship between fecundity and

7 relative male density (Fig. 1a) makes it a difficult but important function to estimate

8 empirically.

Male mating strategies

10 As well as the problems of finding a mate, female fitness itself may be directly and

11 negatively affected by the behaviour of males in the population. Sexual conflict,

12 loosely defined as occurring when males and females do not share a common interest

13 (Chapman et al. 2003, Arnqvist and Rowe 2005, Tregenza et al. 2006), can reduce

14 female fitness through factors such as male harassment (e.g. Réale et al. 1996). A

15 consequence of anisogamy is that it is often more advantageous for males to mate

16 multiply than for females (reviewed in Kokko et al. 2006). Increased mating rates may

17 cause a reduction in female fitness through male harm, but whether this has

18 population consequences is debated (Kokko and Brooks 2003, Rowe and Day 2006).

19 The extent of male harassment will depend on the mating rate (Arnqvist et al. 2005),

20 which in turn may be profoundly influenced by both the sex ratio (Le Galliard et al.

21 2005) and the density of individuals (Kokko and Rankin 2006). Altering the sex ratio

22 or density of males in the population could increase the extent to which harassment

23 affects population processes, and thus bears examination in the context of this paper.

1   If there are costs of mating, these will depend not only on the sex ratio and density of

2   individuals, but will be inextricably linked to the mating system; if matings impose

3   costs on females, those mating with only one male should suffer less than multiply

4   mating females.

5   We therefore extend the simple model above to account for male harassment. The

6   same assumptions about both males and females apply as above. However, now we

7   introduce the function h to describe additional female mortality due to male

8   harassment. The dynamics are now described by the following equations:

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

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

11 Equations 2a and 2b describe the dynamics of both males and females, respectively.

12 The first expressions deal with birth, and the latter deal with death, in a manner

13 similar to equation (1). In this model we are interested in how the mating rate affects

14 female survival, and so we must take into account the fact that an increasing mating

15 rate has a negative impact on survival. The *per capita* mortality h due to harassment

16 of females is determined by the density of males and females, and we provide an

17 example that makes use of the following function:

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

19 Here k scales the intensity of harassment. One could envisage that the harassment

1 experienced by females depends either on the sex ratio or, alternatively, more directly

2 on male density irrespective of the number of males per female. To be able to model

3 either extreme as well as intermediate cases, we include the parameter α that

4 measures the extent to which the mating system depends on either sex ratio or male

5 density ($\alpha = 0$ denotes a sex-ratio determined mating system, and $\alpha = 1$ denotes a

6 mating system determined by male density). The parameter γ determines how strongly

7 harassment depends on either of the factors mentioned above. When $\gamma = 0$, then

8 harassment occurs independently of either the proportion or number of males in the

9 population.

10 The model can be investigated for varying levels of male mortality δ_M (Figure 2). As

11 male mortality decreases, the population becomes more male-biased, and there is an

12 increase in female mortality which causes the overall population size to decline

13 (Figure 2a). The model described here incorporates a positive feedback between male

14 density and population density (Crespi 2004); the more males there are in the

15 population, the more females will suffer from harassment females. This reduces the

16 number of females in the population relative to males, which increases the level of

17 harassment, and the process may continue until population persistence is threatened.

18 The final outcome depends on the mating system (Figure 2a). Catastrophic outcomes

19 can occur if the mating system is influenced more strongly by the proportion of males

20 in the population, rather than absolute density. This results in the complete extinction

21 of the population, where harassment drives reaches disproportionate levels where the

22 population can no longer be sustained (Figure 2a, III). This is in stark contrast to the

23 somewhat unrealistic case where the level of harassment is independent of the

24 proportion or density of males ($\gamma = 0$, Figure 2a, I). In this case the population density

11

1   remains unchanged regardless of the density of males; in such a case an asexual

2   approximation would be appropriate.

3   As discussed above, our model shows that the results of harassment should depend

4   very much on the extent to which the mating rate depends on the sex ratio or

5   population density. This has long been realised in behavioural ecology, and several

6   studies of sexual conflict have manipulated male harassment by simply altering the

7   sex ratio (e.g. Holland and Rice 1999, Wigby and Chapman 2004). Obviously,

8   manipulating the mating rate is one way in which females can reduce the impact of

9   male harassment (Arnqvist and Nilsson 2000), and in systems in which sexual conflict

10   is prevalent, an increase in the mating rate will impose more costs on the females,

11   subsequently reducing population density. If costs increase with mating rate, females

12   are predicted to mate at an intermediate rate in order to maximise their fitness

13   (Arnqvist and Nilsson 2000).

14   A similar result to that shown in Figure 2 has been studied in the common lizard

15   *Lacerta vivipara*. By simply manipulating the adult sex ratio, Le Galliard and

16   colleagues found that male-biased populations were much more prone to sexual

17   conflict than were female-biased populations (Le Galliard et al. 2005). Comparing

18   female and male biased populations, the authors found a severe decline in both female

19   survival and fecundity under male bias (Le Galliard et al. 2005). A greater rate of

20   injury to females, revealed by a higher number of mating scars, gave strong support to

21   the prediction that more males would lead to more harassment. If a higher relative

22   density of males in a population increases female mortality, then the sex-ratio should

23   become more male-biased in the future, perpetuating a high level of harassment in the

24   population. A model revealed that if such harassment continued, the positive feedback

1 between male density and decline female densities could ultimately result in the

2 population would be driven extinct within 40 years (Le Galliard et al. 2005).

3 The resulting extinction may be seen as something analogous to the tragedy of the

4 commons (Hardin 1968, Rankin and Kokko 2006), as it is to the male's advantage to

5 compete for females, even if this reduces female survival. While there have been a

6 number of studies examining the influence of sexual selection in general on

7 population density and extinction risk (reviewed in Kokko and Brooks 2003), to our

8 knowledge this is the first looking at the population-level consequences of sexual

9 conflict as a result of sex-ratio manipulations.

10 The extent to which sexual conflict affects population processes is still in its infancy.

11 The study of Le Galliard and colleagues (Le Galliard et al. 2005) remains unique, in

12 that it explicitly considers the population consequences of male harassment. However,

13 the capacity for such consequences is large, as there are many examples in the

14 literature of how males can affect female fitness through various mating strategies.

15 Males of red-sided garter snakes *Thamnophis sirtalis parietalis* which are too eager to

16 mate can end up strangling the females, a factor which no-doubt increases female

17 mortality (Shine et al. 2001). In feral sheep, sexual harassment by males has also been

18 shown to increase female mortality during the mating season (Réale et al. 1996).

19 One of the most curious examples of sexual conflict is the spiked penis of the been

20 weevil *Callosobruchus maculatus* (Crudgington and Siva-Jothy 2000). It is known

21 that these spines puncture the female reproductive tract during mating, and it has been

22 suggested that females kick males to reduce the cost of mating (Crudgington and

23 Siva-Jothy 2000). One study found that the spines may have evolved as a side-

13

1   adaptation, rather than to aid males in sperm competition, demonstrated by the fact

2   that preventing females from kicking during their second copulation did not make the

3   second mates more successful in sperm competition (Edvardsson and Tregenza 2005).

4   The role of female counteradaptations is clearly underexplored. Female resistance

5   may itself incur fecundity or survival costs through investment in avoidance strategies

6   (Croft et al. 2006), and thus it may not be sufficient enough to buffer the effect of

7   male harm on population densities.

8   The prevalence of sexual conflict in the animal kingdom leads to the inevitable

9   question of how male harassment can persist, given that it has the potential to impose

10   extreme costs on the population. Population ecology itself may offer one explanation.

11   If males can have a negative effect on population density, then they effectively change

12   the environment under which selection operates (Kokko and Rankin 2006). The

13   reduction in the absolute numbers of males and females may make it less

14   advantageous for males to attempt to monopolise females, resulting in less overall

15   sexual harassment, and a lesser impact on population processes. However, empirical

16   evidence is so far both limited and conflicting (Kokko and Rankin 2006). There is

17   also the question whether males can exhibit sufficiently fast evolutionary responses to

18   counteract a process that occurs over ecological time (Figure 2). The feedback

19   between population processes and behaviour may be an important factor influencing

20   the behaviour, and further study is much needed.

21   Mating with many partners inevitably increases the risk of contracting sexually

22   transmitted diseases (STDs), a factor which can be seen as having the same effect as

23   male harassment when it reduces female lifespan or fecundity. The model presented

24   above can also be interpreted in terms of the risk to a female of contracting a sexually

1   transmitted disease, where a higher mating rate will lead to more individuals

2   becoming infected with STDs, and thus a lower population density. Sexually

3   transmitted diseases are often expected to be more prevalent in females than in males,

4   mainly due to the variance in male reproductive success that leaves some males

5   without a chance to mate (Thrall et al. 2000). The sex of a host can also make a

6   difference to the transmission of parasites, thus male behaviour can also matter in the

7   spread of disease in general and not just in the context of STDs (Skorping and Jensen

8   2004).

9   *Infanticide*

10   Another way in which male behaviour may negatively affect female fitness is

11   infanticide. In the above examples we have seen that removing males can, under some

12   circumstances, lead to higher population densities through freeing resources and

13   reducing the level of harassment of females. Even though infanticide when performed

14   by males is a 'negative' behaviour in terms of population performance, it differs from

15   the earlier examples in that it can increase when males are removed. Killing males can

16   result in male replacement, and the replacing male may kill the offspring of any

17   previously present males in order to increase his reproductive success (Swenson et al.

18   1997, Møller 2004, Whitman et al. 2004). Selective hunting of males has been shown

19   to result in infanticide in both brown bears (*Ursus arctos*) and African lions (*Panthera*

20   *leo*). In lions, removing a male typically makes a coalition more vulnerable to a

21   takeover by an outside male (Whitman et al. 2004). When this happens, the incoming

22   male will typically evict all older male lions, and kill all cubs under 9 months old

23   (Whitman et al. 2004).

1   Modelling the impact of infanticide on population density suggests that an increase in

2   infanticide caused by removing males from the population can increase the risk of

3   population extinction (Whitman et al. 2004). However, this result depends on the age

4   of the males that are hunted, and reducing the hunting of younger males should allow

5   them to rear a cohort of young, reducing the prevalence of infanticide (Whitman et al.

6   2004). In brown bears, infanticide caused by selective hunting can lead to a dramatic

7   decline in cub survival (Swenson et al. 1997). Comparing populations with and

8   without selective hunting of males revealed suggested that infanticide was responsible

9   for reduced cub survival, which led the author's to predict that removing one adult

10   male from the population was equivalent to killing between 0.5 and 1 female

11   (Swenson et al. 1997). Hunted populations of bears are predicted to be highly

12   susceptible to population extinction (Wieglus et al. 2001), and infanticide may be one

13   important factor of this. Finally, there is experimental support for the importance of

14   infanticide in shaping population dynamics: a field experiment in which male root

15   voles (*Microtus oeconomus*) were removed nearly halved population growth

16   (Andreassen and Gundersen 2006).

17   Infanticide, in combination with the possibility of sperm limitation, could exacerbate

18   the effects of selectively hunting males, as fecundity is reduced both by decreasing the

19   probability that a female is fertilized and an increased likelihood of infanticide. In the

20   barn swallow, *Hirundo rustica*, for example, male quality was negatively associated

21   with the degree of infanticide in the population due to the ability of males to defend

22   nests against infanticidal males (Møller 2004). However, the same study also found

23   that, at lower population densities, infanticide was less prevalent, most like due to a

24   relatively higher proportion of males that are able to find a mate (Møller 2004). Such

1 a density-dependent effect could potentially reduce the risk that infanticide poses to

2 the population by reducing its prevalence as the population approaches low density

3 (see also Kokko and Rankin 2006).

4 *Not all males are nasty*

5 As a caveat, it should be noted that males can also influence female fitness in a

6 positive way, by providing direct benefits for females they mate with (Møller and

7 Jennions 2001). In this paper we have contrasted the fundamental reason why females

8 require males, i.e. their fertilization ability, with several potential negative effects that

9 males can have on female fitness.

10 In species with biparental care (Trivers 1972), removing the social mate can have

11 particularly negative impacts, as the social mate is probably the only male willing to

12 provide paternal care, and he may also defend the female against other male intruders

13 (Sergio and Bogliani 2001). It has been shown that male parental care can increase the

14 survival and number of offspring (Johnson et al. 1993, Reid et al. 2002, Wright 2006).

15 Consider a case where a single-parent brood has lower survival than a brood

16 biparentally cared for. Despite a trade-off between abandoning a nest and offspring

17 survival, females may benefit by abandoning a brood to nest elsewhere if this allows

18 them to found a new nest (Székely and Cuthill 2000). Thus, if females use male

19 parental care efforts in this way, the reproductive output of the population could

20 significantly increase: such a solution is possible if two parents caring each for their

21 own brood (as, for example, in some shorebirds) result in more surviving offspring

22 than two parents caring for the same brood. In general, removing males can have a

1   significant influence on population recruitment in species with paternal or biparental

2   care.

3   Males can also provide direct benefits to females through substances transferred in

4   seminal fluids (Møller and Jennions 2001). Because of this, females mating at

5   intermediate mating rates may have lower fitness than those with higher mating rates,

6   as they miss out on the beneficial nuptial gifts provided by males (Arnqvist et al.

7   2005). For such situations, we look at the case when $k = -1$, in the model presented by

8   equation 2, to look at how increased mating may increase female fecundity through

9   direct benefits provided by males (figure 2b). In such a case, we find that density

10   increases with the proportion of males, and again this depends on whether the mating

11   rate is based on the sex ratio or the absolute density of males. Interestingly, after a

12   certain amount of male mortality, male deaths no longer have a discernable influence

13   on the absolute density, suggesting that the effects of direct benefits are mostly

14   important when there are very many males in the population (figure 2b).

Sexual dimorphism and resource use

16   In Figures 1 and 2, we assumed a simple form of density dependence in which males

17   and females had equal effects on the carrying capacity: adding one individual of either

18   sex diminishes resource availability equally between both sexes. However, sexual

19   selection often leads to size dimorphism (Fairbairn 1997). In birds and mammals,

20   males are often larger than females, while female-biased sexual size dimorphism

21   (hereafter SSD) predominates among invertebrates and poikilothermic vertebrates

22   (Fairbairn 1997). Assuming that males and females use the same niche, resource use

23   increases with body size, and the resource in question plays a central role in density

18

1 dependence, we can expect that sex ratios will have an effect on resource availability

2 and hence the growth rate of a population, with obvious management implications

3 (e.g. Langvatn and Loison 1999, Matsuda et al. 1999, Clutton-Brock et al. 2002).

4 We can illustrate this phenomenon using the model above (equation 1). For

5 simplicity, we shall now assume that sperm is not limiting, and that therefore $f(F,M) =$

6 1. Equation 1 can still be used to describe the dynamics, but $g_i(F,M)$ is now written as

7 $g_i(F,M) = (\theta_M M + \theta_F F)\delta_i$, where θ represents the effect of males and females on

8 the carrying capacity. We can scale θ_M and θ_F so that they are relative to each other:

9 $\theta = \theta_M / \theta_F$, so the function becomes $g_i(F,M) = (\theta M + F)\delta_i$. This allows us to re-

10 write equation 1 as:

$$\frac{dM}{dt} = brF - (\theta M + F)\delta_M M$$
$$\frac{dF}{dt} = b(1-r)F - (\theta M + F)\delta_F F$$

11 (4)

12 If sexes do not differ in their mortalities, we predict that high values of θ diminish

13 equilibrium population sizes: male-biased sexual size dimorphism has a negative

14 effect on populations (Figure 3a). However, large body size often also means higher

15 mortality under resource limitation. Males that allocate disproportionately to

16 ornaments or weapons, are larger, or behave more aggressively than females put

17 themselves at risk (Kodric-Brown et al. 2006, Møller and Nielsen 2006). There is

18 indeed evidence for greater sensitivity of males to poor conditions, that often

19 correspond to high density (e.g. Gaskin et al. 2002, Kokko and Rankin 2006). Hence

20 any effect of a difference in resource consumption may be buffered by males dying

19

1 off at a larger rate than females at higher densities (Figure 3b).

2 Kokko & Brooks (2003) showed in a similar model that increased male vulnerability

3 can increase population sizes when males consume a larger proportion of resources

4 than females. This will compensate for their negative effect on population growth, and

5 may even mean that strong male-biased SSD increases equilibrium population sizes

6 compared with a one-sex model (Figure 3b). The equivalent effects happen with

7 female-biased SSD, but as a mirror image: if large females die at high density due to

8 their high energy requirements, the resulting male-biased populations do not allow

9 high population growth, and the population will equilibrate sooner (i.e. at lower

10 density).

11 How likely are strong effects of SSD on population growth? The question of male vs.

12 female resource use has been most extensively studied in ungulates (for a review see

13 Mysterud 2000), where resource use differences can be strong and they also pose

14 interesting management questions as hunters are mostly interested in males (Clutton-

15 Brock et al. 2002). For example, in a study of moose *Alces alces*, a strong correlation

16 between sex-ratio and population density was observed, and it was found that males

17 were smaller when sex-ratios were more female biased (Solberg and Saether 1994).

18 Other taxa appear to have attracted less interest in this respect, but given the ubiquity

19 of SSD, resource use should provide ample opportunities for study. For example, an

20 interesting case is provided by hermit crabs *Diogenes nitidimanus* that rely on sand

21 snail shells (*Umbonium moniliferum*) for shelter (Asakura 1995). Male crabs are

22 larger than females, and appear to be less discriminating in their shell use. Males also

23 seem to be stronger intraspecific competitors for vacant shells than females, which

20

1	may restrict female growth as shell-limited individuals restrain growth until a larger

2	shell is available. Males, however, also have higher mortality, which may indicate

3	greater sensitivity to shell-limitation stress, and the natural populations are

4	consequently female-biased (Asakura 1995).

5	However, the situations depicted by Figures 3a & b do not form an exhaustive list of

6	the possible effects of resource use of males and females. Below, we review prospects

7	and evidence for population effects of two further factors that can influence resource

8	use: correlated responses to selection, and sexual segregation.

9	*Female traits as correlated responses to selection on males*

10	Sexually selected traits are characteristics that improve the access to reproductive

11	partners. Unless both sexes suffer from limited access to mates (e.g. due to low

12	mobility), such selective pressures should be felt by one sex only. However, perfect

13	sex-limited expression of traits does not evolve easily in an instant. Many traits, body

14	size included, are influenced by multiple loci, and selection pressure in one sex often

15	produces a correlated response in the other, leading to a deviation from the optimal

16	trait size in both sexes (e.g. Chippindale et al. 2001). Such correlations can break

17	down over time, but significant evolutionary lags are often expected (Rhen 2000).

18	Consequently, females can exhibit traits that are suboptimal regarding female

19	reproductive performance. This can be hypothesized to have a negative impact on

20	population growth, but we are not aware of any studies explicitly testing the idea.

21	There is evidence, however, for some of the components of the hypothesis: in the case

22	of body size with male-biased SSD, females can evolve to be larger as a correlated

23	response (Fairbairn 1997, Andersson and Wallander 2004). Large body size

1   typically implies small growth rates ("slow-fast" life history continuum, e.g. lizards:

2   Clobert et al. 1998), birds: (Saether and Engen 2002, Saether et al. 2002), and this

3   remains true even in fishes despite the fact that largest-bodied females often have the

4   highest fecundity (Goodwin et al. 2005, Reynolds et al. 2005). Large body size also

5   correlates with low population densities across many taxa (Colinvaux 1978,

6   Blackburn and Gaston 1999, Saether and Engen 2002). In principle, negative effects

7   of other sexually selected traits could have similar effects on population performance,

8   but we are not aware of any studies showing this, and moreover, it often requires

9   careful experimentation to test whether the expression of a sexually selected trait in a

10 female is a correlated response to selection on males, or an independently adaptive

11 trait (e.g. Emlen et al. 2005).

12 **Sexual segregation**

13 For simplicity, our models (Figures 1-3) ignore the possibility of sexual segregation in

14 niche use. Given the often markedly different body sizes of females and males, it is

15 perhaps surprising that their feeding niches are so often identical: for example, in a

16 study of shorebird sexual dimorphism, this fact allowed Székely et al. (2004) to use

17 bill length as a variable that is subject to functional selection pressure rather than

18 sexual selection. The Huia bird (*Heteralocha acutirostris*) is an example of a species

19 where bill shape and length differ widely between the sexes, the female's bill being

20 long and curved, the male's strong and short. This does not necessarily mean that the

21 feeding niches evolved to be separate, however: it has been hypothesized that the bird

22 foraged in pairs, the male breaking up rotting tree trunks and the female gaining

23 access to insect prey using the thin curved bill.

1 Sadly, empirical tests can no longer be performed as the species only persisted in New

2 Zealand until the early 20th century (http://www.terranature.org/huia.htm). Still, the

3 uniqueness of Huia type bill dimorphism does pose the question why vertebrate

4 species do not more often opt for wholly divergent foraging options for males and

5 females. Extreme sexual size dimorphism in some fishes form perhaps the best

6 examples (in extreme cases, dwarf males merge with females, e.g. Pietsch 2005). In

7 general, invertebrates show perhaps better examples of drastic resource partitioning

8 between the sexes than vertebrates. Males and females of the Mediterranean hermit

9 crabs *Calcinus tubularis* differ dramatically in their shelter use. Males use loose

10 shells, and females inhabit attached tubes (Gherardi 2004), and this resource

11 partitioning reduces competition between the sexes. In insects, adult stages often

12 differ in their feeding habits. For example, females of most mosquito species need

13 vertebrate blood to form eggs, while both sexes feed on nectar (Foster 1995). Whether

14 this has population dynamic consequences is unclear, however, as the dynamics of

15 many insect populations is largely determined in the larval stage.

16 Milder forms of differentiated resource use (ecological segregation) between the sexes

17 appears common in vertebrates, however (e.g. Mysterud 2000). For example, both

18 sexes of southern giant petrels (*Macronectes giganteus*) feed mainly on penguin and

19 seal carrion, but the smaller females also feed extensively on fish, squid and

20 crustaceans (Forero et al. 2005). Sexual segregation refers to situations where males

21 and females can in principle utilize the same resource, but the sexes differ

22 behaviourally such that their resource utilization patterns become different. This has

23 implications for population growth as well as correct estimation of vital rates and

24 resighting probabilities (Härkönen et al. 1999). There is an ongoing debate on the

1 reasons behind segregation, particularly in ungulates (Ruckstuhl and Neuhaus 2006),

2 but possibilities across taxa are likely to extend beyond the 'social selection' and

3 'activity budget' hypotheses mostly discussed in the ungulate literature.

4 A likely determinant of sexual segregation is that males (particularly when they are

5 the larger sex) are also behaviourally dominant, and drive females into using poorer

6 microhabitats. Good evidence for this exists e.g. in wintering migratory birds: stable

7 isotope studies have revealed that male American redstarts *Setophaga ruticilla* occupy

8 the best (mangrove) habitat, forcing females and juveniles to over-winter in sites

9 (inland scrub) that do not allow for good performance (Marra 2000). An experiment

10 that removed old, dominant males led to females and juveniles upgrading to

11 mangrove. These birds maintained body mass from winter to spring, departed earlier

12 on spring migration, and returned at a higher rate in the following winter (Studds and

13 Marra 2005). On a larger spatial scale, the wintering areas of many birds are

14 segregated, so that the distances migrated can differ significantly between the sexes

15 (Myers 1981, Cristol et al. 1999, Nebel et al. 2002). This can occur over oceans too:

16 Black-browed albatross *Thalassarche melanophrys* females over-winter several

17 degrees further north and west than males (Phillips et al. 2005), as do female giant

18 petrels (Gonzalez-Solis et al. 2000). Whether this relates to site quality is unclear, but

19 in the case of female giant petrels, their longer trips and foraging further west forced

20 them into areas with more long-line fishing (a significant human-induced mortality

21 risk, Gonzalez-Solis et al. 2000).

22 A mammalian study also shows a counterexample where males are forced into poorer

23 habitats despite male-biased sexual size dimorphism: most males of Galapagos sea

24 lions (*Zalophus californianus wollebaeki*) have to use suboptimal inland habitats, due

1 to a combination of strong intrasexual selection and female avoidance of male

2 harassment (Wolf et al. 2005). Avoidance of sexual harassment probably deserves

3 much more attention as a factor influencing the spatial distribution of individuals (e.g.

4 Agrillo et al. 2006), yet unlike the sea lion example, in general it does not guarantee

5 that females have access to superior habitats. In guppies, sexual harassment has been

6 shown to drive females into areas of high predation risk (Croft et al. 2006). Males,

7 being the more vulnerable sex in the presence of predators, avoid these dangerous

8 areas, which highlights the complexity of ways in which sexual dimorphism can

9 impact female fitness.

10 Sexual segregation may diminish the effect of males on population densities, as

11 resource partitioning means that males and females will not be in direct competition

12 for resources. However, this conclusion is reversed if segregation occurs as a result of

13 dominant males who prevent females from using preferred resources. Ours is not

14 meant to be an exhaustive list of sexual segregation and the associated differences in

15 habitat or resource use, but it highlights the various possibilities how intraspecific

16 competition can alter the resources available to female reproduction. Insofar this

17 means poorer resources for females, the effect of males is likely to be negative; if this

18 leads to higher mortality of females too, the effect might be amplified, as females then

19 have to compete for resources in a male-biased population.

20 **Discussion**

21 We have shown that males can have a diverse range of effects on models of

22 population density: resource use alone predicts that the relative density of males will

23 often influence population growth, and there are several other mechanisms that imply

1   that "males matter". The direction of the change depends on the behaviour of the

2   sexes, and the extent to which each sex contributes to density-dependent processes.

3   There are many instances where the removal of males appears to have little effect on

4   population persistence, indicated by examples such as extreme sex ratio bias in the

5   face of male killing *Wolbachia* (Dyson and Hurst 2004), or the simple observation

6   that populations subjected to selective harvesting of males can be sustainable if it is

7   not excessive (Milner-Gulland and Lhagvasuren 1998). However, persistence does not

8   mean that population growth has not been impacted: in the example of butterfly

9   system subject to Wolbachia, dearth of males caused a 57% reduction in average

10   female fecundity (Dyson and Hurst 2004).

11   The importance of males in population dynamics is not limited to conservation action.

12   Malarial pest control programmes have mostly focused on the biology of the female,

13   and taking male biology into account can bring valuable information to help control

14   the disease (Ferguson et al. 2005). As such, functions should be considered as

15   plausible examples representing biological control programmes have benefited by

16   factoring males into population dynamics, and the realisation of the role males may

17   play in population dynamics obviously has potential benefits in both pest control

18   (Ferguson et al. 2005, Schliekelman et al. 2005) and conservation biology. Males

19   have also been an important factor in recent demographic studies on humans (e.g.

20   Löfstedt et al. 2004). A result of the one-child family policy in China, for example,

21   has resulted in a higher number of abortions of female foetuses relative to male

22   foetuses, a factor which has resulted in strong male-bias in some areas (Löfstedt et al.

23   2004, Hesketh et al. 2005). The results of this may be just as severe for human

24   populations as they are for animal populations, especially with regard to male

1 harassment of females and the socio-economic problems that male populations bring

2 to society (Hesketh and Xing 2006).

3 One-sex models of population dynamics are highly competent at describing

4 population dynamics. Based on our simple models and the view from the literature,

5 we can expect surprising deviations from the predicted if male dependence of

6 population dynamics has not been incorporated in the dynamical explanation.

7 Empirically derived graphs depicting changes in population growth (or more

8 explicitly still, changes in the numbers of females and males separately) at various

9 male and female densities would be a welcome sight in the literature.

10 *Future directions*

11 Very few studies have actively looked at how the adult sex ratio has had an impact on

12 population size, and the examples covered in this paper show that removing males can

13 range from having no effect (e.g. Dyson and Hurst 2004), to a positive effect (e.g. Le

14 Galliard et al. 2005) or a negative effect (e.g. Milner-Gulland et al. 2003).

15 Mathematically, the best population growth is expected in female-biased populations

16 (Ovidiu Vlad 1989), thus it is remarkable how we lack studies that relate population-

17 wide sex ratios and population densities to reproductive output (most such studies are

18 concerned with detecting sperm limitation, Danthanarayana and Gu 1991, Hines et al.

19 2003, Milner-Gulland et al. 2003, Levitan 2004). But then, there are surprisingly few

20 studies that have ever attempted the far simpler task of graphing population growth

21 against population density: Sibly & Hone (2002) found only 25.

22 There are therefore still many gaps in our knowledge of how males affect population

23 dynamics. It is important to note that the   processes given in table 1 can be divided

1 into either "evolutionary" or "ecological" problems, according to the attention they

2 have attracted, even though we have shown here that all processes listed are capable

3 of altering population densities and thus being ecologically important. For example,

4 sexual conflict has remained in the realm of evolutionary biology, where researches

5 are interested in questions such as why females mate multiply (Arnqvist and Rowe

6 2005), while very little remains on how such behaviours can influence density (but

7 see Kokko and Brooks 2003, Le Galliard et al. 2005). Similarly, parental care and

8 nuptial gifts have been primarily studied from an evolutionary angle, and the potential

9 effects of their absence on population dynamics remain unexplored. In contrast,

10 infanticide has been studied from a population and conservation perspective (Swenson

11 et al. 1997, Møller 2004, Whitman et al. 2004) in addition to its evolutionary roots

12 (O'Connor 1978, Young and Clutton-Brock 2006). Meanwhile, there have been a

13 number of studies on how differential resource use might influence density, or how

14 the sex ratio could affect female fertilisation rate, but studies on the latter are rather

15 conflicting, with some systems appearing almost immune to the effects of sperm

16 limitation.

17 What should be clear from our paper is that, with the exception of studies on

18 ungulates, the vast majority of situations in which males might "matter" have been

19 studied by their influence on individual female fitness rather than population-wide

20 reproductive output. The strength of density-dependence in birth and death rates is

21 likely to affect the extent to which higher female productivity will increase population

22 density. As a result, rather than just looking at per female productivity, we strongly

23 advocate investigating the role of males on population dynamics in a population

24 setting.

1 *Model limitations*

2 The models presented in the chapters are illustrative, but certainly simplistic. This

3 reflects the lack of two-sex models describing how different aspects of male

4 behaviour can influence population densities. There have been a number of two-sex

5 models of population dynamics, but these have generally focused on the specific

6 problems of Allee effects (Berec et al. 2001, Engen et al. 2003, Bessa-Gomes et al.

7 2004) and stability (Caswell and Weeks 1986, Doebeli and Koella 1994, Lindström

8 and Kokko 1998, Ranta et al. 1999, Flatt et al. 2001), rather than aiming at solid

9 predictions of population densities despite the importance of such a measure for

10 population management. Our functions should be considered as plausible examples

11 representing first steps of the required modelling effort. For example, our density-

12 dependent mortality g is rather simplistic, but allows us to spell the intuitive reasoning

13 behind the relative contributions of males and females to density dependence.

14 Similarly, the function f, which describes females fecundity as a function of male and

15 female density, is based on evidence from one study, showing that males only become

16 limiting at highly female-biased sex-ratios (Milner-Gulland et al. 2003). Other

17 functions could be used to incorporate different mating systems (see Bessa-Gomes et

18 al. 2004). Similarly, male harassment could be modelled in a different way,

19 incorporating both juvenile and adult age classes (Le Galliard et al. 2005) or being

20 more explicit about the exact mating system. There is clearly much room for further

21 theoretical advances in this field too.

22 *Other effects*

23 In our review we mainly concentrated on effects of males on equilibrium population

1 densities, but the presence of males may also have an influence on the stability of the

2 equilibrium (Doebeli and Koella 1994, Flatt et al. 2001). While some studies have

3 found that sex does not necessarily affect population dynamics (Castillo-Chavez and

4 Huang 1995), others have found that a small amount of sexual reproduction can

5 stabilize population dynamics (Doebeli and Koella 1994, Flatt et al. 2001). However,

6 the stabilising effect of sex often depends on the details of the mating system:

7 deviations from monogamy often mean that sexual reproduction can destabilize

8 dynamics rather than stabilize it (Caswell and Weeks 1986, Lindström and Kokko

9 1998, Ranta et al. 1999). Unstable dynamics generally occurs at high growth rates,

10 and the mixed results on stability make sense in the light of our current results: we

11 generally find that various aspects of male behaviour can either promote or hinder

12 population growth, thus future models should be explicit about considering a wide

13 enough range of processes if they are to make general conclusions.

14 Our study concentrated on direct costs and benefits provided by males.

15 Recombination is known to have many benefits for the population, and has been used

16 as a major argument for why sex is so prevalent (Hadany and Feldman 2005), and the

17 type of males present as well as female mate choice may affect the effective

18 population size (Wedekind 2002). We have ignored the question of whether the

19 presence of males can provide genetic benefits to females (for recent reviews see

20 Andersson and Simmons 2006, Kokko et al. 2006), and whether competition between

21 males can decrease the mutational load of sexual populations (Radwan 2004). How

22 immediately such effects would show up in a study of population dynamics is

23 currently unknown.

1 *Conclusion*

2 All models are always approximations (Levins 1966) and ecology and evolution has

3 certainly progressed substantially with single-sex models. However, with our

4 increasing understanding of the effects that individual behaviour has on population

5 dynamics (Sutherland 1996) and the pressing need to be able to adequately predict

6 how populations will respond to anthropogenic change, it is increasingly necessary to

7 consider that males male also have an important role in population processes. This is

8 particularly important if populations exist at sex ratios or densities that have not been

9 frequently encountered in the evolutionary past. Whether planning actions of

10 conservation management or pest control, one should not forget the potential of males

11 in influencing the dynamics of those populations. We thus encourage more systematic

12 study to the effects that males have on population dynamics.

13 **Acknowledgements**

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14

1 **Figure legends**

2 Figure 1 – (a) The fertilization probability of a female as a function of the adult sex

3 ratio (ASR, proportion of adult males). (b) The influence of male mortality on the

4 equilibrium population density (i.e. the total number of males and females) for

5 different sensitivities to ASR (I-IV). The different lines represent different

6 sensitivities of fertilization probability to changes in the ASR: $c=0$ (I), $c=0.01$ (II),

7 $c=0.1$ (III), c=1.0 (IV). The adult sex ratio is manipulated by changing the primary

8 sex-ratio r. Other parameters are $b=50$, $\delta_F=10$ and $\delta_M=10$.

9 Figure 2 – The equilibrium population density (total number of males and females) as

10 a function of male mortality, where males inflict direct costs on females (figure 2a,

11 $k=1$) or provide direct benefits (figure 2b, $k=-1$). Three scenarios are represented by

12 the lines: I Male harassment of females not influenced by male density ($\gamma=0$), II male

13 harassment of females influenced by male density ($\gamma=1$, $\alpha=1$) and III male harassment

14 of females influenced by the sex ratio ($\gamma=1$, $\alpha=0$). Other parameters are $b=50$, $\delta_F=10$

15 and $r=0.5$. The dotted line represents the point where the population is driven to

16 extinction; zero is the only stable equilibrium in this case. Only stable equilibrium

17 points are shown. Note the difference in scale between figure 2a and figure 2b.

18 Figure 3 – The equilibrium population density (i.e. the total number of males and

19 females) as a function of (a) male contribution to density-dependence (the amount that

20 males consume relative to females, which is given by θ) and (b) male mortality (δ_M)

21 under higher male resource competition. Mortality is given by the function $g_i=(\theta M+F)$

22 δi, where i denotes the respective sex. In (a) $\delta_M=10$, while in (b) $\theta =2$. Other

23 parameters are $b=50$, $\delta_F=10$, and $r=0.5$.

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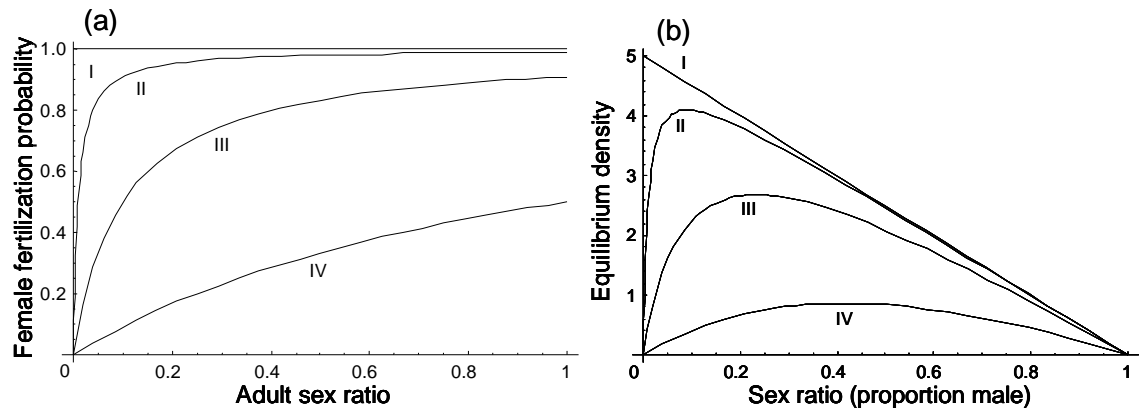
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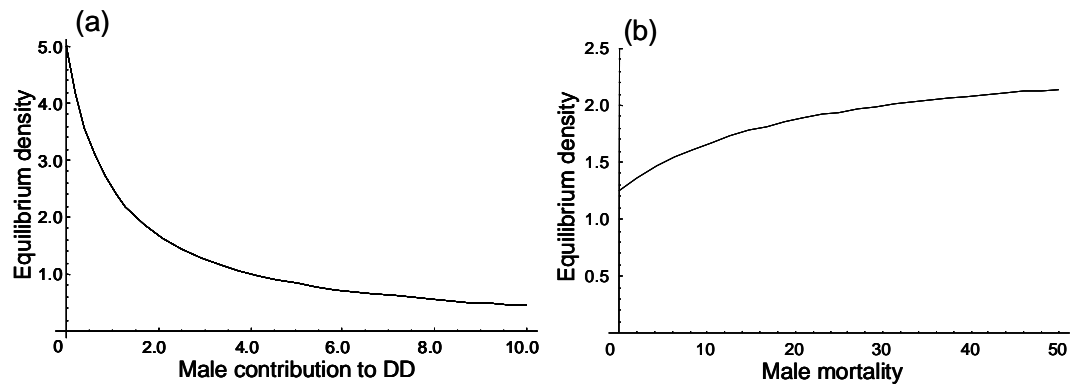
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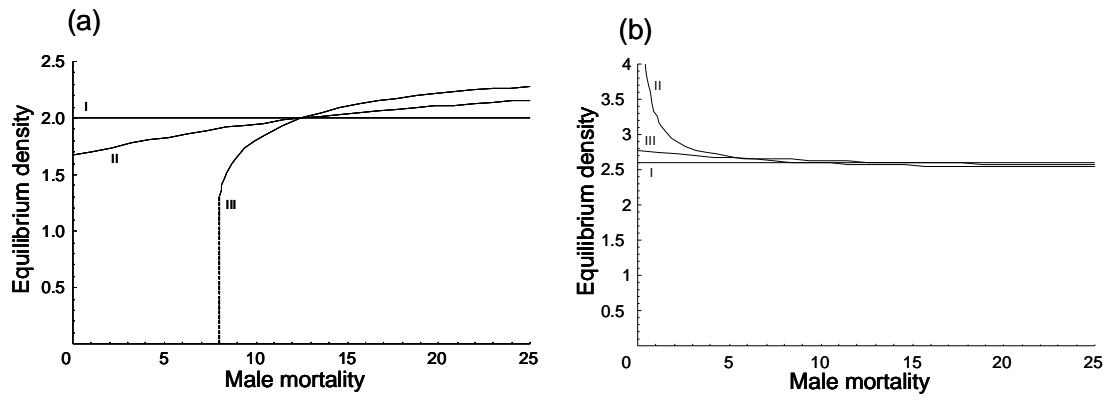
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1   Figure 3

1   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

2