PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B

rstb.royalsocietypublishing.org

Review

Cite this article: Holman L, Kokko H. 2013 The consequences of polyandry for population viability, extinction risk and conservation. Phil Trans R Soc B 368: 20120053.
http://dx.doi.org/10.1098/rstb.2012.0053

One contribution of 14 to a Theme Issue 'The polyandry revolution'.

Subject Areas:
evolution, ecology

Keywords:
mating systems, sexual conflict, cost of sex, demography, persistence

Author for correspondence:
Luke Holman
e-mail: luke.holman@anu.edu.au

Royal Society Publishing
Informing the science of the future

The consequences of polyandry for population viability, extinction risk and conservation

Luke Holman and Hanna Kokko

Centre of Excellence in Biological Interactions, Division of Ecology, Evolution and Genetics, Research School of Biology, Australian National University, Canberra, Australian Capital Territory 0200, Australia

Polyandry, by elevating sexual conflict and selecting for reduced male care relative to monandry, may exacerbate the cost of sex and thereby seriously impact population fitness. On the other hand, polyandry has a number of possible population-level benefits over monandry, such as increased sexual selection leading to faster adaptation and a reduced mutation load. Here, we review existing information on how female fitness evolves under polyandry and how this influences population dynamics. In balance, it is far from clear whether polyandry has a net positive or negative effect on female fitness, but we also stress that its effects on individuals may not have visible demographic consequences. In populations that produce many more offspring than can possibly survive and breed, offspring gained or lost as a result of polyandry may not affect population size. Such ecological 'masking' of changes in population fitness could hide a response that only manifests under adverse environmental conditions (e.g. anthropogenic change). Surprisingly few studies have attempted to link mating system variation to population dynamics, and in general we urge researchers to consider the ecological consequences of evolutionary processes.

1. Introduction

A large shift in our understanding of mating systems occurred in the 1970s when birds, the most conspicuously monogamous animals, were shown to be promiscuous. This finding was quickly realized to have important consequences for population management, as illustrated by an unsuccessful attempt to control a perceived agricultural pest, red-winged blackbirds, by vasectomizing males. Bray *et al*. [1] were surprised to find that females paired with sterilized males remained fertile, suggesting that females mate with extra-pair males. At the time, such findings were big news, because they showed that variation in mating systems was a significant and understudied predictor of population dynamics, which could be a key to the success of both pest management and conservation programmes. Since then, much theory has been developed to contrast the population-level consequences of monogamy and multiple mating [2–5], including factors causally underlying mate availability, such as the temporally varying number of males per female [6,7].

The study by Bray *et al*. [1] also illustrates that monandry was long taken as the null model. After Bateman [8] highlighted that fruitfly females benefit less (and sometimes not at all) from multiple mating than do males, the presumed ubiquity of monandry seemed so obvious as to be beneath empirical investigation. Lest the reader now feel condescending towards earlier researchers, it is prudent to note how strongly this belief continues to the present day. Monogamy is still a common assumption in evolutionary and ecological models, and the number of studies seeking to explain polyandry (reviewed in [9,10]) far outweighs the number investigating the evolution of monandry. Although this bias may simply reflect a greater number of polyandrous species, the popular research question 'Why do females mate multiply?' appears to

carry with it the implicit assumption that monandry does not warrant special investigation.

This view of monandry as a null model for female behaviour may be incorrect: it is illuminating to ask why individuals of either sex would evolve behaviour any more sophisticated than mating every time a potential mate is encountered [11]. Monandry requires a complete loss of female receptivity after one mating or, in the case of social and genetic monogamy, specific acceptance of mating advances by one male, but not others. The propensity of females to reject additional mates is also able to respond to selection [12,13]. In short, monandry is an evolved outcome that requires an explanation. We therefore consider polyandry a more suitable null model, at least in species where individuals typically encounter multiple potential mates.

Defining the scope of this review requires stating precisely what we mean by polyandry. A behavioural ecology textbook usually introduces the reader to monogamy, polygyny, polyandry and polygamy/polygynandry, depending on whether no-one, males only, females only or both sexes mate multiply [14,15]. Given that multiple mating by both sexes has proved to be commonplace [10,16], one might expect polygynandry to have swamped all other terminology. However, this is decidedly not the case: a Web of Science topic search for *polygynandr** (conducted on 18 July 2012) yielded 138 hits, a meagre result compared with 1860 for *polyandr** and 3243 for *polygyn**. This appears to reflect confusion over whether 'polyandry' and 'polygyny' are defined via the ability of one sex to control access to mates via social pair bonds [17] ([15] recommends 'promiscuity' for cases where no such bonds exist), or if polyandry is taken to simply mean that a female mates multiply, whether or not the system is also polygynous. It appears that common usage has shifted away from defining polygyny and polyandry as mutually exclusive alternatives (as in [14,15,17]). Here, we define polyandry in its broad sense (as in [9,13,16,18]): populations in which females sometimes mate with more than one male, and/or have their eggs fertilized by more than one male, are polyandrous. Nevertheless, the diversity of polyandrous mating systems presents us with a clear challenge. As we will see below, it matters greatly whether multiple matings occur rapidly enough that sperm of different males compete over fertilization of the eggs.

With this review, we aim to identify routes by which polyandry can affect population fitness, with a focus on conservation biology. We also attempt to link individual-level effects of polyandry to their demographic consequences, although we conclude that existing data make it difficult to do so reliably. Polyandry is shown to have a great many potential positive and negative effects on populations, and we endeavour to synthesize these and highlight potentially fruitful avenues for future research.

2. Multiple mating modifies the cost of sex

Whether a female is monandrous or polyandrous depends on mate encounter rates as well as on the behaviour of males and females when encounters happen; the behaviours themselves evolve according to the net fitness consequences of polyandry for the individuals involved, and the cost they pay to either resist or to seek additional matings. Even if polyandry has a net negative effect on female inclusive fitness, it can persist if the costs of resistance would outweigh its benefits ('convenience polyandry'; [19–21]). Note also that stochastic variation in mate availability might make some females monandrous and others polyandrous even if they use identical behavioural rules [11,22].

Whatever the selective forces (if any) behind polyandry, its consequences are profound. This is especially true when polyandry occurs within a breeding cycle, leading males to be uncertain about the parentage of their mates' offspring, because uncertain paternity is a core reason why male parental care tends to be less common than female care [23,24]. Curiously, this holds true even in systems where females mate multiply in order to receive care from more than one male: care effort per male is still predicted to decline with polyandry [24]. This means that polyandry influences a fundamental property of two-sex systems: the famous twofold cost of sex [25]. Under specific conditions, asexual reproduction doubles the fitness of individual females and thus population fitness. However, the cost of sex is only exactly twofold when a suite of surprisingly stringent assumptions is met: specifically, the existence of males should have no effect on female reproductive output. For example, there should be no paternal care, no harmful male harassment of females, no mate or sperm limitation, no genetic benefits of sexual selection, and a male must be equivalent to a female in intraspecific competition for food and other resources [25].

Polyandry is expected to increase the cost of sex in the great majority of cases. By selecting against paternal investment, polyandry increases the cost of sex [23,24]. Further, it can favour male traits that displace females from their phenotypic optimum; below, we review such instances in the context of intra- and inter-locus sexual conflict, which can increase the cost of sex beyond the twofold baseline that arises in the total absence of paternal investment. Sexual conflict, of course, can also exist under monandry or even monogamy: if there is a biased operational sex ratio, selection may favour traits that improve competition for mates despite reducing productivity at the mated stage. In general, however, polyandry greatly increases the opportunity for sexual conflict [26], and thus we expect much of the cost of sex to be a direct consequence of polyandry.

3. Demographic consequences of inter-locus sexual conflict

Inter-locus sexual conflict occurs when the sexes have differing optimal outcomes in a male–female interaction [27]. It may occur in all mating systems except those in which strict lifetime monogamy is the only option and the sex ratio is even [28]. Because it can produce sperm competition, polyandry creates the potential for conflict over female-mating rate—for example, males may attempt to prevent their mates from mating with another male. Sexual conflict over female-mating rate may, therefore, be stronger in polyandrous than monandrous species. Conversely, sexual conflict over the mating rate may sometimes be lower in polyandrous species, because females are mating at a rate that is closer to the male optimum. Polyandry is similarly expected to affect sexual conflict over a range of other traits. For example, polyandry can select against male care [23,24,29] and promote the evolution of harmful competitive

adaptations [26]. A few studies, which we will now review, have addressed how inter-locus sexual conflict affects demographic parameters. However, we note that there is ample scope for additional research.

Studies of desertion in birds provide evidence that reduced male care can cause a population-wide decline in productivity. For example, penduline tits often desert their nest in the hope that their partner will stay and rear the eggs alone. Deserting is thought to be advantageous on average, even though the parent left behind often deserts as well (reviewed in [30]). This conflict leads to very many nests (30–40%) being deserted by both parents, and this wasted effort may substantially reduce the number of young produced each year. Although biparental desertion might be an extreme example, reduced productivity when males do not care for young generalizes to a very broad pattern: in a dataset of 980 bird species, female-only care led to a 20 per cent reduction of productivity compared with other types of care [31].

Male harassment and copulation attempts have been shown to depress female survival and fecundity in several diverse taxa (e.g. water striders [32], lizards [33], sea lions [34], *Drosophila* [35]). Experimental evolution studies manipulating the mating system have provided some of the strongest evidence that polyandry selects for both elevated male harm and costly female resistance to that harm [36–40]; for example, Crudgington *et al*. [41] showed that males evolved under polyandry courted females more frequently, and that females housed with these males produced fewer progeny than females interacting with males evolved under monogamy. Additionally, female dung flies evolved under polyandry were found to be less fecund than monogamous females when mating only once, implying that female adaptations to male harm have a cost that outweighs the potential genetic benefits of sexual selection [40].

In a twist to the conflict over mating rates, males may attempt to increase their fitness by imposing a suboptimally low future mating rate on their female mates [28]. Adaptations such as mating plugs [42] and mate guarding are, therefore, potentially harmful to female fitness. Mate guarding appears particularly harmful to female reproduction when it makes females unable to escape senescent [43] or sperm-depleted males [44]. However, mate guarding is a good example of a male-mating adaptation that can actually increase female fitness, e.g. if the mate performs vigilance duties or deters harassment from other males. In gammarids, guarded females had a shorter inter-moult duration suggesting a benefit of being guarded [45], and female crickets guarded by a male were less likely to be predated [46]. Male attempts to increase fertilizations gained with a particular female can also occur after mating: in *Drosophila* and other insects, males transfer seminal fluid proteins that inhibit further matings and induce females to lay more eggs in the short term [47], at a cost to female lifetime reproductive success [48].

Another detrimental effect of polyandry is its positive effect on the incidence of sexually transmitted infections (STIs). These infections likely have population dynamic consequences, particularly when the parasite sterilizes, but does not kill the host, leaving it to mate and compete with uninfected individuals [49]. Confounding this problem is the prediction that males should often be selected to invest less in avoiding disease or clearing infections than females [50]. Lowered male immune defence should exacerbate sexual conflict over mating rates in the case of STIs, and turn males into easy targets for pathogens, in turn increasing the incidence of disease in females [51].

4. Does it matter?

There is abundant evidence that female lifetime productivity can be reduced by male adaptations to polyandry (for further examples see [26]). However, the extent to which such negative effects show up in measures of population performance (ultimately affecting extinction rate) is much less clear, principally because population dynamics are not solely driven by juvenile production. Demographically, male-induced harm may have no visible effects as long as the birth rate remains greater than the death rate: for example, many juveniles may experience density-dependent mortality, and adult populations are then expected to be of similar size in each generation regardless of variation in female fecundity. The relevant life-history stage determining population limitation is crucial here. However, changes in the environment (for example, anthropogenic impact) can adversely affect the birth and death rates, and this may push a population below the threshold of positive growth; populations with greater female survival and fecundity are expected to be more robust to such challenges. High levels of conflict may therefore weaken the capacity of populations to persist in a challenging environment.

It is curious that few studies of sexual conflict have considered the full life-history consequences, together with the relevant ecology, to determine how conflict impacts population growth. In a slightly different context, that of within-sex conflict for breeding opportunities, intraspecific conflict was estimated to have slowed down the recovery of Seychelles magpie robins from 'Critically Endangered' status by 33 per cent [52]. Given that every year spent at a low population size elevates the species-wide vulnerability to environmental hazards [53], it appears possible that conflict makes populations more vulnerable whenever it slows down population growth. By extension, male–female conflict, too, may have real population consequences. Bearded vultures provide an example of such a conflict that is pertinent to conservation biology (the species is endangered in Europe; [54]). This species exhibits bi-parental care, which should lower the cost of sex (because a hypothetical asexual vulture would not raise its young as efficiently as a sexual pair). However, vulture pairs are sometimes joined by an additional male who was not able to find a female of his own. Joining a pair presumably affords males greater fitness than making no attempt to breed, but trios rear substantially fewer offspring than do pairs (likely as a result of antagonism between the males). This male-driven behaviour is a concern when designing conservation efforts.

Theoretical [55] and empirical [33] work suggests that inter-locus sexual conflict coupled with a male-biased adult sex ratio can be very damaging. Male–male competition for matings and fertilizations is essentially a zero-sum game, in which the limiting resource (females/eggs) can diminish as competition becomes more intense. Sexual selection may come to resemble a tragedy of the commons, where the harmful fallout of male–male competition increases female mortality, leading to even stronger competition (and, therefore more harm) for the remaining females, potentially

driving females extinct unless their resistance compensates sufficiently [55]. In principle, this might mean that removing males could in some cases improve the performance of endangered populations. Conservationists are understandably reluctant to consider such extreme measures without good scientific backing. Indeed, intuitive predictions have not always been supported by data. One might expect that males would have a strongly negative effect on population-wide reproductive output in the hihi, *Notiomystis cincta*, a bird with a fierce mating system in which males pin down females in face-to-face forced copulations. However, despite intense harassment, adult sex ratio had little or no effect on adult female survival or the number of fledglings per female [56]. This highlights that the apparent severity of male harm can be misleading. Infanticide is another potential problem for conservation by male removal: in many mammals (e.g. bears, lions), removing paired males can cause unpaired males to kill offspring belonging to the removed males, meaning that removing males could actually negatively affect population growth. Such infanticide would also exacerbate the impact of hunting targeted at males.

Perhaps, the clearest cases of male harm with real-life conservation concern are found in heterospecific contexts. If costs of mating are low for males, males are expected to mate relatively indiscriminately, and the eagerness to mate can extend to heterospecific matings. In *Skiffia bilineata*, a goodeid fish native to Mexico, forced copulations by invasive guppies are a clear threat to native populations [57]. Still, males are not always the sex that causes the majority of the damage during an invasion. While indiscriminate mating habits underlie the problem of feral ruddy ducks, *Oxyura jamaicensis*, hybridizing with the globally threatened white-headed duck *Oxyura leucocephala* [58], a genetic study has found that most crosses in the wild are between female ruddy ducks (the invasive species) and male white-headed ducks [59].

Another context where male harassment can really matter is when it selects for sexual segregation. Although sexual segregation is not always a consequence of sexual conflict over mating rates [60], females have been shown to accept sub-optimal habitat, either to avoid harmful mating attempts by males [61] or because males are behaviourally dominant and force females into inferior habitat in the non-breeding season [62,63]. When sexual segregation is pronounced, conservation measures that protect only part of a species' range might only protect one sex (for a case study on large pelagic sharks and the threat from fisheries see [64]).

Given that current methods for pest management, conservation and hunting/harvesting often alter the adult sex ratio, the links between male traits, male abundance, sexual segregation and population performance appear understudied [65]. The most popular experimental approach is to contrast monogamy with multiple mating, although it would perhaps be more realistic to consider the scenario in which females always encounter multiple males, but the male : female ratio (or the frequency with which females encounter males) varies. In an intriguing experiment of the latter type, Edward *et al*. [66] found that *Drosophila melanogaster* females experienced a shorter lifespan when exposure to males was increased, but because they also laid eggs earlier in life, this rescheduling of their life history resulted in a net benefit if the population was assumed to be growing (life-history theory predicts that the importance of early-life reproduction is elevated in populations that are expanding in size; [67]).

The above arguments illustrate that it is difficult to predict *a priori* the extent to which inter-locus sexual conflict affects population persistence. Male harm may be substantial, but it could be largely mitigated by female counter-adaptations, or might be insufficient to have much impact on population productivity in populations that, despite conflict, still produce many more progeny than can possibly survive. Future studies could aim to quantify explicitly how male harm that has evolved in response to polyandry affects population persistence in a changing environment, and there is a clear need for more theory integrating the ecological and evolutionary consequences of sexual conflict.

5. Demographic consequences of intra-locus sexual conflict

Intra-locus sexual conflict refers to the situation where the optimal phenotype differs between the sexes, leading to an evolutionary compromise that is suboptimal for either sex [27]. Intra-locus conflict might have important consequences for demography; for example, if there is sex-specific selection on a shared trait such as body size, and selection on males moves females off their phenotypic optimum because of cross-sex genetic correlations, female productivity and, therefore, population persistence may be reduced. To our knowledge, no studies have tested for a link between the degree of polyandry and the intensity of intra-locus conflict. However, it seems reasonable to assume that polyandry intensifies intra-locus conflict in many cases, because it imposes additional sex-specific selection pressures relative to monandry and monogamy, as described in §2.

The extent to which sex-specific selection affects population performance probably depends greatly on how much intra-locus conflict has been resolved through the evolution of sexual dimorphism, e.g. through sex linkage or sex-biased gene expression [68,69]. For example, many costly male sexually selected traits such as antlers are absent or reduced in females, which could improve female productivity and, therefore, population fitness. However, recent experiments with *Gnatocerus cornutus* beetles demonstrate 'hidden' intra-locus conflict that exists even when sexual trait expression is limited to males [70]. Beetles were selected for large or small mandibles, a trait that is only well developed in males; as expected, males from the large-mandible lines were more successful at fighting and gaining mates. Even though females lack well-developed mandibles, female fitness was negatively correlated with male mandible size across selection lines because of correlated responses to selection in non-sex-specific morphological traits. This experiment illustrates that female trait evolution will be adversely affected by selection on male-specific traits whenever the latter are genetically correlated with traits expressed in females. Given the ubiquity of genetic correlations among traits, it seems likely that substantial intra-locus conflict will exist even in species with strong sexual dimorphism (though sexual dimorphism should certainly help; [71,72]).

In this context, it is good to remember that selection on males would still negatively impact population growth even if intra-locus conflict were completely resolved through the evolution of sex-limited gene expression. For example, if males grow faster for the duration of parental care, mothers may have to provision sons more (at a cost to daughters);

this applies even if growth has evolved to follow precisely optimal sex-specific trajectories. In principle, mothers may then be selected to produce fewer sons, which would mitigate this conflict; however, full compensation of this type might be rare [73, pp. 22, 74]. Connallon *et al*. [69] also point out that genes that are only expressed in one sex (and, therefore subject to selection half as often) are expected to harbour more deleterious mutations, such that intra-locus conflict imposes a genetic load even after it has been resolved. Additionally, allowing males to approach their phenotypic optimum might amplify any negative consequences of males on population demography, for example, if the better-adapted males were more able to harass females or compete with them for food or territories. 'Risky' male-specific traits (e.g. singing, bright coloration, lowered investment in immunity) might also increase predation and parasite pressure on females, because the males represent easier targets that encourage population growth in natural enemies [5,51,75]. Finally, some of these male adaptations may reduce the density of males to the point where females become mate- or sperm-limited, compromising population fitness. The frequency of 'evolutionary suicide' caused by exaggerated sexual traits that harm the survival of the male is debatable [76,77], in part because selection for trait exaggeration should weaken as the operational sex ratio moves towards females. While sperm limitation does occur in nature [78], we are not aware of evidence showing this to be a consequence of too few males surviving their massive investment in sexual traits. In an intriguingly direct link to multiple mating, however, Charlat *et al*. [79] discuss the special case of *Wolbachia*-infected butterfly populations, where female-mating frequency increases as males become rarer, triggering a cycle of increasing depletion of male-mating resources and female promiscuity. The potential population dynamic consequences appear intriguing, as do cases of male scarcity owing to sex ratio distorting selfish genetic elements [80].

Lastly, many male- and female-imprinted genes are thought to reflect sexual conflict resulting from polyandry over provisioning of the developing foetus in placental mammals, in a similar fashion to conflict over parental care [81,82]. Loci of paternal origin in the offspring are predicted to draw more resources from the mother than are maternal loci, because males may not be the father of offspring produced later in the female's life. Such genomic tug-of-war has been proposed to be a causative agent of human diseases including preeclampsia and mental illness [83,84].

6. Does sexual selection oppose or augment natural selection?

If sexual selection is indeed stronger under polyandry, how does this impact population fitness? Above, we have mainly considered direct demographic effects of male and female trait divergence under polyandry, but long-term population performance also depends on population-level characteristics such as mutation load and adaptation rate. Most studies consider how these traits respond to sexual selection or the presence of sexually antagonistic alleles, which usually leaves the precise link to polyandry undefined. This is likely because the link between polyandry and the strength of sexual selection is understudied. Sexual selection may tend to increase with the degree of polyandry (e.g. by generating conflict over mating rate, and facilitating both pre- and post-copulatory sexual selection), but one could also conceivably make the opposite prediction: in the extreme case in which all females mate with all locally available males, pre-copulatory selection disappears. Intriguingly, we are not aware of any systematic comparative tests that compare the strength of pre-copulatory sexual selection with the degree of promiscuity, although it has been noted that extra-pair fertilizations in birds can either intensify or weaken sexual selection, depending on the covariance between within-pair and extra-pair success [85].

For the purposes of the following section, we tentatively assume that polyandry is positively correlated with the intensity of sexual selection across taxa and then review the population-level consequences of sexual selection, while reminding the reader that this link is relatively unexplored.

(a) Sexual selection and population fitness

Theoreticians have argued that sexual selection might have a number of beneficial effects on populations, such as accelerating the removal of deleterious alleles and the fixation of beneficial ones, because males carrying inferior genes should have reduced reproductive success [86–92]. Crucial to this argument is the assumption that genes affecting male reproductive success also have beneficial effects on traits that affect population fitness [69]. For example, an allele conferring high attractiveness in males might also increase fecundity when expressed in females. If loci affecting male reproductive success tend not to affect any other traits, sexual selection might have little effect on population fitness. Conversely, if a sufficient number of alleles that increase male-mating success are detrimental when expressed in females (or cause the males to harm or compete with females), sexual selection would oppose natural selection and lower population fitness [69,93].

A number of recent studies have attempted to measure whether sexual selection has a positive, negative or negligible effect on female or population fitness, with mixed results (reviewed in [90,94]). Some of the strongest evidence comes from selection experiments in *Drosophila* spp. McGuigan *et al*. [95] studied mutation accumulation lines with and without the opportunity for sexual selection. Male mating success was higher in sexually selected lines, and the majority of *de novo* mutations affecting male mating success pleiotropically affected female productivity in the same direction, suggesting that sexual selection increases both sexual and non-sexual fitness. There was also a non-significant trend for sexual selection to reduce extinction rate. Morrow *et al*. [96] eliminated selection on one sex and measured the change in fitness of the other, and found that the fitness of both sexes declined when either males or females were prevented from responding to selection, suggesting that sexually concordant genetic variation outweighs antagonistic variation. However, the fitness of the unselected sex declined more rapidly, demonstrating the presence of significant amounts of antagonistic variation. Sharp & Agrawal [97] measured the selective consequences of eight deleterious alleles on viability and female fecundity as well as male mating success, and found that in seven out of eight cases natural and sexual selection were aligned (the eighth locus was under sexually antagonistic selection); this is in broad agreement with a large transcriptomic study indicating sexually antagonistic selection on around 8 per cent of

all genes [98]. Another study evolved maladapted *D. melanogaster* populations under enforced monogamy or promiscuity; sexual selection imposed a net cost on productivity, and sexual selection did not improve egg-to-adult viability [99]. Studies of bulb mites *Rhizoglyphus robini* have also produced evidence that male–male competition is beneficial for populations; sexual selection was found to improve viability [100] and female fecundity [101], and to reduce the rate of extinction [102].

A few studies have examined whether sexual selection accelerates adaptation to a novel environment [91], which might have important implications for the long-term persistence of populations. In *Callosobruchus maculatus* beetles, populations with the opportunity for sexual selection adapted more rapidly to a novel food source than those without. However, two studies of *Drosophila* found no such evidence: Holland [103] found no difference in the rate at which polyandrous and monogamous populations adapted to thermal stress, whereas Rundle *et al*. [104] found no effect of sexual selection on adaptation to novel food. Bonduriansky [105] also raised the intriguing possibility that sexual selection increases the rate of adaptation and ecological diversification by pushing species off their naturally selected phenotypic optimum, allowing them to cross fitness valleys to reach higher peaks in the adaptive landscape.

(b) Post-copulatory sexual selection and population fitness

Some genetic elements adversely affecting population fitness might have no effect on male mating success, but might be a handicap in post-copulatory sexual selection, such that they could only be screened out by polyandrous females. A fascinating example is provided by studies of *Drosophila pseudoobscura* populations harbouring an X-linked selfish genetic element that distorts both Mendelian segregation and the sex ratio by killing the Y-bearing sperm of male carriers. Males with this element pass it on in 100 per cent of their gametes, but are very poor sperm competitors [106]. Females mating with a carrier and non-carrier male therefore produce predominantly non-carrier offspring. Females in experimental populations containing the selfish genetic element evolved higher levels of polyandry [13], and populations prevented from being polyandrous were more likely to be driven extinct by a shortage of males caused by the spread of the selfish genetic element [80]. Post-copulatory screening against carrier males is especially important because females appear to be unable to distinguish between carrier and non-carrier males prior to mating [107]. Selfish genetic elements that harm male fertility may be common, suggesting a taxonomically widespread benefit of polyandry to population persistence [108]. Accordingly, a recent study of the selfish t haplotype in *Mus domesticus*, another segregation distorter that works by impairing non-carrier sperm in males, found evidence that polyandry may explain the puzzlingly low frequency of the t allele in wild populations [109].

(c) Complexities and unresolved issues

Although these studies suggest that pre- and post-copulatory sexual selection can improve population fitness by improving mean genetic quality in at least some taxa, it is important to recall that demography matters too: male–male competition can also have strongly detrimental effects on female productivity that might more than cancel any population-level genetic benefits. After it was first established that male harm is widespread, several authors speculated that females mating to harmful males might recoup some or all of their lost direct fitness through indirect benefits such as 'sexy sons' [110–113]. The extent to which this actually occurs is debated, and likely varies among taxa [114–118]. However, even though heritable male reproductive success might partially or fully offset female direct fitness lost to inter-locus sexual conflict, we stress that indirect benefits from sexy sons do not diminish the costs of male harm to population viability. This is because male–male competition, by virtue of being a zero-sum game over paternity, tends to select for traits that have a negative impact on the rate of population growth. If male–male competition that harms females is to have a positive effect on population fitness, we must additionally assume a genetic correlation between naturally selected traits and sexually selected, harmful traits. This is not so far-fetched; for example, large male body size can simultaneously predict mating success and harm to females [119], but might also indicate 'good genes' that increase the viability of both male and female offspring. In short, the net effect of sexual selection on population fitness depends on the direct effects of male–male competition on female survival and fecundity, the indirect effects on offspring survival and fecundity, but *not* the indirect effects on offspring reproductive success.

Adding to this complexity, a recent study [120] highlighted that the relative amount of genetic variation with sexually antagonistic or sexually concordant fitness effects depends on the population's evolutionary history. Populations near their adaptive peak were found to harbour relatively more sexually antagonistic genetic variation than those adapting to a new environment, because loci with sexually concordant fitness effects are predicted to lose genetic variation in stable environments (in contrast to sexually antagonistic loci). Furthermore, sexually selected traits might interfere with the operation of natural selection. In *D. melanogaster*, highly-fecund females are more attractive to males and therefore experience more male harm, depressing their fitness and weakening natural selection on female fecundity [35].

To sum up, it is far from clear how polyandry affects population fitness via its putative effects on the strength of sexual selection. Solving this question requires not only that we know how selection operates on males and females and the extent to which gene expression is sex-limited [69], but also that we appreciate how the fitness of each sex affects population demography [65], and, in general, how polyandry influences the strength of pre- and post-copulatory sexual selection. There is tremendous potential for feedback between ecology and evolution that leaves much fertile ground for future empirical and theoretical research.

7. Inbreeding avoidance and genetic benefits of post-copulatory sexual selection

Inbreeding may reduce population viability by increasing the expression of deleterious recessive phenotypes and eroding the genetic variation required to respond to novel biotic and abiotic environmental challenges [121]. In many species,

individuals (especially females) avoid mating with close relatives, which increases the heterozygosity and potentially the fitness of their offspring relative to random mating [122]. Polyandry gives the possibility of a second, post-copulatory round of sexual selection to screen out close relatives, as well as low-quality males [18,85].

In a number of species, males have reduced success in post-copulatory sexual selection if they are closely related to the female. For example, female *Gryllus bimaculatus* crickets mating with both an unrelated male and a brother store fewer sperm from the brother, greatly reducing his share of paternity [123]. Similarly, red junglefowl *Gallus gallus* store fewer sperm when mating with their brothers [124]. In *Poecilia reticulata* guppies, female ovarian fluid causes the sperm of close relatives to swim more slowly than sperm of unrelated males, lowering the number of eggs fertilized by related males following polyandry [125]. Blue tits constrained to pair with close relatives by social monogamy seek extra-pair copulations with other males, reducing inbreeding depression in their offspring [126]. Evidence for post-copulatory inbreeding avoidance has also been found in mammal, reptile, amphibian and plant species, although there are several counter-examples in which it was searched for but not detected (reviewed in [127]). Whether females evolve mechanisms that disfavour related males' sperm likely depends on the relative costliness and frequency of inbreeding [127]. In species where females often encounter their relatives and cannot avoid mating with them, e.g. in species that typically live in small and fragmented populations, post-copulatory avoidance of inbreeding may significantly enhance female and population fitness. However, species that have only recently been reduced to small population sizes by human activity are less likely to possess post-copulatory blocks against inbreeding, because these would not have been needed at their original population sizes; polyandry might, therefore, do relatively little to increase outbreeding.

Even when levels of inbreeding are held constant, potential sires may differ greatly in their genetic compatibility. The majority of loci have epistatic fitness effects (i.e. the relative fitness of different alleles depends on other loci), so the optimum male is one whose genes will interact favourably with those of the female when brought together in the offspring. Low fitness of hybrids between genetically divergent groups ('outbreeding depression') is thought to be predominantly caused by the break-up of co-adapted complexes of epistatically interacting loci, which can select for mate choice for individuals from the same genetic group [128,129]. The frequency of maladaptive hybridization can be increased by anthropogenic environmental change (e.g. habitat loss and artificial introductions), making genetic compatibility of potential importance to conservation.

Polyandry might facilitate post-copulatory sexual selection against incompatible males in some species [18], with beneficial consequences for population viability. For example, the endangered Gouldian finch *Chloebia gouldiae* occurs in two distinct races, which are easily distinguished by their head colour, which is either black or red (other colours are also rarely observed). Inter-morph matings produce poor quality offspring, many of which do not survive to maturity [130]. Females frequently engage in extra-pair copulations, and there is a strong post-copulatory bias towards same-morph males; females paired with an opposite-morph male can, therefore, receive both paternal care and healthy offspring by being polyandrous [131]. Polyandry coupled with the strong genetic incompatibility between the morphs means that population fitness is likely to be significantly higher than one would predict from the high number of mixed-morph breeding pairs observed in nature (20%; [132]). In *Drosophila*, populations of *Drosophila yakuba* experimentally evolved in sympatry with the closely related *Drosophila santomea* evolved post-copulatory mechanisms that reduced the proportion of their eggs fertilized by the other species in only ten generations (hybrids are largely sterile): sympatrically evolved *D. yakuba* that mated with a conspecific lost his sperm more quickly from storage and therefore remated more quickly than controls [133]. Additionally, populations of *Tribolium* beetles that had recently experienced a genetic bottleneck evolved higher rates of polyandry, likely because polyandrous females had a greater proportion of their eggs fertilized by genetically compatible males [134]. Many more studies have found greater offspring viability in polyandrous females, implying that genetic benefits of post-copulatory sexual selection may be widespread [16].

Post-copulatory sexual selection can also provide 'good genes' whenever success in sperm competition or cryptic female choice is genetically correlated with traits under natural selection [135]. An interesting example of conservation importance is provided by studies of hybridization between farmed and wild fish, such as salmon and cod. Farmed fish escape in considerable numbers, and may potentially introduce their domesticated (maladapted) genes into wild populations [136]. Salmon and cod are polyandrous, so the competitiveness of farmed males in both pre-and post-copulatory sexual selection is a key predictor of gene flow from farmed to wild stocks. In some cases farmed males are highly competitive [137], increasing the ecological impact of escapees, whereas in others they are less competitive [138]. These results underpin the importance of mating system variation to conservation biology and local adaptation in general.

Lastly, polyandry may allow females who have mated but subsequently encounter a better-quality male to 'trade-up', especially in species with last-male sperm precedence [139]. Post-copulatory sexual selection could, therefore, augment mate choice, amplifying any population-level benefits [90] of the latter. However, this also has the flipside that effective population sizes (see §9) can be reduced if the successful sires constitute a smaller subset of all males.

8. Evolutionary consequences of elevated within-family genetic diversity

Polyandry frequently causes mixed paternity within the clutches of individual females, meaning that similarly aged offspring may be half-siblings. This increase in within-family genetic diversity may have far-reaching evolutionary consequences, and have both positive and negative effects on population viability.

Sibling rivalry, which is ultimately caused by the difference in relatedness between an individual to itself versus its sibling, is predicted to be more intense in broods containing half-siblings [140]. Conflicts among siblings may reduce productivity if they lead to the evolution of costly competitive traits such as begging [141]. Conflicts among siblings can be intense, as exemplified by tadpoles of some toads and salamanders, which develop into cannibalistic morphs at high densities, potentially leading to population collapses

[142]. Studies suggest that cannibals are less likely to develop in highly related groups [143] and may refrain from eating close kin [144], suggesting a possible population-level cost of polyandry. Conflicts might also be more subtle; for example, the evolution of dispersal under offspring control depends on the degree of relatedness among siblings. Polyandry could select for either higher or lower dispersal distances depending on how it modifies sibling conflict relative to parent–offspring conflict [145]. Dispersal ability is a key predictor of persistence, especially in fragmented populations or those affected by environmental change, highlighting another potentially important evolutionary consequence of polyandry for population fitness.

An alternative possibility is that increased within-family genetic diversity resulting from polyandry actually reduces competition among siblings by allowing them to occupy more distinct ecological niches. Elevated offspring performance in polyandrous broods is often assumed to result from 'good genes' gained during post-copulatory sexual selection, but recent work highlights that reduced competition may provide a widespread alternative possibility. Two studies of marine invertebrates found that polyandry elevated offspring performance even when pre- or post-copulatory sexual selection was experimentally precluded, suggesting that genetic diversity benefits families [146,147].

By increasing within-family genetic diversity, polyandry may also affect the efficacy of selection when selection is relatively soft and groups are composed of siblings [148]. Polyandry should increase the mean variance in fitness among competing siblings relative to monandry, because some offspring patrilines are expected to be fitter than others. Increased variance in fitness makes selection more effective, leading to more rapid adaptation [149], at least in traits that affect competition among siblings (which may or may not also increase population persistence). In other words, polyandry improves the mean competitiveness of individuals that survive sibling competition because it pits strong competitors against weaker ones more often than does monandry, similar to 'seeding' in sports such as tennis. The population-level benefits of this process should be especially pronounced if low-quality individuals die early in development and then free up resources for their fitter siblings. Many birds produce an excess of offspring in every clutch, and may even expedite the deaths of the weakest by treating them roughly [150]. In insects such as flies and butterflies, females often lay many eggs on a food resource, and the death of some individuals leaves more for the others. Broods with a high variance in fitness may lose the weaker individuals more quickly, increasing the number or quality of surviving offspring. Polyandry might therefore provide direct and indirect benefits, even when males that produce high-quality offspring are not more successful in sexual selection.

9. Effect of polyandry on the effective population size

The effective population size (N_e) is a major determinant of the fixation probabilities of both beneficial and detrimental alleles. As N_e increases, the relative importance of stochastic changes in allele frequency (genetic drift) declines, such that negatively selected alleles have a greater chance of drifting to fixation in smaller populations (reviewed in [151]). Conversely, beneficial mutations have a lower chance of being lost owing to drift before they can fix. Small populations are therefore expected to accumulate more deleterious mutations and fewer beneficial ones than larger populations. The decline in fitness may further reduce N_e (e.g. by reducing fecundity or survival), increasing the rate of fitness decline and trapping the population in an accelerating downward spiral (the 'extinction vortex' or 'mutational meltdown', [152,153]).

The same set of reasons that make it difficult to predict whether polyandry intensifies or weakens sexual selection also lead to different possible relationships between polyandry and N_e. Polyandry generally increases N_e relative to monogamy [154], but if it combines with paternity skew (e.g. because of last-male sperm precedence) towards specific males, N_e will be negatively affected. Polyandry can therefore help protect against extinction if a large number of males mating elevate N_e, but the opposite result is also possible.

10. How does it all add up?

Above, we have highlighted a plethora of ways in which polyandry could positively and negatively affect population fitness, and consequently rates of extinction. We also emphasize that most of the putative links between polyandry and population fitness often have no visible demographic effects. For example, male-induced reductions in female fecundity, or genetic benefits of post-copulatory sexual selection, will have negligible demographic consequences if females are still able to produce many more progeny than can survive at density-dependent equilibrium. Positive and negative effects of polyandry on demographic parameters may only become important once birth and death rates are modified by environmental change. This, of course, makes testing the ideas challenging: for example, a healthy population may show little evidence that male harm reduces population growth rates or densities, yet this harm could make the population more vulnerable if an adverse change in the environment erodes the 'buffer' of surplus young.

The indirect nature of this link might explain why polyandry and sexual selection have received mixed support as predictors of extinction risk. For example, sexually dichromatic birds were found to have a higher rate of local extinctions in a 21 year dataset of North American bird counts [155], and testis size predicts current perceived risk of extinction in a dataset of 1030 birds [156], but there is no such effect in a dataset comprising 1007 species of mammals (see also [94,157]). More large-scale ecological and comparative studies appear welcome in this context. For example, in antbirds, dichromatic species and those with presumed stronger sexual signalling (measured as song pitch) have larger ranges, supporting the idea that sexual selection and natural selection might act in synergy. However, cause and effect will often be difficult to disentangle. For example, extra-pair paternity in birds covaries with higher population-wide genetic variability [158]. Does polyandry maintain much variability in this case (for why it can do so see [85]), or does the presence of high genetic variability increase the benefits for females of seeking extra-pair copulations? Another type of study that appears surprisingly rare, both in an ecological and evolutionary context, is the simple manipulation of adult male and female numbers. For example, in a correlative study, a high proportion of male

frogs diminished froglet survival [159]; in an experimental study, lizard demography proceeded in a downwards spiral in enclosures that were initialized with a male-biased population [33]. As a whole, it appears that too few studies consider the ecological consequences of sexual conflict in a manner fully informed by population ecology; much remains to be done.

We thank Jean Clobert and an anonymous reviewer for helpful comments on the manuscript.

References

1. Bray OE, Kennelly JJ, Guarino JL. 1975 Fertility of eggs produced on territories of vasectomized red-winged blackbirds. *Wilson Bull.* **87**, 187–195.
2. Bessa-Gomes C, Legendre S, Clobert J. 2010 Discrete two-sex models of population dynamics: on modelling the mating function. *Acta Oecologica* **36**, 439–445. (doi:10.1016/j.actao.2010.02.010)
3. Bessa-Gomes C, Clobert J, Legendre S, Møller AP. 2003 Modeling mating patterns given mutual mate choice: the importance of individual mating preferences and mating system. *J. Biol. Syst.* **11**, 205–219. (doi:10.1142/S0218339003000853)
4. Bessa-Gomes C, Legendre S, Clobert J. 2004 Allee effects, mating systems and the extinction risk in populations with two sexes. *Ecol. Lett.* **7**, 802–812. (doi:10.1111/j.1461-0248.2004.00632.x)
5. Boukal DS, Berec L, Křivan V. 2008 Does sex-selective predation stabilize or destabilize predator–prey dynamics? *PLoS ONE* **3**, e2687. (doi:10.1371/journal.pone.0002687)
6. Calabrese JM, Fagan WF. 2004 Lost in time, lonely, and single: reproductive asynchrony and the Allee effect. *Am. Nat.* **164**, 25–37. (doi:10.1086/421443)
7. Calabrese JM, Ries L, Matter SF, Debinski DM, Auckland JN, Roland J, Fagan WF. 2008 Reproductive asynchrony in natural butterfly populations and its consequences for female matelessness. *J. Anim. Ecol.* **77**, 746–756. (doi:10.1111/j.1365-2656.2008.01385.x)
8. Bateman AJ. 1948 Intra-sexual selection in *Drosophila*. *Heredity* **2**, 349–368. (doi:10.1038/hdy.1948.21)
9. Arnqvist G, Nilsson T. 2000 The evolution of polyandry: multiple mating and female fitness in insects. *Anim. Behav.* **60**, 145–164. (doi:10.1006/anbe.2000.1446)
10. Jennions MD, Petrie M. 2000 Why do females mate multiply? A review of the genetic benefits. *Biol. Rev.* **75**, 21–64. (doi:10.1111/j.1469-185X.1999.tb00040.x)
11. Kokko H, Mappes J. In press. Multiple mating by females is a natural outcome of a null model of mate encounters. *Entomol. Exp. Appl*. (doi:10.1111/j.1570-7458.2012.01296.x)
12. Harano T, Miyatake T. 2009 Bidirectional selection for female propensity to remate in the bean beetle, *Callosobruchus chinensis*. *Popul. Ecol.* **51**, 89–98. (doi:10.1007/s10144-008-0112-6)
13. Price TAR, Hodgson DJ, Lewis Z, Hurst GDD, Wedell N. 2008 Selfish genetic elements promote polyandry in a fly. *Science* **322**, 1241–1243. (doi:10.1126/science.1163766)
14. Davies NB, Krebs JR, West SA. 2012 *An introduction to behavioural ecology*, 4th edn. Chichester, UK: Wiley-Blackwell.
15. Davies NB. 1991 Mating Systems. In *Behavioural ecology: an evolutionary approach* (eds JR Krebs, NB Davies), pp. 263–294, 3rd edn. Oxford, UK: Blackwell.
16. Slatyer RA, Mautz BS, Backwell PRY, Jennions MD. 2012 Estimating genetic benefits of polyandry from experimental studies: a meta-analysis. *Biol. Rev.* **87**, 1–33. (doi:10.1111/j.1469-185X.2011.00182.x)
17. Emlen ST, Oring LW. 1977 Ecology, sexual selection, and the evolution of mating systems. *Science* **197**, 215–223. (doi:10.1126/science.327542)
18. Zeh JA, Zeh DW. 1997 The evolution of polyandry. II. Post-copulatory defences against genetic incompatibility. *Proc. R. Soc. Lond. B* **264**, 69–75. (doi:10.1098/rspb.1997.0010)
19. Wolff JO, Macdonald DW. 2004 Promiscuous females protect their offspring. *Trends Ecol. Evol.* **19**, 127–134. (doi:10.1016/j.tree.2003.12.009)
20. Rowe L. 1992 Convenience polyandry in a water strider: foraging conflicts and female control of copualtion frequency and guarding duration. *Anim. Behav.* **44**, 189–202. (doi:10.1016/0003-3472(92)90025-5)
21. Arnqvist G. 2006 Sensory exploitation and sexual conflict. *Phil. Trans. R. Soc. B* **361**, 375–386. (doi:10.1098/rstb.2005.1790)
22. Bleu J, Bessa-Gomes C, Laloi D. 2012 Evolution of female choosiness and mating frequency: effects of mating cost, density and sex ratio. *Anim. Behav.* **83**, 131–136. (doi:10.1016/j.anbehav.2011.10.017)
23. Kokko H, Jennions M. 2012 Sex differences in parental care. In *The evolution of parental care* (eds N Royle, PT Smiseth, M Kölliker). Oxford, UK: Oxford University Press.
24. Kokko H, Jennions MD. 2008 Parental investment, sexual selection and sex ratios. *J. Evol. Biol.* **21**, 919–948. (doi:10.1111/j.1420-9101.2008.01540.x)
25. Lehtonen J, Jennions MD, Kokko H. 2012 The many costs of sex. *Trends Ecol. Evol.* **27**, 172–178. (doi:10.1016/j.tree.2011.09.016)
26. Arnqvist G, Rowe L. 2005 *Sexual conflict*. Princeton, NJ: Princeton University Press.
27. Chapman T, Arnqvist G, Bangham J, Rowe L. 2003 Sexual conflict. *Trends Ecol. Evol.* **18**, 41–47. (doi:10.1016/S0169-5347(02)00004-6)
28. Hosken DJ, Stockley P, Tregenza T, Wedell N. 2009 Monogamy and the Battle of the Sexes. *Annu. Rev. Entomol.* **54**, 361–378. (doi:10.1146/annurev.ento.54.110807.090608)
29. Kokko H. 1999 Cuckoldry and the stability of biparental care. *Ecol. Lett.* **2**, 247–255. (doi:10.1046/j.1461-0248.1999.00075.x)
30. Bleeker M, Kingma SA, Szentirmai I, Szekely T, Komdeur J. 2005 Body condition and clutch desertion in penduline tit *Remiz pendulinus*. *Behaviour* **142**, 1465–1478. (doi:10.1163/156853905774831855)
31. Sibly RM, Witt CC, Wright NA, Venditti C, Jetz W, Brown JH. 2012 Energetics, lifestyle, and reproduction in birds. *Proc. Natl Acad. Sci. USA* **109**, 10937–10941. (doi:10.1073/pnas.1206512109)
32. Eldakar OT, Wilson DS, Dlugos MJ, Pepper JW. 2010 The role of multilevel selection in the evolution of sexual conflict in the water strider *Aquarius remigis*. *Evolution* **64**, 3183–3189. (doi:10.1111/j.1558-5646.2010.01087.x)
33. Le Galliard J-F, Fitze PS, Ferrière R, Clobert J. 2005 Sex ratio bias, male aggression, and population collapse in lizards. *Proc. Natl Acad. Sci. USA* **102**, 18231–18236. (doi:10.1073/pnas.0505172102)
34. Gerber LR, González-Suárez M, Hernández-Camacho CJ, Young JK, Sabo JL. 2010 The cost of male aggression and polygyny in California sea lions (*Zalophus californianus*). *PLoS ONE* **5**, e12230. (doi:10.1371/journal.pone.0012230)
35. Long TAF, Pischedda A, Stewart AD, Rice WR. 2009 A cost of sexual attractiveness to high-fitness females. *PLoS Biol.* **7**, e1000254. (doi:10.1371/journal.pbio.1000254)
36. Tilszer M, Antoszczyk K, Salek N, Zajac E, Radwan J. 2006 Evolution under relaxed sexual conflict in the bulb mite *Rhizoglyphus robini*. *Evolution* **60**, 1868–1873. (doi:10.1554/06-060.1)
37. Gay L, Hosken DJ, Eady P, Vasudev R, Tregenza T. 2011 The evolution of harm: effect of sexual conflicts and population size. *Evolution* **65**, 725–737. (doi:10.1111/j.1558-5646.2010.01181.x)
38. Michalczyk L, Millard AL, Martin OY, Lumley AJ, Emerson BC, Gage MJG. 2011 Experimental evolution exposes female and male responses to sexual selection and conflict in *Tribolium castaneum*. *Evolution* **65**, 713–724. (doi:10.1111/j.1558-5646.2010.01174.x)
39. Edward DA, Fricke C, Chapman T. 2010 Adaptations to sexual selection and sexual conflict: insights from experimental evolution and artificial selection. *Phil. Trans. R. Soc. B* **365**, 2541–2548. (doi:10.1098/rstb.2010.0027)
40. Martin OY, Hosken DJ, Ward PI. 2004 Post-copulatory sexual selection and female fitness in *Scathophaga stercoraria*. *Proc. R. Soc. Lond. B* **271**, 353–359. (doi:10.1098/rspb.2003.2588)

41. Crudgington HS, Fellows S, Snook RR. 2010 Increased opportunity for sexual conflict promotes harmful males with elevated courtship frequencies. *J. Evol. Biol.* **23**, 440–446. (doi:10.1111/j.1420-9101.2009.01907.x)
42. Fromhage L. 2012 Mating unplugged: a model for the evolution of mating plug (dis-)placement. *Evolution* **66**, 31–39. (doi:10.1111/j.1558-5646.2011.01406.x)
43. Dean R, Cornwallis CK, Løvlie H, Worley K, Richardson DS, Pizzari T. 2010 Male reproductive senescence causes potential for sexual conflict over mating. *Curr Biol* **20**, 1192–1196. (doi:10.1016/j.cub.2010.04.059)
44. Montrose VT, Harris WE, Moore PJ. 2004 Sexual conflict and cooperation under naturally occurring male enforced monogamy. *J. Evol. Biol.* **17**, 443–452. (doi:10.1046/j.1420-9101.2003.00654.x)
45. Galipaud M, Dechaume-Moncharmont F-X, Oughadou A, Bollache L. 2010 Does foreplay matter? *Gammarus pulex* females may benefit from long-lasting precopulatory mate guarding. *Biol. Lett.* **7**, 333–335. (doi:10.1098/rsbl.2010.0924)
46. Rodríguez-Muñoz R, Bretman A, Tregenza T. 2011 Guarding males protect females from predation in a wild insect. *Curr. Biol.* **21**, 1716–1719. (doi:10.1016/j.cub.2011.08.053)
47. Avila FW, Sirot LK, LaFlamme BA, Rubinstein CD, Wolfner MF. 2011 Insect seminal fluid proteins: identification and function. *Annu. Rev. Entomol.* **56**, 21–40. (doi:10.1146/annurev-ento-120709-144823)
48. Wigby S, Chapman T. 2005 Sex peptide causes mating costs in female *Drosophila melanogaster*. *Curr. Biol.* **15**, 316–321. (doi:10.1016/j.cub.2005.01.051)
49. Knell RJ, Webberley KM. 2004 Sexually transmitted diseases of insects: distribution, evolution, ecology and host behaviour. *Biol. Rev.* **79**, 557–581. (doi:10.1017/s1464793103006365)
50. Rolff J. 2002 Bateman's principle and immunity. *Proc. R. Soc. Lond. B* **269**, 867–872. (doi:10.1098/rspb.2002.1959)
51. Skorping A, Jensen KH. 2004 Disease dynamics: all caused by males? *Trends Ecol. Evol.* **19**, 219–220. (doi:10.1016/j.tree.2004.02.006)
52. López-Sepulcre A, Norris K, Kokko H. 2009 Reproductive conflict delays the recovery of an endangered social species. *J. Anim. Ecol.* **78**, 219–225. (doi:10.1111/j.1365-2656.2008.01475.x)
53. Ferrière R, Dieckmann U, Couvet D. 2004 *Evolutionary conservation biology*. Cambridge, UK: Cambridge University Press.
54. Carrete M, Donázar JA, Margalida A, Bertran J. 2006 Linking ecology, behaviour and conservation: does habitat saturation change the mating system of bearded vultures? *Biol. Lett.* **2**, 624–627. (doi:10.1098/rsbl.2006.0498)
55. Rankin DJ, Dieckmann U, Kokko H. 2011 Sexual conflict and the tragedy of the commons. *Am. Nat.* **177**, 780–791. (doi:10.1086/659947)
56. Ewen JG, Thorogood R, Armstrong DP. 2011 Demographic consequences of adult sex ratio in a reintroduced hihi population. *J. Anim. Ecol.* **80**, 448–455. (doi:10.1111/j.1365-2656.2010.01774.x)
57. Valero A, Macías Garcia C, Magurran AE. 2008 Heterospecific harassment of native endangered fishes by invasive guppies in Mexico. *Biol. Lett.* **4**, 149–152. (doi:10.1098/rsbl.2007.0604)
58. Smith GC, Henderson I. 2007 A model for the management of the invasive ruddy duck to reduce interbreeding pressure on the white-headed duck. *Int. J. Pest Manage.* **53**, 335–339. (doi:10.1080/09670870601185214)
59. Muñoz-Fuentes V, Vilà C, Green AJ, Negro JJ, Sorenson MD. 2007 Hybridization between white-headed ducks and introduced ruddy ducks in Spain. *Mol. Ecol.* **16**, 629–638. (doi:10.1111/j.1365-294X.2006.03170.x)
60. Ruckstuhl K, Neuhaus P. 2006 *Sexual segregation in vertebrates*. Cambridge, UK: Cambridge University Press.
61. Darden SK, Croft DP. 2008 Male harassment drives females to alter habitat use and leads to segregation of the sexes. *Biol. Lett.* **4**, 449–451. (doi:10.1098/rsbl.2008.0308)
62. Marra PP. 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. (doi:10.1093/beheco/11.3.299)
63. Marra PP, Holmes RT. 2001 Consequences of dominance-mediated habitat segregation in American redstarts during the nonbreeding season. *Auk* **118**, 92–104. (doi:10.1642/0004-8038(2001)118[0092:codmhs]2.0.co;2)
64. Mucientes GR, Queiroz N, Sousa LL, Tarroso P, Sims DW. 2009 Sexual segregation of pelagic sharks and the potential threat from fisheries. *Biol. Lett.* **5**, 156–159. (doi:10.1098/rsbl.2008.0761)
65. Rankin DJ, Kokko H. 2007 Do males matter? The role of males in population dynamics. *Oikos* **116**, 335–348. (doi:10.1111/j.0030-1299.2007.15451.x)
66. Edward DA, Fricke C, Gerrard DT, Chapman T. 2011 Quantifying the life-history response to increased male exposure in female *Drosohpila melanogaster*. *Evolution* **65**, 564–573. (doi:10.1111/j.1558-5646.2010.01151.x)
67. Stearns SC. 1992 *The evolution of life histories*. Oxford, UK: Oxford University Press.
68. Poissant J, Wilson AJ, Coltman DW. 2010 Sex-specific genetic variance and the evolution of sexual dimorphism: a systematic review of cross-sex genetic correlations. *Evolution* **64**, 97–107. (doi:10.1111/j.1558-5646.2009.00793.x)
69. Connallon T, Cox RM, Calsbeek R. 2010 Fitness consequences of sex-specific selection. *Evolution* **64**, 1671–1682. (doi:10.1111/j.1558-5646.2009.00934.x)
70. Harano T, Okada K, Nakayama S, Miyatake T, Hosken DJ. 2010 Intralocus sexual conflict unresolved by sex-limited trait expression. *Curr. Biol.* **20**, 2036–2039. (doi:10.1016/j.cub.2010.10.023)
71. Rankin DJ, Arnqvist G. 2008 Sexual dimorphism is associated with population fitness in the seed beetle *Callosobruchus maculatus*. *Evolution* **62**, 622–630. (doi:10.1111/j.1558-5646.2007.00315.x)
72. Arnqvist G, Tuda M. 2010 Sexual conflict and the gender load: correlated evolution between population fitness and sexual dimorphism in seed beetles. *Proc. R. Soc. B* **277**, 1345–1352. (doi:10.1098/rspb.2009.2026)
73. West S. 2009 *Sex allocation*. Princeton, NJ: Princeton University Press.
74. Magrath MJL, Van Lieshout E, Pen IDO, Visser GH, Komdeur JAN. 2007 Estimating expenditure on male and female offspring in a sexually size-dimorphic bird: a comparison of different methods. *J. Anim. Ecol.* **76**, 1169–1180. (doi:10.1111/j.1365-2656.2007.01292.x)
75. Zuk M, Kolluru GR. 1998 Exploitation of sexual signals by predators and parasitoids. *Q. Rev. Biol.* **73**, 415–438. (doi:10.1086/420412)
76. Kokko H, Brooks R. 2003 Sexy to die for? Sexual selection and the risk of extinction. *Annal. Zool. Fenn.* **40**, 207–219.
77. Worman CO, Kimbrell T. 2008 Getting to the hart of the matter: did antlers truly cause the extinction of the Irish elk? *Oikos* **117**, 1397–1405. (doi:10.1111/j.2008.0030-1299.16608.x)
78. Wedell N, Gage MJG, Parker GA. 2002 Sperm competition, male prudence and sperm-limited females. *Trends Ecol. Evol.* **17**, 313–320. (doi:10.1016/S0169-5347(02)02533-8)
79. Charlat S, Reuter M, Dyson EA, Hornett EA, Duplouy A, Davies N, Roderick GK, Wedell N, Hurst GDD. 2007 Male-killing bacteria trigger a cycle of increasing male fatigue and female promiscuity. *Curr. Biol.* **17**, 273–277. (doi:10.1016/j.cub.2006.11.068)
80. Price TAR, Hurst GDD, Wedell N. 2010 Polyandry prevents extinction. *Curr. Biol.* **20**, 471–475. (doi:10.1016/j.cub.2010.01.050)
81. Moore T, Haig D. 1991 Genomic imprinting in mammalain development: a parental tug-of-war. *Trends Genet.* **7**, 45–49. (doi:10.1016/0168-9525(91)90040-w)
82. Queller DC. 1994 Male–female conflict and parent–offspring conflict. *Am. Nat.* **144**, S84–S99. (doi:10.1086/285654)
83. Haig D. 1993 Genetic conflicts in human pregnancy. *Q. Rev. Biol.* **68**, 495–532. (doi:10.1086/418300)
84. Crespi B. 2008 Genomic imprinting in the development and evolution of psychotic spectrum conditions. *Biol. Rev.* **83**, 441–493. (doi:10.1111/j.1469-185X.2008.00050.x)
85. Webster MS, Pruett-Jones S, Westneat DF, Arnold SJ. 1995 Measuring the effects of pairing success, extra-pair copulations and mate quality on the opportunity for sexual selection. *Evolution* **49**, 1147–1157. (doi:10.2307/2410439)
86. Siller S. 2001 Sexual selection and the maintenance of sex. *Nature* **411**, 689–692. (doi:10.1038/35079578)
87. Agrawal AF. 2001 Sexual selection and the maintenance of sexual reproduction. *Nature* **411**, 692–695. (doi:10.1038/35079590)
88. Whitlock MC. 2000 Fixation of new alleles and the extinction of small populations: drift load, beneficial alleles, and sexual selection. *Evolution* **54**,

1855–1861. (doi:10.1554/0014-3820(2000)054[1855:fonaat]2.0.co;2)

89. Manning JT. 1984 Males and the advantage of sex. *J. Theor. Biol.* **108**, 215–220. (doi:10.1016/S0022-5193(84)80067-3)
90. Whitlock MC, Agrawal AF. 2009 Purging the genome with sexual selection: Reducing mutation load through selection on males. *Evolution* **63**, 569–582. (doi:10.1111/j.1558-5646.2008.00558.x)
91. Lorch PD, Proulx S, Rowe L, Day T. 2003 Condition-dependent sexual selection can accelerate adaptation. *Evol. Ecol. Res.* **5**, 867–881.
92. Roze D, Otto SP. 2012 Differential selection between the sexes and selection for sex. *Evolution* **66**, 558–574. (doi:10.1111/j.1558-5646.2011.01459.x)
93. Prasad NG, Bedhomme S, Day T, Chippindale AK. 2007 An evolutioary cost of separate genders revealed by male-limited evolution. *Am. Nat.* **169**, 29–37. (doi:10.1086/509941)
94. Candolin U, Heuschele J. 2008 Is sexual selection beneficial during adaptation to environmental change? *Trends Ecol. Evol.* **23**, 446–452. (doi:10.1016/j.tree.2008.04.008)
95. McGuigan K, Petfield D, Blows MW. 2011 Reducing mutation load through sexual selection on males. *Evolution* **65**, 2816–2829. (doi:10.1111/j.1558-5646.2011.01346.x)
96. Morrow EH, Stewart AD, Rice WR. 2008 Assessing the extent of genome-wide intralocus sexual conflict via experimentally enforced gender-limited selection. *J. Evol. Biol.* **21**, 1046–1054. (doi:10.1111/j.1420-9101.2008.01542.x)
97. Sharp NP, Agrawal AF. 2008 Mating density and the strength of sexual selection against deleterious alleles in *Drosophila melanogaster*. *Evolution* **62**, 857–867. (doi:10.1111/j.1558-5646.2008.00333.x)
98. Innocenti P, Morrow EH. 2010 The sexually antagonistic genes of *Drosophila melanogaster*. *PLoS Biol.* **8**, e1000335. (doi:10.1371/journal.pbio.1000335)
99. Hollis B, Houle D. 2011 Populations with elevated mutation load do not benefit from the operation of sexual selection. *J. Evol. Biol.* **24**, 1918–1926. (doi:10.1111/j.1420-9101.2011.02323.x)
100. Radwan J. 2004 Effectiveness of sexual selection in removing mutations induced with ionizing radiation. *Ecol. Lett.* **7**, 1149–1154. (doi:10.1111/j.1461-0248.2004.00681.x)
101. Radwan J, Unrug J, Śnigórska K, Gawrońska K. 2004 Effectiveness of sexual selection in preventing fitness deterioration in bulb mite populations under relaxed natural selection. *J. Evol. Biol.* **17**, 94–99. (doi:10.1046/j.1420-9101.2003.00646.x)
102. Jarzebowska M, Radwan J. 2010 Sexual selection counteracts extinction of small populations of the bulb mites. *Evolution* **64**, 1283–1289. (doi:10.1111/j.1558-5646.2009.00905.x)
103. Holland B. 2002 Sexual selection fails to promote adaptation to a new environment. *Evolution* **56**, 721–730. (doi:10.1554/0014-3820(2002)056[0721:ssftpa]2.0.co;2)
104. Rundle HD, Chenoweth SF, Blows MW. 2006 The roles of natural and sexual selection during adaptation to a novel environment. *Evolution* **60**, 2218–2225. (doi:10.1111/j.0014-3820.2006.tb01859.x)
105. Bonduriansky R. 2011 Sexual selection and conflict as engines of ecological diversification. *Am. Nat.* **178**, 729–745. (doi:10.1086/662665)
106. Price TAR, Bretman AJ, Avent TD, Snook RR, Hurst GDD, Wedell N. 2008 Sex ratio distorter reduces sperm competitive ability in an insect. *Evolution* **62**, 1644–1652. (doi:10.1111/j.1558-5646.2008.00386.x)
107. Price T, Lewis Z, Smith D, Hurst G, Wedell N. 2012 No evidence of mate discrimination against males carrying a sex ratio distorter in *Drosophila pseudoobscura*. *Behav. Ecol. Sociobiol.* **66**, 561–568. (doi:10.1007/s00265-011-1304-1)
108. Price T, Wedell N. 2008 Selfish genetic elements and sexual selection: their impact on male fertility. *Genetica* **132**, 295–307. (doi:10.1007/s10709-007-9173-2)
109. Manser A, Lindholm AK, König B, Bagheri HC. 2011 Polyandry and the decrease of a selfish genetic element in a wild house mouse population. *Evolution* **65**, 2435–2447. (doi:10.1111/j.1558-5646.2011.01336.x)
110. Kokko H. 2005 Treat 'em mean, keep 'em (sometimes) keen: evolution of female preferences for dominant and coercive males. *Evol. Ecol.* **19**, 123–135. (doi:10.1007/s10682-004-7919-1)
111. Parker GA. 1979 Sexual selection and sexual conflict. In *Sexual selection and reproductive competition in insects* (eds MS Blum, NA Blum), pp. 123–166. New York, NY: Academic Press.
112. Cordero C, Eberhard WG. 2003 Female choice of sexually antagonistic male adaptations: a critical review of some current research. *J. Evol. Biol.* **16**, 1–6. (doi:10.1046/j.1420-9101.2003.00506.x)
113. Pizzari T, Snook RR. 2003 Sexual conflict and sexual selection: Chasing away paradigm shifts. *Evolution* **57**, 1223–1236. (doi:10.1111/j.0014-3820.2003.tb00331.x)
114. Le Galliard JF, Cote J, Fitze PS. 2008 Lifetime and intergenerational fitness consequences of harmful male interactions for female lizards. *Ecology* **89**, 56–64. (doi:10.1890/06-2076.1)
115. Orteiza N, Linder JE, Rice WR. 2005 Sexy sons from re-mating do not recoup the direct costs of harmful male interactions in the *Drosophila melanogaster* laboratory model system. *J. Evol. Biol* .**18**, 1315–1323. (doi:10.1111/j.1420-9101.2005.00923.x)
116. Garcia-Gonzalez F, Simmons LW. 2010 Male-induced costs of mating for females compensated by offspring viability benefits in an insect. *J. Evol. Biol.* **23**, 2066–2075. (doi:10.1111/j.1420-9101.2010.02065.x)
117. Head ML, Hunt J, Jennions MD, Brooks R. 2005 The indirect benefits of mating with attractive males outweigh the direct costs. *PLoS Biol.* **3**, e33. (doi:10.1371/journal.pbio.0030033)
118. Cameron E, Day T, Rowe L. 2003 Sexual conflict and indirect benefits. *J. Evol. Biol.* **16**, 1055–1060. (doi:10.1046/j.1420-9101.2003.00584.x)
119. Pitnick S, García-González F. 2002 Harm to females increases with male body size in *Drosophila melanogaster*. *Proc. R. Soc. Lond. B* **269**, 1821–1828. (doi:10.1098/rspb.2002.2090)
120. Long TAF, Agrawal AF, Rowe L. 2012 The effect of sexual selection on offspring fitness depends on the nature of genetic variation. *Curr. Biol.* **22**, 204–208. (doi:10.1016/j.cub.2011.12.020)
121. Falconer DS, Mackay TFC. 1996 *Introduction to quantitative genetics*. Harlow, UK: Pearson Education.
122. Brown JL. 1997 A theory of mate choice based on heterozygosity. *Behav. Ecol.* **8**, 60–65. (doi:10.1093/beheco/8.1.60)
123. Bretman A, Newcombe D, Tregenza T. 2009 Promiscuous females avoid inbreeding by controlling sperm storage. *Mol. Ecol.* **18**, 3340–3345. (doi:10.1111/j.1365-294X.2009.04301.x)
124. Pizzari T, Lovlie H, Cornwallis CK. 2004 Sex-specific, counteracting responses to inbreeding in a bird. *Proc. R. Soc. Lond. B* **271**, 2115–2121. (doi:10.1098/rspb.2004.2843)
125. Gasparini C, Pilastro A. 2011 Cryptic female preference for genetically unrelated males is mediated by ovarian fluid in the guppy. *Proc. R. Soc. B* **278**, 2495–2501. (doi:10.1098/rspb.2010.2369)
126. Foerster K, Delhey K, Johnsen A, Lifjeld JT, Kempenaers B. 2003 Females increase offspring heterozygosity and fitness through extra-pair matings. *Nature* **425**, 714–717. (doi:10.1038/nature01969)
127. Ala-Honkola O, Manier MK, Lüpold S, Pitnick S. 2011 No evidence for postcopulatory inbreeding avoidance in *Drosophila melanogaster*. *Evolution* **65**, 2699–2705. (doi:10.1111/j.1558-5646.2011.01317.x)
128. Tregenza T, Wedell N. 2000 Genetic compatibility, mate choice and patterns of parentage. *Mol. Ecol.* **9**, 1013–1027. (doi:10.1046/j.1365-294x.2000.00964.x)
129. Dobzhansky T. 1951 *Genetics and the origin of species*. New York: Columbia University Press.
130. Pryke SR, Griffith SC. 2009 Postzygotic genetic incompatibility between sympatric color morphs. *Evolution* **63**, 793–798. (doi:10.1111/j.1558-5646.2008.00584.x)
131. Pryke SR, Rollins LA, Griffith SC. 2010 Females use multiple mating and genetically loaded sperm competition to target compatible genes. *Science* **329**, 964–967. (doi:10.1126/science.1192407)
132. Pryke SR, Griffith SC. 2007 The relative role of male versus female mate choice in maintaining assortative pairing among discrete colour morphs. *J. Evol. Biol.* **20**, 1512–1521. (doi:10.1111/j.1420-9101.2007.01332.x)
133. Matute DR. 2010 Reinforcement of gametic isolation in *Drosophila*. *PLoS Biol.* **8**, e1000341. (doi:10.1371/journal.pbio.1000341)
134. Michalczyk Ł, Millard AL, Martin OY, Lumley AJ, Emerson BC, Chapman T, Gage MJG. 2011 Inbreeding promotes female promiscuity. *Science* **333**, 1739–1742. (doi:10.1126/science.1207314)
135. Yasui Y. 1997 A 'good-sperm' model can explain the evolution of costly multiple mating by females. *Am. Nat.* **149**, 573–584. (doi:10.1086/286006)

136. Grant W. 2012 Understanding the adaptive consequences of hatchery–wild interactions in Alaska salmon. *Environ. Biol. Fish.* **94**, 325–342. (doi:10.1007/s10641-011-9929-5)
137. Garant D, Fleming IA, Einum S, Bernatchez L. 2003 Alternative male life-history tactics as potential vehicles for speeding introgression of farm salmon traits into wild populations. *Ecol. Lett.* **6**, 541–549. (doi:10.1046/j.1461-0248.2003.00462.x)
138. Skjaeraasen JE, Meager JJ, Karlsen Ø, Mayer I, Dahle G, Rudolfsen G, Ferno A. 2010 Mating competition between farmed and wild cod *Gadus morhua*. *Mar. Ecol. Prog. Ser.* **412**, 247–258. (doi:10.3354/meps08670)
139. Pitcher TE, Neff BD, Rodd FH, Rowe L. 2003 Multiple mating and sequential mate choice in guppies: females trade up. *Proc. R. Soc. Lond. B* **270**, 1623–1629. (doi:10.1098/rspb.2002.2280)
140. Godfray HCJ. 1995 Signaling of need between parents and young: parent–offspring conflict and sibling rivalry. *Am. Nat.* **146**, 1–24. (doi:10.1086/285784)
141. Haskell D. 1994 Experimental evidence that nestling begging behaviour incurs a cost due to nest predation. *Proc. R. Soc. Lond. B* **257**, 161–164. (doi:10.1098/rspb.1994.0110)
142. Dercole F, Rinaldi S. 2002 Evolution of cannibalistic traits: scenarios derived from adaptive dynamics. *Theor. Popul. Biol.* **62**, 365–374. (doi:10.1016/s0040-5809(02)00008-4)
143. Pfennig DW, Collins JP. 1993 Kinship affects morphogenesis in cannibalistic salamanders. *Nature* **362**, 836–838. (doi:10.1038/362836a0)
144. Pfennig DW, Reeve HK, Sherman PW. 1993 Kin recognition and cannibalism in spadefoot toad tadpoles. *Anim. Behav.* **46**, 87–94. (doi:10.1006/anbe.1993.1164)
145. Starrfelt J, Kokko H. 2010 Parent–offspring conflict and the evolution of dispersal distance. *Am. Nat.* **175**, 38–49. (doi:10.1086/648605)
146. Aguirre JD, Marshall DJ. 2012 Does genetic diversity reduce sibling competition? *Evolution* **66**, 94–102. (doi:10.1111/j.1558-5646.2011.01413.x)
147. McLeod L, Marshall DJ. 2009 Do genetic diversity effects drive the benefits associated with multiple mating? A test in a marine invertebrate. *PLoS ONE* **4**, e6347. (doi:10.1371/journal.pone.0006347)
148. Wade MJ. 1985 Soft selection, hard selection, kin selection, and group selection. *Am. Nat.* **125**, 61–73. (doi:10.1086/284328)
149. Frank SA, Slatkin M. 1992 Fisher's fundamental theorem of natural selection. *Trends Ecol. Evol.* **7**, 92–95. (doi:10.1016/0169-5347(92)90248-A)
150. Townsend HM, Anderson DJ. 2007 Production of insurance eggs in Nazca boobies: costs, benefits, and variable parental quality. *Behav. Ecol.* **18**, 841–848. (doi:10.1093/beheco/arm056)
151. Whitlock MC, Bürger R. 2004 Fixation of new mutations in small populations. In *Evolutionary conservation biology* (eds R Ferrière, U Dieckmann, D Couvet), pp. 155–170. Cambridge, UK: Cambridge University Press.
152. Gilpin ME, Soulé ME. 1986 Minimum viable populations: processes of species extinction. In *Conservation biology: the science of scarcity and diversity* (ed. ME Soulé). Sunderland, MA: Sinauer.
153. Lynch M, Gabriel W. 1990 Mutation load and the survival of small populations. *Evolution* **44**, 1725–1737. (doi:10.2307/2409502)
154. Balloux F, Lehmann L. 2003 Random mating with a finite number of matings. *Genetics* **165**, 2313–2315.
155. Doherty PF, Sorci G, Royle JA, Hines JE, Nichols JD, Boulinier T. 2003 Sexual selection affects local extinction and turnover in bird communities. *Proc. Natl Acad. Sci. USA* **100**, 5858–5862. (doi:10.1073/pnas.0836953100)
156. Morrow EH, Pitcher TE. 2003 Sexual selection and the risk of extinction in birds. *Proc. R. Soc. Lond. B* **270**, 1793–1799. (doi:10.1098/rspb.2003.2441)
157. Morrow EH, Fricke C. 2004 Sexual selection and the risk of extinction in mammals. *Proc. R. Soc. Lond. B* **271**, 2395–2401. (doi:10.1098/rspb.2004.2888)
158. Petrie M, Doums C, Møller AP. 1998 The degree of extra-pair paternity increases with genetic variability. *Proc. Natl Acad. Sci.* USA **95**, 9390–9395.
159. Lodé T. 2009 For a few males more: do changes in sex ratio predict reproductive success and offspring survival? *Evol. Ecol. Res.* **11**, 95–107.