

# Sexual selection can both increase and decrease extinction probability: reconciling demographic and evolutionary factors

Carlos Martínez-Ruiz and Robert J. Knell\*

School of Biological and Chemical Sciences, Queen Mary University of London, London E1 4NS, UK

## Summary

1. Previous theoretical models of the effect of sexual selection on average individual fitness in a population have mostly predicted that sexually selected populations should adapt faster and clear deleterious mutations more quickly than populations where sexual selection is not operating.
2. While some laboratory studies have supported these predictions, others have not and studies of field systems have tended to find negative effects of sexual selection, or no effect. The negative effects of sexual selection found in field and other studies are usually ascribed to the costs associated with strong sexual selection acting on the population.
3. Here, using an individual-based model that allows feedback between demographic and evolutionary processes, we find that sexual selection can lead to both increases and decreases in population-level fitness measures such as extinction probability and adaptation rate. Whether fitness increases or decreases depends on a variety of environmental and demographic factors including the nature of environmental change, the carrying capacity of the environment, the average fecundity of the population in question and the strength of condition dependence.
4. In many cases, our model predicts that sexual selection leads to higher extinction probability in small populations because of an increased risk of demographic stochasticity, but lower extinction probability in larger populations because of faster adaptation rates. This is consistent with field studies that have mostly focussed on very small populations such as recently introduced birds, and tend to find negative effects, and also with laboratory studies that tend to use larger populations and have tended to find positive effects.
5. These findings go at least some way towards an understanding of the apparent contradictions between theoretical predictions, laboratory studies and field data.

**Key-words:** adaptation, climate change, environmental change, evolution, extinction, individual-based model, sexual selection

## Introduction

Sexual selection, whereby organisms compete for matings or fertilizations rather than for resources such as food or space, is a pervasive and powerful driver of evolution. Nowadays, it is recognized as being responsible for much of the morphological and behavioural diversity that we see in the animal kingdom (Andersson 1994). Recently, our improved understanding of the fundamental mechanisms of sexual selection has led to a number of studies that propose a role for 'good-genes' sexual selection in

determining rates of adaptation and extinction (Houle & Kondrashov 2002; Lorch *et al.* 2003; Plesnar-Bielak *et al.* 2012; Lumley *et al.* 2015). The formulation of the 'genetic capture' model has played a major role in this, as this model seems to have resolved the so-called lek paradox (Rowe & Houle 1996; Kotiaho *et al.* 2001). This new possibility has generated a debate on whether sexual selection facilitates or hinders adaptation to new environments (Candolin & Heuschele 2008), which may have deep implications for the conservation of sexually selected species facing environmental change (e.g. Sorci *et al.* 1998).

Genetic capture, the proposed mechanism behind good-genes sexual selection, posits that secondary sexual display

\*Correspondence author. E-mail: r.knell@qmul.ac.uk

traits are 'condition-dependent', meaning that their expression is affected by the bearer's overall health and well-being (Rowe & Houle 1996; Kotiaho *et al.* 2001; Cotton *et al.* 2006). Lorch *et al.* (2003) argued that when the environment changes, those individuals that are best suited to the new environment will have the best condition and therefore the highest expression of sexually selected traits. Because sexual selection leads to reproductive skew in favour of those individuals with the greatest expression of display traits, this will lead to those individuals contributing a high proportion of offspring to the next generation, thus rapidly spreading their alleles in the population and enhancing the rate of adaptation. This idea has gained empirical support from experiments carried out with the bulb mite *Rhizoglyphus robini* (Plesnar-Bielak *et al.* 2012) and *Drosophila melanogaster* (Long *et al.* 2012). The latter study also found evidence for further beneficial effects of sexual selection, and the authors suggested that sexual selection could also improve the average individual fitness in a population whenever most of the variance in condition depends on large inputs of maladaptive alleles (Long *et al.* 2012). In other words, sexual selection could be beneficial not only under environmental change but also when the population experiences inbreeding depression or migration. This is in accordance with previous ideas of sexual selection being effective at purging alleles with small deleterious effects (Whitlock 2000), which has been observed empirically several times (e.g. Jarzebowska & Radwan 2010; Lumley *et al.* 2015).

Arguments based on the genic capture – condition dependence model of sexual selection, therefore indicate that sexual selection should lead to faster adaptation to new environments and a lower probability of extinction [although see Reding *et al.* (2013) for an example where sexual signalling is independent of condition], and these predictions are supported by several laboratory studies. A variety of field studies, however, give conflicting results, finding that sexual selection is either neutral or appears to increase extinction probability. Sorci *et al.* (1998) analysed the persistence of bird species following introduction to New Zealand and found that sexually dimorphic species were more likely to become extinct following introduction. Doherty *et al.* (2003) analysed 21 years' worth of data on American bird communities and found that sexual selection increased the risk of local extinction. Morrow & Fricke (2004) analysed a large data set of mammal species and found no relationship between sexual size dimorphism or relative testis size and extinction probability, but more recently Bro-Jørgensen (2014) showed that bovid species with relatively large horns tend to be assessed by the IUCN as at greater risk of extinction.

These negative or neutral relationships between sexual selection and survival or extinction probability in the field are usually ascribed to the inherent costs of sexual selection that can affect demography (Kokko & Brooks 2003) and adaptation rates (Candolin & Heuschele 2008).

Sexual selection leads to a decrease in the effective population size ( $N_e$ ) because non-attractive individuals are less likely to reproduce (Kokko & Brooks 2003). A reduced  $N_e$  would facilitate inbreeding and genetic drift, leading to the fixation of maladaptive alleles (Keller & Waller 2002). Furthermore, exaggerated sexual signals or displays are themselves costly, displacing males' populations from their optimal fitness peaks (Promislow 1992; Bonduriansky 2011). Increased mortality in males caused by these extra costs can cause a bias in the sex ratio (Clutton-Brock *et al.* 1997; Kokko & Brooks 2003), thus reducing further the effective population size. Tanaka (1996) predicted with a theoretical model that this burden of sexual selection, added to that of stress caused by environmental change, would eventually lead to extinction.

Environmental variability itself has also been pointed out as a factor influencing the benefits or the costs of sexual selection on fitness. Kokko & Brooks (2003) showed with a simple theoretical model that a low perturbation rate could lead to a decrease in sexual display diversity and to an increased extinction probability when facing catastrophic changes. Long *et al.* (2012) found that in 'off-peak' populations, sexual selection was, overall, beneficial for average individual fitness in a population, but that it may be detrimental when the population is at its average individual fitness peak.

To make the picture more complex, all of these costs could be offset by different mechanisms. The decrease in  $N_e$  would be compensated by an effective purging of maladaptive genes arising from genetic drift and inbreeding (Jarzebowska & Radwan 2010). Condition dependence would limit the exaggeration of costly sexual displays during environmental stress (Kokko & Brooks 2003; Candolin & Heuschele 2008), and moreover, it would facilitate adaptation, thus limiting the extinction probability of the population (Lumley *et al.* 2015). Sexual conflict has also been found to maintain genetic diversity (Foerster *et al.* 2007), which would make populations more plastic when facing environmental changes (Bonduriansky 2011).

There is thus a wide range of factors interacting in different and complex ways that may determine the effect of sexual selection on population fitness, on adaptation rates and on overall resilience to change. As a result, making predictions about the effect of sexual selection is difficult, and importantly, most of the models that have been used to try to understand the role of sexual selection in determining adaptation rates or population fitness do not take into account the feedback between evolutionary and ecological processes, and those that include some kind of ecological dimension are often limited. For instance, Tanaka (1996) took into account environmental variability, but disregarded condition dependence; Lorch *et al.* (2003) took into account condition dependence and environmental variation, but did not account for population size. The lack of complex interactions between evolution and ecology in these models is most likely due to two

main reasons: first, because the questions addressed were somewhat different to those posed here, and while modellers were exploring the fundamental aspects of the relationship between sexual selection and population fitness, it was prudent to favour simplicity over realism, and secondly, because computational tools at that time were not powerful enough to model and interpret complex interactions between demographic, evolutionary and environmental factors.

In this study, we investigate the circumstances under which sexual selection hinders or facilitates adaptation using an individual-based model (IBM) allowing more complex feedback and interactions between evolutionary and ecological processes. IBMs are a powerful approach to simulate poorly understood evolutionary process, as they generate complex outputs from inputting a set of simple rules observed in nature (DeAngelis & Mooij 2005). This IBM simulates a population evolving under variable environments with different degrees of sexual selection and condition dependence, allowing us to investigate the effect of a set of different factors that will influence the strength of sexual selection, the carrying capacity and fecundity of the population, the environmental changes the populations will face and how and to what extent the traits are condition-dependent. It is likely that these factors will affect the costs and benefits in fitness of sexual selection, thus altering its net effect on the population. It is expected that costs of sexual selection will become more important as fecundity and population size decreases (Kokko & Brooks 2003), whereas the benefits of sexual selection are expected to be more evident in variable environments, where the input of maladaptive alleles is higher (Long *et al.* 2012). These benefits should be more evident as the sexual displays are more honest (i.e. more condition-dependent), because females will prefer good-quality mates.

### Model description

An IBM was used to simulate the complex effects arising from mate choice in a sexually selected species under a variety of scenarios of environmental change. The model was written and run in R (R Core Team, 2014), and we describe it in detail in Appendix S1 (Supporting Information) using the Overview-Design-Details (ODD) scheme proposed by Grimm *et al.* (2006).

All simulations started with an initial population of 100 individuals of randomly (drawn from uniform distributions) allocated sexes and ages breeding in a non-spatially structured environment. It was assumed that there was a single important environmental factor varying along a continuous axis, such as temperature or salinity, represented by an arbitrary single number for the whole environment. Each individual experienced this mean environmental value plus a small normally distributed random element drawn ('individual environment') to account for local climatic effects and phenotypic

variation. The degree of adaptation to the environment was modelled by a continuous variable called '*environmental genotype*' and the squared difference (mismatch) between the *environmental genotype* of each individual and the environment affected survival and reproduction, with high levels of mismatch between environmental genotype and environment leading to poorer *condition*. The squared rather than the absolute difference was taken to measure condition due to computational economy. The squared difference allows a tighter relationship between environment and phenotype. This allows the population to evolve faster, thus requiring fewer time steps to simulate and therefore fewer computational resources.

Each individual had a second 'genotype' value, '*sexual genotype*', which defined the strength of preference in females and allocation in sexual display in males. The size of a male's sexual display trait was determined by both its sexual genotype and by its condition, with the extent of condition dependence being a further variable in the model.

The overall potential strength of sexual selection was determined by adjusting the number of males that each female assessed before choosing a mate. The greater the number of males assessed per female, the stronger the potential reproductive skew and therefore pressure of sexual selection in the male population. To produce non-sexually selected populations, this value was set to 1, meaning that each female assessed only one male, giving mating which is effectively random. Each female chooses a mate from the pool of available males depending on the relative magnitude of their sexual display, on the degree of preference of a female and on a random factor drawn from a normal distribution. This added stochasticity accounts for the effects of spatial distribution of the populations, by which a male can be dominant locally, without necessarily displaying the most exaggerated sexual display of the whole population. It also allows for alternative reproductive strategies by which males bypass female mate choice, such as sneaky behaviours, mimicry or harassment (Gross 1996). As a result of this system of mate determination, females who are less choosy are less likely to mate with the male with the largest display. The environmental genotype, female choosiness and the degree of allocation into male display traits are inherited by any offspring making them able to evolve in the model, allowing feedback between sexual selection and demographic factors.

Each simulation lasted for 1000 time steps. Every time step, the environment could vary depending on the type of simulation, the options being a sudden step change, continuous directional change, random change or no change. After any environmental change was calculated, condition and all features depending on it were recalculated and the age increased by one in each individual. These features were then used to calculate each individual's death probability. Death was more likely if an individual was very young or old, if it had a poor condition

and, in males, if it had a large sexual display. The surviving individuals then mated according to the females' preferences and the males' sexual displays. Females only mated once each time step, but males could mate repeatedly. Females then reproduced, giving a variable number of offspring depending on the condition of each female and on the value of a parameter determining the degree of female fecundity. New individuals were then assigned a random sex, age 0 and an environmental and sexual genotype depending on that of the parents. The new individuals joined the population and the next time step started.

The modelled population was allowed to evolve with different levels of sexual selection strength (from none to strong), with varying levels of carrying capacity, fecundity, strength and timing of condition dependence in sexual displays and types of environmental change; 100 replicates were run for each combination of factors, giving a total of 43 200 runs. The values for each parameter used and their mathematical description are shown in Tables S1 and S2, respectively. The effects of these factors were assessed measuring their impact and that of their interactions in the observed patterns of population dynamics, exaggeration and cost of sexual display, and adaptation.

White *et al.* (2014) made a number of arguments against the use of frequentist statistics designed for hypothesis testing, such as *P*-values obtained from ANOVAS, for interpreting the output of simulation models such as the present one. Chief among these is the sensitivity of *P*-values to sample size, meaning, first, that the large sample sizes often obtained from simulation outputs can produce statistically significant effects that are biologically meaningless, and secondly, that a non-significant result can often be made into a significant one simply by running more simulations. It is more appropriate to describe the importance of each factor by using a measure of effect size such as partial  $\eta^2$ , which can be defined as the variance in the dependent variable explained by a particular predictor once the variance by other predictors has been excluded (Cohen 1973). Only the factors or interactions causing medium and large effect sizes were plotted and compared [medium effect sizes:  $\eta^2 > 0.059$  and  $\eta^2 < 0.138$ ; big effect sizes:  $\eta^2 > 0.138$ , according to Cohen's guidelines (Cohen 1988)]. For obtaining the partial  $\eta^2$  values, an ANOVA including the five abovementioned factors and all possible interactions between them was performed for each dependent variable (more details in Supporting Information). All the analyses were performed in R version 3.1.1 (R Core Team, 2014). The partial  $\eta^2$  was calculated using the package LSR (Navarro 2015), and the plots were generated using the packages PLYR (Wickham 2011), RCOLORBREWER (Neuwirth 2014) and GGPlot2 (Wickham 2009).

In order to test the effect of sexual selection on  $N_e$ , a further two hundred simulations were run with the numbers of males and females breeding recorded for each time step (more details in Supporting Information).

## Results

### SIMULATION OUTPUTS

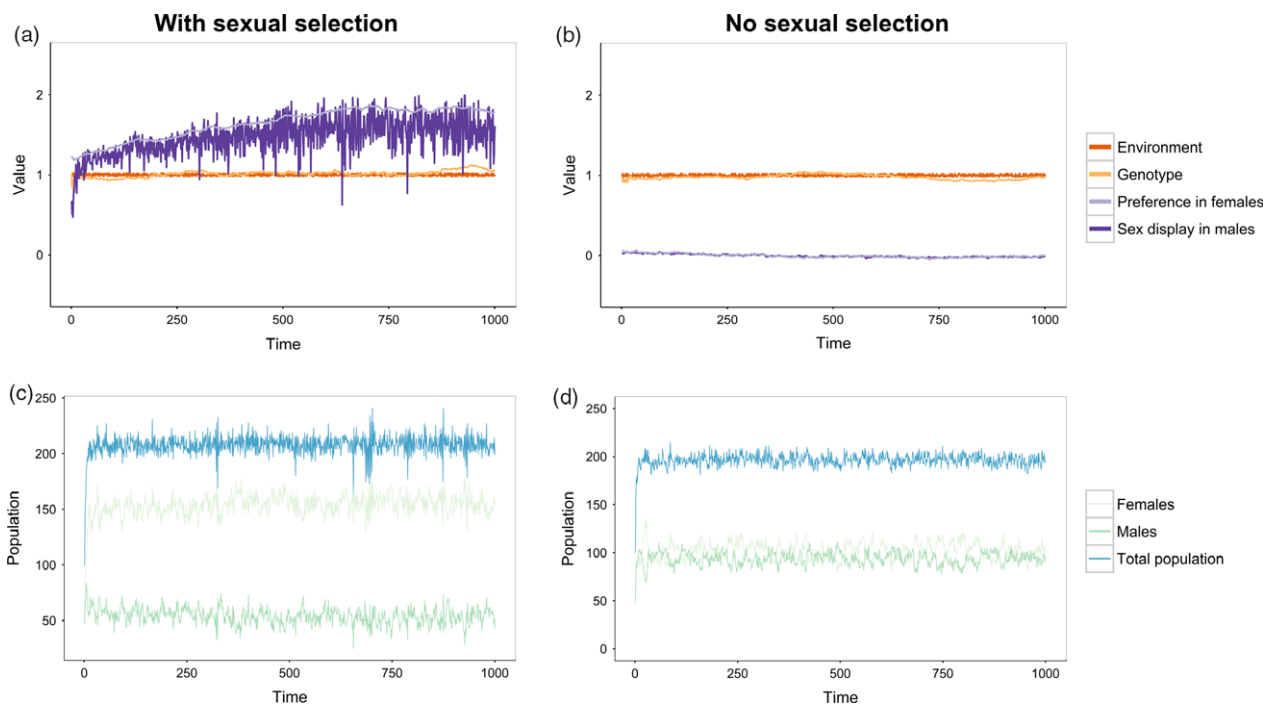
When simulations were carried out in the absence of environmental change (Fig. 1), the *sexual genotype* value increased in those populations with sexual selection operating (SS+) until it reached an apparent equilibrium, and female preference and the expression of male display increased correspondingly. Simultaneously, the sex ratio became more female biased. Without sexual selection (SS-), the sex ratio remained balanced during the whole simulation.

Figures 2 and S1 show examples of simulation outputs with environmental change. Whenever the environment changes, the population size drops, as does the expression of sexual displays in males when sexual selection is operating. In these SS+ populations, the population drop appears to affect females disproportionately such that the sex ratio becomes more even. In fact, this effect is caused by the death rate of males increasing less than that of females as a consequence of condition-dependent expression of the display trait: this interacts with environmental stress to cause reduced displays during these times. Because the increased death rate experienced by males is related to the expression of their display traits, these males experience a death rate that is much closer to that of the females when under severe environmental stress, balancing the sex ratio. Although display in males is reduced when the environmental mismatch is high due to condition dependence, the expression of female preference increases, albeit slowly, even when there is considerable mismatch between the environment and the population. When the environment changes, the population evolves and the *environmental genotype* variable can be seen to track the *environmental value*.

### SIMULATION EXPERIMENTS

Sexual selection had a marked effect on all the model outputs (Table 1), either directly (as with expression of the sexual trait, the amount of environmental mismatch and mean life span) or in interaction with another factor, usually population size (simulation time and expression of the sexual trait) or the type of environment variation (extinction probability, the amount of environmental mismatch and mean life span). Figure 3a shows the probabilities of extinction for the range of parameter values explored here. Without environmental variation, extinction probability was always higher in SS+ populations, especially when the population was small. When the environment was allowed to change, sexual selection either increased or decreased extinction probability depending on the nature of environmental change, the carrying capacity and the fecundity of individuals in the populations simulated.





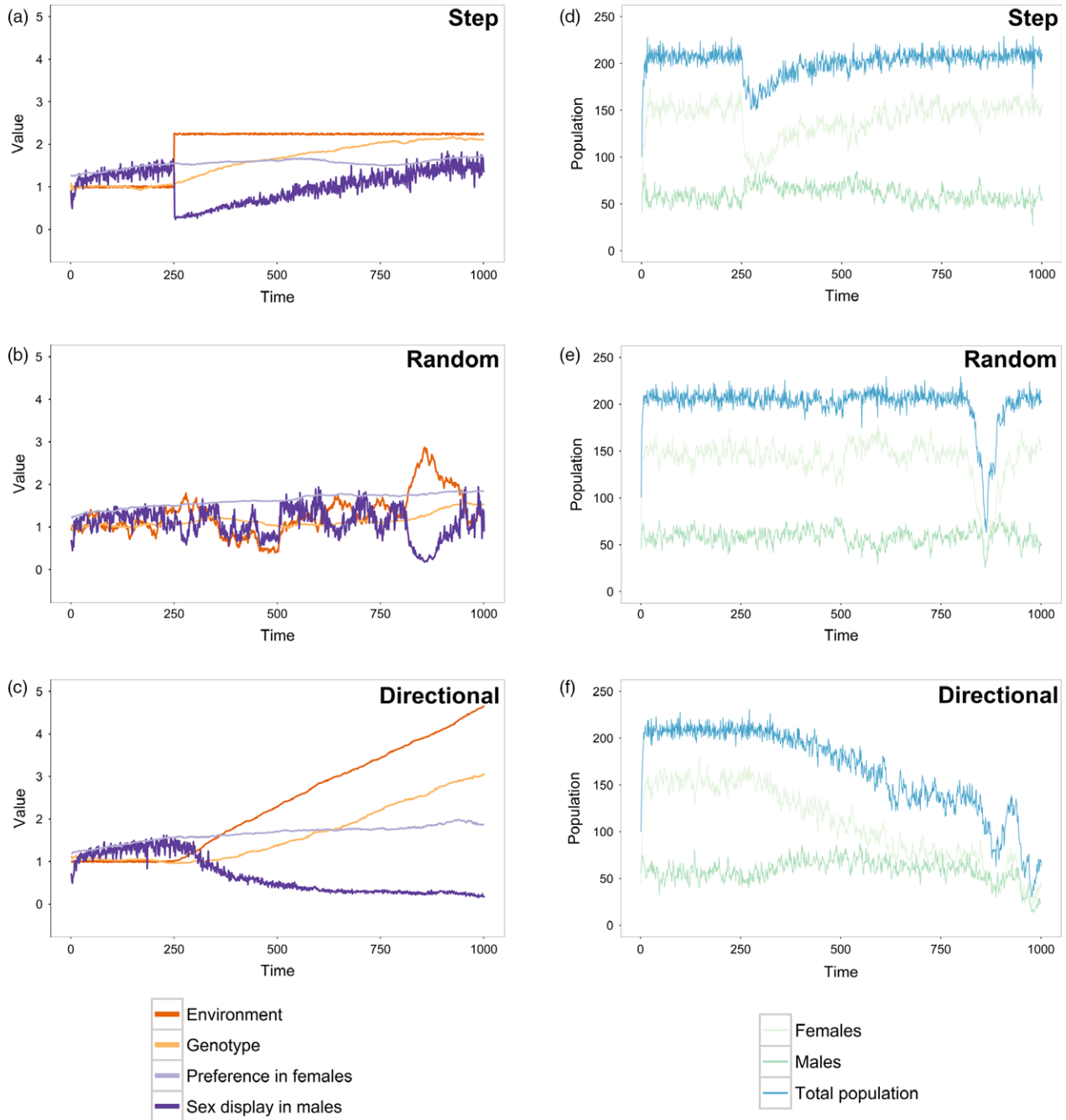
**Fig. 1.** Example of simulation outputs in which the environmental variation has been set to ‘none’. Populations in a and c are under sexual selection, whereas those in b and d mate randomly. (a and b) The median of the *environmental genotype* (dark orange), the mean of the sexual display in males (*sex trait* for males, dark purple), the mean of preference in females (*sex trait* for females, light purple) as well as the *environmental value* (light orange) for each time step. (c and d) The population size of every time step for males (dark green), females (light green) and the total population (blue). In this example, the values of the factors were 200 (medium–high) for *carrying capacity*, 5 (high) for *fecundity*, 10 (medium) for *strength of condition dependence* and in the sexually selected population, 5 (medium) for *strength of sexual selection*.

When facing directional environmental change, all SS– populations eventually became extinct. SS+ populations, by contrast, were sometimes able to persist and their probability of extinction decreased with increasing fecundity and carrying capacity such that high fecundity, large populations all survived for the entire period of the simulation when sexual selection was strong. When environmental change followed a random trajectory, almost all the populations went extinct when fecundity was low, regardless of whether sexual selection was operating. At higher fecundities, sexual selection affected extinction probability differently depending on the carrying capacity, with the beneficial effect of sexual selection increasing at higher carrying capacities. For instance, when both fecundity and the carrying capacity were high (5 and 500, respectively), the extinction probability was 0.21 in SS– against an extinction probability of 0.06 in SS+ populations. When environmental change was modelled as a step change, low fecundity populations almost all became extinct regardless of population size or the strength of sexual selection. When fecundity was higher, larger populations were mostly able to persist and there is some indication of an effect of sexual selection on the probability of persistence, especially when fecundity = 3 (medium) and the population carrying capacity is 100. For the smallest populations, however, SS+ populations were more likely to become

extinct when faced with an environmental step change than SS– populations.

Even though the strength of condition dependence had a small effect overall on extinction probability (partial  $\eta^2 = 0.016$ , see Table 1 for more details), its effect was noteworthy (Fig. 3b). In SS+ populations, as the strength of condition dependence increased, extinction probability decreased. This effect was most evident when fecundity was not at its minimum and the carrying capacity was very low. In this case, the extinction probability dropped from 0.86 to 0.48 (partial  $\eta^2 = 0.14$ , a strong effect size), and it is notable that the negative effect of sexual selection on extinction probability in small populations is neutralized when condition dependence is strong. Additionally, most of the SS+ populations evolving without condition dependence went extinct under any type of environmental change (results not shown).

The effect of sexual selection on adaptation can be estimated by looking at the mean *mismatch* between the *environmental genotype* and the value for the environment (Fig. 4) – when the environment is changing, populations that adapt more quickly will have lower values for this mismatch. Sexual selection affected *mismatch* differently depending on the type of environmental variation. The most dramatic effect was seen under step environmental change. In this scenario, SS– populations had a mean mismatch ( $0.63 \pm \text{SD of } 0.06$ ), which was close to twice



**Fig. 2.** Example of simulation outputs for populations under sexual selection in which the environmental variation has been set to ‘step’ (a, d), ‘random’ (b, e) and ‘directional’ (c, f). (a, b and c) The median of the *environmental genotype* (light orange), the mean of the sexual display in males (*sex trait* for males, dark purple), the mean of preference in females (*sex trait* for females, light purple) as well as the *environmental value* (dark orange) for each time step. (d, e and f) The population size of every time step for males (dark green), females (light green) and the total population (blue). In this example, the values of the factors were 200 (medium–high) for *carrying capacity*, 5 (high) for *fecundity*, 10 (medium) for *strength of condition dependence* and 5 (medium) for *strength of sexual selection*.

that of SS+ ones ( $0.38 \pm 0.04$ ). Under directional changes, there were no SS– populations that did not become extinct to compare with the SS+ populations, but presumably *mismatch* would be lower in the latter, as Figs 2c and S1c suggest quicker adaptation rates in SS+ populations, which would explain why all SS– populations went extinct when facing directional changes. Random and no environmental

changes do not yield any clear *mismatch* pattern depending on the effect of sexual selection.

The life span of individuals in the simulations was strongly affected by sexual selection and also by environment and fecundity (Fig. S3). Condition dependence strength also had a strong effect on life span (Table 1), although the amount of variation explained is small

**Table 1.** Effect sizes of all factors tested and their combinations on all dependent variables

Factors	Size effect (partial $\eta^2$ )				Mean life span
	Extinction probability	Time to extinction	Expression of sexual trait	Degree of environmental mismatch	
<b>K</b>	<b>0.2152</b>	<b>0.2481</b>	<b>0.5351</b>	0.0074	0.0132
<b>CD</b>	0.0159	0.0138	<b>0.6525</b>	0.0008	<b>0.1407</b>
<b>SS strength</b>	0.0028	0.0032	<b>0.4086</b>	<b>0.3438</b>	<b>0.9179</b>
<b>Environment</b>	<b>0.4951</b>	<b>0.1767</b>	<b>0.7667</b>	<b>0.8850</b>	<b>0.8138</b>
<b>Fecundity</b>	<b>0.4386</b>	<b>0.4390</b>	0.0115	0.0216	<b>0.8760</b>
<b>K × CD</b>	0.0126	0.0073	<b>0.0769</b>	0.0008	0.0018
<b>K × SS strength</b>	0.0572	<b>0.0645</b>	<b>0.1284</b>	0.0055	0.0004
CD × SS strength	0.0065	0.0055	0.0170	0.0008	0.0090
<b>K × Environment</b>	0.0373	0.0396	<b>0.0787</b>	0.0138	0.0134
<b>CD × Environment</b>	0.0091	0.0034	0.0138	0.0006	<b>0.0893</b>
<b>SS strength × Environment</b>	<b>0.0958</b>	0.0033	0.0303	<b>0.3928</b>	<b>0.5677</b>
K × Fecundity	0.0211	0.0090	0.0366	0.0007	0.0028
CD × Fecundity	0.0012	0.0001	0.0027	0.0002	0.0016
SS strength × Fecundity	0.0222	0.0468	0.0030	0.0073	0.0388
<b>Environment × Fecundity</b>	<b>0.2419</b>	0.0289	0.0280	<b>0.0615</b>	<b>0.1237</b>

Factors are as follows: **K**, carrying capacity; **CD**, strength of condition dependence; **SS strength**, strength of sexual selection (i.e. amount of males from which a female chooses its mate); **environment**, type of environmental change; **fecundity**, maximum number of offspring per female.

The values of partial  $\eta^2$  were obtained by fractionating the variance of each dependent variable with ANOVAS. Values in boldface show medium and big effect sizes on the variables; those in light grey have medium effect sizes ( $\eta^2 > 0.059$  and  $\eta^2 < 0.138$ ) and those in dark grey have big effect sizes ( $\eta^2 > 0.138$ ) according to Cohen's standards (1988). Factors in boldface have a medium or big effect size in at least one response variable. The '×' indicates interaction between factors. Only two-way interactions are shown, as more complex interactions have only a small effect sizes, except for the triple interaction K:environment:fecundity, which has a medium effect size (partial  $\eta^2 = 0.0822$ ) for extinction probability.

relative to the effect of sexual selection intensity, the environment and fecundity. SS+ individuals had a shorter mean life span ( $4.59 \pm 0.45$  years for all SS+ populations) than SS- ones ( $5.6 \pm 0.68$  years for all SS- populations). A set of further simulations showed that the effect of sexual selection on life span was much stronger in males than in females (partial  $\eta^2 = 0.98$  for males and 0.23 for females). Males from SS+ populations had a mean life span of  $4.25 \pm 0.75$  time steps, whereas SS- males had a mean life span of  $7.79 \pm 0.47$  steps, very similar to that of females in both SS- and SS+,  $8.02 \pm 0.56$  and  $8 \pm 0.5$ , respectively.

Strongly sexually selected populations generated higher mean values of *sexual trait* (Fig. S4), but only when the carrying capacity and condition dependence were high enough. For instance, without environmental variation and at a high carrying capacity, there was little difference in the *sexual trait* value between weak and strong sexual selection when condition dependence was weak ( $1.78 \pm 0.04$  vs.  $1.88 \pm 0.23$ ). The difference became more evident, however when the sexual display was highly condition-dependent ( $1.38 \pm 0.04$  vs.  $1.64 \pm 0.04$ ). Strong condition dependence resulted in lower values of *sex trait*, especially under directional environmental change, where *sex trait* dropped from  $1.24 \pm 0.1$  to  $0.93 \pm 0.08$  when comparing non-extinct SS+ populations under weak and strong condition dependence, respectively. Although these differences may not seem remarkable, it is important to

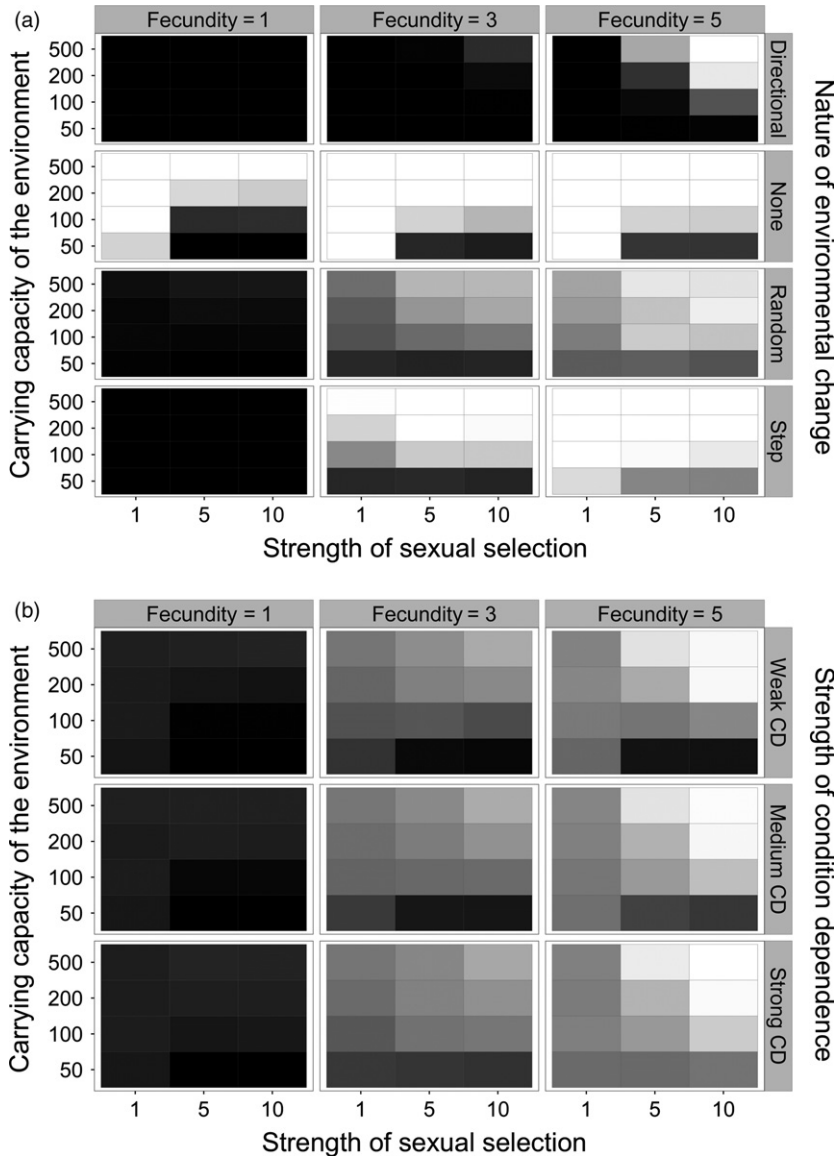
consider that *sex trait* was analysed for both males and females and that the latter were not subject to condition dependence (as seen in Fig. 2). The results here shown are therefore most likely underestimated.

As expected, SS+ had a lower  $N_e$  than SS- populations (more details in Supporting Information).

## Discussion

By using an IBM that allows feedback between demographic and evolutionary processes, we find that sexual selection can both increase and decrease average individual fitness in a population depending on a variety of factors. These include the carrying capacity of the environment, how fecund the individuals in the population are, the nature of environmental variation and the degree of condition dependence of the sexual displays.

Long *et al.* (2012) argued that sexual selection should be beneficial in situations in which genetic variance depends on large inputs of maladaptive alleles, such as environmental changes. Our results support this and show also that the type of environmental change is important in determining the effects of sexual selection. When the environmental change is directional and harsh conditions are maintained for long periods of time, sexually selected populations are less vulnerable to extinction than populations mating randomly. Directional environmental change means that all generations are some distance from their



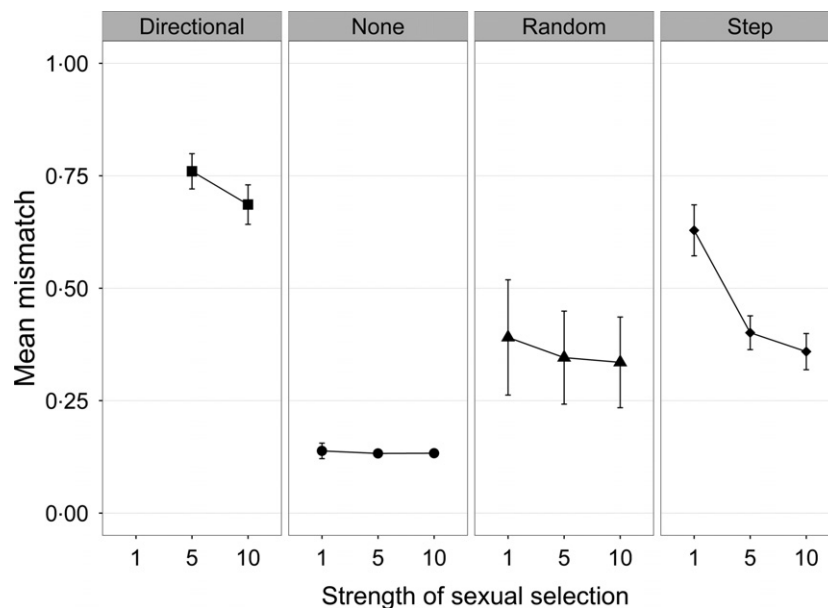
**Fig. 3.** Heatmaps showing the risk of extinction depending on carrying capacity ( $y$ -axis), fecundity (varies by column), sexual selection (SS) strength ( $x$ -axis) and either environmental variation (a, by row) or condition dependence (CD) (b, by row). Each square accounts for a single combination of levels of each factor. Darker squares represent higher extinction risk, and lighter ones represent lower extinction risk. The levels ‘directional’, ‘none’, ‘random’ and ‘step’ refer to types of environmental change. As a general trend, extinction decreases as fecundity and carrying capacity increase. The effects of environment and sexual selection are variable depending on the interaction between each other and with carrying capacity and fecundity. Although condition dependence did not have a large effect size, it was plotted because it has interesting effects on extinction risk. As CD increases, extinction risk decreases provided that there is sexual selection.

fitness optimum and that there is a constant input of maladaptive alleles because what was adaptive in one generation will become maladaptive in later generations as the environment alters. Under these circumstances, sexual selection leads to less adapted males acquiring relatively few mates, whereas those males who happen to be best adapted to the new environment will achieve much higher mating success than they would in a randomly mating system. This allows the sexually selected populations to adapt faster, ‘tracking’ the changing environment more efficiently. Without environmental variation, the input of maladaptive alleles is low and consequently sexual selection has no benefits but is still costly. Moreover, as noted by Kokko & Brooks (2003), the absence of environmental variation limits the diversity of sexual displays, which are highly exaggerated due to a lack of harsh conditions. As a result, the cost of sexual selection increases, but there is no benefit because there are no maladaptive alleles to purge.

When the environmental change is random, sexually selected populations are more likely to persist except when the carrying capacity is low, but the effect of sexual selection is not as great as in other scenarios: some SS– populations persisted and some SS+ populations became extinct, even when fecundity and carrying capacities were high. This appears to be because under random environmental change there are some periods when the environment is relatively stable, and some periods of sudden change. In the former case, sexual selection has an adverse effect because of its cost, whereas in the latter it allows faster adaptation and is therefore beneficial. As a consequence of these two differing effects, the effect of sexual selection on population persistence is weaker in this case.

Sexually selected populations that went extinct facing large step changes in the environment lasted for longer and had an overall higher fitness than non-sexually selected ones, suggesting that again, sexual selection





**Fig. 4.** Mean mismatch of all simulations depending on sexual selection (SS) strength and environmental variation. Error bars represent the standard error of the mean. Only simulations in which the population did not go extinct were selected. Combinations of factors not showed here led to the extinction of the population in all simulations. The levels 'directional', 'none', 'random' and 'step' refer to types of environmental change.

facilitates adaptation, allowing a quick response to a catastrophic environmental change. Overall, however, sexual selection did not appear to have a strong effect on extinction probability in this scenario. This lack of detectable effects may be caused by demographic effects overriding the effect of sexual selection, as all populations with low fecundity went extinct and even at higher fecundity levels only those with large carrying capacities survived.

In our simulations, males from sexually selected populations lived shorter lives than those of non-sexually selected ones, giving the increased female/male ratio observed. This effect was expected (Kokko & Brooks 2003), and it is common in nature, for example in populations of red deer (Clutton-Brock *et al.* 1997), Soay sheep (Coulson *et al.* 2001) and lions (Loveridge *et al.* 2007). This is likely to be the reason why sexually selected populations with low carrying capacity and low fecundity are more vulnerable to extinction than non-sexually selected ones in our simulations. Small populations under sexual selection have fewer males than non-sexually selected ones of the same size and mortality in sexually selected males is higher than those in populations with random mating. These small populations of males with high rates of mortality will be more vulnerable to stochastic demographic effects, and there will be an increased probability that, for example, all males in the population die at the same time due to stochastic events. Without males, the females remaining cannot reproduce and the entire population goes extinct. These results suggest that populations under sexual selection would be prone to Allee effects because under sexual selection, population density and fitness would be positively correlated. This observation is similar to that made by other authors, such as Møller & Legendre (2001) or Shaw & Kokko (2014) who hypothesized that sexual selection could be a key driver for Allee

effects. Without the burden of sexual selection, the sex ratio is close to 0.5 and therefore the population of males is larger, making it more resilient to stochastic effects. This effect of sexual selection in small populations has not been explicitly tested empirically, but it would explain why introductions to islands of dimorphic species of birds were more likely to fail than those of monomorphic ones in the study performed by Sorci *et al.* (1998).

Condition dependence of the sexual display has shown to be a key factor in determining the effect of sexual selection. Without condition dependence (i.e. dishonest sexual displays), the cost of sexual selection is excessive for most sexually selected populations simulated. However, once condition dependence is acting, the effect of its strength in the sexually selected populations is rather limited. If the sexual display does not signal the quality of the bearer honestly, there are no indirect benefits in the population for costly exaggerated sexual displays. In this situation, sexual selection still has costs, but no benefits. If the sexual display does not signal the quality of the bearer honestly, there are no indirect benefits in the population for costly exaggerated sexual displays. In this situation, sexual selection still has costs, but no benefits. Consequently, there is an additional burden to the populations' fitness apart from that arising from environmental stress, as described by Tanaka (1996), which eventually leads to the extinction of the population.

In this study, sexual selection was assumed to show only indirect benefits through 'good genes'. It is important to remember that not all sexually selected traits have necessarily evolved due to the indirect benefits of 'good genes'. There are other well-known mechanisms that can generate costly exaggerated sexual displays without necessarily evolving condition dependence (Pomiankowski & Iwasa 1998; Ryan & Cummings 2013), and if there are direct benefits of female preference, these could increase

population fitness without the need of indirect benefits through ‘good genes’ (Kirkpatrick & Ryan 1991). In such a scenario, however, males might be paying a high cost because they would not benefit from indirect effects of ‘good genes’. Future work could study how these processes balance each other, and under which conditions and to what extent their relative importance impacts adaptation and extinction probability.

Despite this, the importance of condition dependence cannot be disregarded. The results obtained here show that not only does condition dependence accelerate adaptation as expected by both theory and empirical observation (Lorch *et al.* 2003; Plesnar-Bielak *et al.* 2012), but that it can also modulate the selective pressure of sexual selection, preventing the exaggeration of the sexual display during harsh environmental conditions. As a consequence, the burden of bearing a large signalling trait is not added to that of environmental stress. As the population becomes adapted to the new environment, exaggerated sexual displays are able to grow again, thus increasing the pressure of sexual selection and accelerating adaptation. This preventive mechanism depending on both condition dependence and phenotypic plasticity has been predicted previously by different authors (e.g. Candolin & Heuschele 2008).

There are likely to be more factors affecting the balance of costs vs. benefits of sexual selection than those included in our model. For example, migration introduces new alleles to the population, which may alter the balance of costs and benefits in a number of ways (Long *et al.* 2012). Sexual conflict is another factor that is likely to alter the costs and benefits (Chapman *et al.* 2003), which has not been explicitly explored here. However, the loss of fertility is a usual outcome of sexual conflict (Kokko & Brooks 2003; Holman & Kokko 2013). If this assumption is correct, the effects of sexual conflict would be similar to that of a loss of fecundity observed here. Further studies are needed to determine to which extent and in which situations sexual conflict adds a cost to sexual selection.

Future models could also simulate population genetics in a more detailed way. In this study, the genetic structure of the population was modelled as genotypes with continuous values rather than as discrete alleles. This was done because condition is assumed to be a large selection target, depending on a large number of alleles (Rowe & Houle 1996), and for the sake of simplicity, the genotype approach was considered adequate for the purposes of this study. The limitation of this approach is that effects such as genetic drift and inbreeding expected to occur in reduced populations could not be tested. Instead, it was assumed that under sexual selection, the reduction in effective population size, predicted by other authors (Kokko & Brooks 2003) and observed in this study, is counteracted by the more efficient purging of maladaptive alleles (e.g. Almbro & Simmons 2014) and that these effects were therefore negligible. Clearly, this is a subject that could be considered in more detail in future work. In

conclusion, sexual selection should not be considered as a process with the same general effect in all populations. Rather, the specific details of the population’s ecology as well as the nature of any environmental change will determine whether sexual selection leads to an overall positive or negative effect on population-level fitness. As a broad generalization, sexual selection appears to be more costly when the population affected is small and has limited growth, either because of low fecundity or by low carrying capacity, and sexual selection is more likely to be costly in stable environments. On the other hand, when the environment is changing rapidly, condition-dependent sexual displays can lead to considerable benefits from sexual selection, especially in larger populations with higher fecundity.

Although the applicability of this model to specific natural systems is limited, this study has generated several hypotheses that could be tested empirically. For instance, large-scale studies comparing extinction probability between sexually and non-sexually selected species have yielded contradictory results (e.g. Doherty *et al.* 2003; Morrow & Fricke 2004). The results of the present study show that sexual selection by itself is a bad predictor of extinction probability, and future work incorporating factors such as population size, population fecundity or the nature of environmental change should predict the extinction risk of sexually vs. non-sexually selected populations more accurately.

Climate change is likely to produce similar types of environmental variation to those simulated here. For instance, constant and steady changes will be faced due to increases in temperature or, in aquatic systems, pH, and extreme events such as storms or heat waves will be more severe and frequent, thus increasing the unpredictability of the environment and increasing the probability of catastrophic events (Stocker *et al.* 2013). In general, sexually selected populations should perform better under environmental change, but only if the population is healthy and large enough. Unfortunately, the latter condition is not likely to be fulfilled in all cases, as many threatened species have reduced habitats due to anthropogenic activities, thus limiting its carrying capacity and potentially increasing the costs of sexual selection. For future conservation decisions, the factors described here should be taken into account to assess the real costs and benefits of sexual selection for each particular case.

### Authors’ contributions

R.K. developed the original concept. C.M.-R. wrote the model code and ran the simulations. C.M.-R. and R.K. interpreted the output and wrote the paper.

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## Data accessibility

Full code for the model is given in Appendix S2.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article.

**Appendix S1.** Model description.

**Appendix S2.** Model code.