Sexually-selected male weapon increases the risk of population extinction under environmental change: an experimental evidence

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Abstract

Exaggerated sexually-selected traits, occurring more commonly in males, help individuals to increase reproductive success, but are costly to produce and maintain. These costs on the one hand may improve population fitness by intensifying selection against maladapted males, but on the other hand may increase the risk of extinction under environmental challenge. However, the impact of sexually selected traits on extinction risk have not been investigated experimentally. We used replicate populations of a male-dimorphic mite, Rhizoglyphus robini, to test if prevalence of an elaborate, sexually-selected weapon affected the risk of extinction under gradual temperature increase (20C per generation). As temperature increased, individual survival decreased, but this effect was much more dramatic in populations with high weapon prevalence, compared to populations in which weapon expression was low. Consequently, the former was significantly more prone to extinction than the latter, with 75% vs 8% populations going extinct, respectively. Extinctions occurred despite partial suppression of the weapon expression at increased temperature, and were not explained by increased male mortality. Our results provide the first, to our knowledge, experimental evidence demonstrating dramatic effect of elaborated sexual traits on the risk of extinction under environmental challenge.

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Abstract

Exaggerated sexually-selected traits, occurring more commonly in males, help individuals to increase reproductive success, but are costly to produce and maintain. These costs on the one hand may improve population fitness by intensifying selection against maladapted males, but on the other hand may increase the risk of extinction under environmental challenge. However, the impact of sexually selected traits on extinction risk have not been investigated experimentally. We used replicate populations of a male-dimorphic mite, *Rhizoglyphus robini*, to test if prevalence of an elaborate, sexually-selected weapon affected the risk of extinction under gradual temperature increase (2^{0} C per generation). As temperature increased, individual survival decreased, but this effect was much more dramatic in populations with high weapon prevalence, compared to populations in which weapon expression was low. Consequently, the former was significantly more prone to extinction than the latter, with 75% vs 8% populations going extinct, respectively. Extinctions occurred despite partial suppression of the weapon expression at increased temperature, and were not explained by increased male mortality. Our results provide the first, to our knowledge, experimental evidence demonstrating dramatic effect of elaborated sexual traits on the risk of extinction under environmental challenge.

Introduction

Darwin developed the theory of sexual selection to explain evolution of traits, such as elaborated antlers or feathers, which by hampering survival, and thus apparently contradicted his theory of natural selection (Darwin 1859, 1871). Darwin's solution highlighted the role of such costly traits in reproductive competition: antlers help males to win in combat over access to females, and colourful feathers make males sexually more attractive. However, he also appreciated that sexual competitiveness is likely to be associated with general health and vigour, and thus sexual selection may be partly aligned with natural selection (Darwin, 1859). In contemporary theory of sexual selection, this is framed in terms of condition-dependence of sexual trait expression, with condition being defined as a trait capturing genetic variation in an individuals' ability to acquire and effectively process resources. This "genic capture" mechanism implies that individuals which are better-adapted and/or less burdened with mutations, should be more likely to reproduce and pass their genes to next generations (Andersson, 1986; Rowe & Houle, 1996).

The degree to which sexual selection is aligned with natural selection is likely to affect the risk of extinction. On the one hand, studies manipulating opportunity for sexual selection experimentally have demonstrated that sexual selection can help adaptation to a novel environment (Long et al., 2012; Plesnar-Bielak et al., 2012; Grieshop et al., 2016; Parrett & Knell, 2018), purge genetic load (Radwan, 2004; McGuigan et al., 2011; Almbro &Simmons, 2014) and in consequence, prevent extinction (Jarzębowska & Radwan, 2010; Plesnar-Bielak et al., 2012; Lumley et al., 2015; Godwin et al., 2020) (but see e.g. Arbuthnott & Rundle, 2012; Chenoweth et al., 2015, for counterexamples). On the other hand, elaborated sexual traits may become a burden to survival, especially during stress associated with environmental changes, which can eventually lead to extinction (Kokko & Brooks, 2003). While expression of condition-dependent sexually selected traits may be supressed under environmental stress, thus alleviating their costs to their bearers, genes underlying these traits may also have negative pleiotropic effects in female productivity and survival (Harano et al., 2010;

Plesnar-Bielak et al., 2014; Lukasiewicz et al. 2020), which could contribute to increased risk of extinction (Kokko & Brooks, 2003).

Comparative work yielded conflicting results: some studies reported increased risk associated with elaboration of male sexually selected traits (Doherty et al., 2003; Morrow & Pitcher, 2003; Martins et al., 2018; Bro-Jørgensen, 2014), while others found no evidence for such relationship (Morrow & Fricke, 2004). These apparent inconsistencies can result from uncontrolled differences in the genetic diversity of populations of their exposure to environmental stressors. This possibility is highlighted by a recent study by Parrett et al. (2019), who found that generally positive effect of sexually selected beetle horns on survival is modulated by a degree of anthropogenic alteration of the habitat. Additional confounding factors may include differences in population sizes (Martinez-Ruiz & Knell, 2017) or in breadths of ecological niches, which can be modulated by the degree of sexual dimorphism (Bonduriansky, 2011; De Lisle & Rowe, 2015). Further progress could be achieved by using an experimental evolution approach, which have grossly contributed to our understanding of the contribution of sexual selection to population fitness (see Cally et al., 2019 for review). However, experimental evolution studies that measured extinction rate so far primarily manipulated mating systems or sex ratio (Plesnar-Bielak et al., 2012; Jarzębowska & Radwan, 2010; Parrett & Knell, 2018; Goodwin et al., 2020), rather than expression of exaggerated sexual traits. Thus, they cannot inform us on how evolution of such traits affects the risk of extinction.

Here, we experimentally assess the risk of extinction associated with the expression in males of a costly, sexually selected weapon under environmental change (gradual increase in ambient temperature by 2^{0} C per generation). Our model species was the male-dimorphic bulb mite *Rhizoglypus robini*, in which some males (but not females) express a sexually selected weapon: thickened third pair of legs. The weapon, expressed only in a fighter male morph is both significantly heritable and costly to produce (Radwan, 1995; Smallegange & Coulson, 2011). Part of the heritability could be due to higher load of deleterious mutations preventing males from expressing costly weapon. Indeed, comparison of inbreeding depression between inbred lines derived from fighters and scramblers indicated that the load of deleterious mutations is higher in the scramblers (Lukasiewicz et al., 2020). Thus, purifying selection should be stronger in populations in which the male weapon is present, possibly decreasing their risk of extinction. Furthermore, condition-dependence of the weapon expression (Radwan, 1995; Smallegange, 2011) should ensure that its direct costs to males can be plastically reduced under environmental challenge. However, females from genetic lines nearly fixed for fighter morph were shown to have lower fitness compared to lines nearly fixed for scrambler morph in two independent populations (Plesnar-Bielak et al., 2014; Lukasiewicz et al., 2020), indicating that genes associated with fighter phenotype can have negative pleiotropic effects on female fitness. This variant of gender load (Rice, 1992; Arnqvist & Tuda, 2010) may compromise population viability and make them more prone to extinction.

We used inbred lines nearly fixed for fighter or scrambler morph to establish outbred populations enriched for fighter or scrambler genes (F and S population respectively), each founded by the same number of genomes to control for initial genetic diversity. These populations were then subjected to an incremental increase in temperature (2°C per generation) to simulate a climate change comparable to that experienced by many species during current global warming (Parrett et al., 2018). We find that under such environmental change, populations enriched for fighter genes faced a significantly elevated risk of extinction. Mortality increased with the level of thermal stress at significantly faster rate among individuals in F populations, but males were not disproportionately more affected than females. Our results therefore imply that evolution of exaggerated sexual traits may have negative pleiotropic effect on fitness of both sexes under environmental challenge, thus increasing the risk of population extinction.

Material and methods

We used inbred lines described in Lukasiewicz et al. (2020), that were inbred via 4 generations of brothersister mating and continued inbreeding for 6 more generations. In brief, mites collected from onion bulbs in Mosina, Wielkopolska, Poznań Poland, and inbred lines were initiated from the first generation of which hatched in the lab. The proportion of both male phenotypes used for crosses reflected that in the original population, giving rise 26 inbred lines founded by fighter males (fighter lines henceforth), and 15 inbred lines founded by scrambler males (scrambler lines). The consecutive generations were established by mating a randomly selected female with her sibling male of the same morph as the male founder. Choosing the same morph as the founder to establish each generation allowed us to maintain differences in morph proportions between F and S inbred lines throughout the inbreeding experiment (Fig. S1).

We established outbred populations enriched for scrambler or fighter genes (F and S populations henceforth) by mixing 12 inbred lines with the highest ratio of the desired morph after 10 generations of brother-sister mating described above. In this way we ensured that genes for the desired morph were also overrepresented among females. Furthermore, using inbred lines ensured effective population sizes of F and S populations were similar (i.e. contained about 24 genes randomly sampled from the original wild population), and that they carried much of the standing genetic variance present in the population collected from the field. We took six protonymphs (second juvenile stage) from each from inbred line (hence, there were 72 founders per population) and expanded them for two generations with random mating. The expanded populations were then subdivided into four F populations and four S populations by transferring 50 randomly selected protonymphs in a new vial. Next generation, each of these F and S populations was further subdivided it two treatments: gradual temperature increase (GTI, with three replicates per subpopulation) and control (one replicate). The GTI populations (FT and ST henceforth) were maintained at 25°C during first generation, with temperature increasing for the next two generations by 2°C, and then maintained at 29°C from third generation on (we did not increase the temperature further as our pilot study indicated that mites are unable to adapt to temperature over 30°C when the temperature increases 2°C per generation). Control populations (FC and SC henceforth) were maintained at 23°C at all generations. Each generation lasted 10 days, with c.a. three days needed for adult eclosion and 7 days for mating and reproduction (mating takes place immediately upon emergence and eggs are laid continuously starting ca. 24 h after mating). Each new generation was started by 50 randomly selected protonymphs. At each generation, we recorded the number of females, scrambler, and fighter males twice: immediately after adults eclosed and at the end of the reproduction period. A population was considered to be extinct if (i) the females did not lay any eggs, (ii) no larvae hatched from the laid eggs, or (iii) no adults of one or both sexes survived to adulthood.

Statistical analyses

None of the control populations went extinct, so we only analysed the effect of morph enrichment on extinction in populations subjected to gradual warming after four generations, using the 'glmer' function from the 'lme4' package in R (Bates et al., 2015; R Core Team, 2021). The extinction was modelled as a binomial response variable (coded 0 for extinction and 1 for survival) with population type (FT vs. ST) entered as a fixed factor and replicate within population as random effect.

To analyse survival of individuals within both GTI and control populations, the effect of treatment (Control vs. GTI populations), population type (F vs. S) and generation (coded as continuous variable) were entered as fixed effects, and population and replicate within population as categorical random effects. A two-variable vector containing the numbers of survived and dead individuals (counted as difference between initial number of juveniles and number of adults at the end of the reproductive period) was a response variable. In order to investigate the effect of founder morph effect on survival of individuals that experienced increased temperature, GTI treatment-specific model with population type and generation as fixed effects was fitted. We similarly analysed sex-specific survival at the adult stage (immature stages cannot be sexed) in GTI populations, with a vector of the numbers of adults which survived and died by the end of reproductive period as a response variable. Finally, we analysed changes in male morph ratio (coded as a two-variable vector containing number of fighters and the number of scramblers) at emergence from nymphs, using GLMM with treatment and generation as fixed factors. The model was run only for F populations data because an evgiuvalent model for S population, as well as a full model with a tree-way interaction, could not be estimated due to high correlation between fixed effects in models including three-way interaction, and quasi compleate separation (a situation when the predictor is associated with nearly uniform value of response variable) in S population. The data were overdispersed in models testing for survival of individuals, sex-specific survival,

and changes in male morph ratio. To account for this, beta-binomial GLMMs were conducted using the 'glmmTMB' function in 'glmmTMB' package (Brooks et al., 2017). The goodness of fit of the models were evaluated based on Akaike information criterion (AIC) by comparing AIC scores between model with the highest order interactions and simplified models, but this only lead to reduction of sex-specific survival model, for which the best fitted model (Δ AIC = 3.2) included two-way interaction between sex and generation, and population type as fixed effects. In all other cases, full models for all response variables had the lowest AIC scores. All statistics were run in R version 4.0.5 (R Core Team, 2021).

Results

The proportion of individuals which survived till the end of the reproduction period in the GTI treatment declined with the increasing temperature (Fig. 1), and the decline was significant when compared to control treatment (Treatment * Generation est. \pm s.e. = -1.004 + 0.228, z = -4.393, p < 0.001; Table S1). Within GTI populations, the survival was affected by the interaction between population type (FT vs. ST) and generation (est. \pm s.e. = 0.538 + 0.184, z = 2.992, p = 0.003; Fig. 1, Table 1). Strikingly, among populations subjected to temperature stress, very few adults survived in FT populations at generation four (Fig. 1) and consequently, nine (75%) of these populations went extinct (Fig. 2). At the same time, only one (8,3%) ST population went extinct, a significantly lower proportion compared to FT populations (est. \pm s.e. = 3.724 + 1.741, z = 2.139, p = 0.032). Interestingly, extinction proceeded despite that expression of fighter morphs in FT populations declined from 76% at first generation to 25% at fourth generation (est. \pm s.e. = -1.598 + 0.218, z = -7.327, p < 0.001; Fig. S2, Table S2). Indeed, the reason for higher extinction of FT did not seem to have been associated with higher male mortality in FT populations, as indicated by the non-significant effect of population type*sex interaction on proportion of surviving adults across four generation (full model: est. \pm s.e. = 0.154 + 0.301, z = 0.511, p = 0.609). However, there was a significant generation * sex interaction (best model: est. \pm s.e. = 0.462 + 0.145, z = 3.184, p < 0.001 Fig. S3; Table S3): in both F and S populations, females survived better than males in early generations, but then in following generations, as temperature increased and survival decreased, the differences between sexes decreased.

Discussion

Costly sexually selected traits may affect viability, especially in stressful environments, and it has long been speculated that, for example, Irish elk (*Megaloceros giganteus*), characterized by extremely elaborated antlers, went extinct when glaciation limited resource availability (Moen et al., 1999; but see O'Driscoll Worman & Kimbrell, 2008). However, the effect of elaborated sexual traits on extinction risk remains unresolved, with comparative analyses yielding conflicting results (Doherty et al., 2003; Morrow & Pitcher, 2003; Martins et al., 2018; Parrett et al., 2019). Our study is the first experimental evidence showing that during the environmental change, the presence of elaborated sexual trait in a population elevates the risk of extinction.

Our results contrast with those obtained by manipulating opportunity sexual selection via mating system and sex ratio, which generally find positive effect of sexual selection on fitness correlates (reviewed in Cally et al., 2019) and population survival (Jarzebowska & Radwan, 2010; Plesnar-Bielak et al., 2012; but see Parrett and Knell 2018). This apparent inconsistency can be reconciled by conceptually separating short-term from long term impacts of sexual selection (Figure 3). In the short timescale, the effects of sexual and natural selection act on phenotypic variation present in a population at a given point in time. Under conditiondependence, both types of selection can to a large extent be aligned, especially during environmental change (Long et al., 2012; Plesnar-Bielak et al., 2012; Parrett & Knell, 2018). However, in the long term, as sexually selected traits get elaborated, extinction risk may be increased, for example by magnifying survival costs to males (Promislow, 1992; Moen et al., 1999), or by causing gender load associated with (partial) expression in females of alleles favoured by sexual selection acting on males (Rice & Chippindale, 2001; Berger et al., 2016).

Our results do not support the hypothesis that rate of extinction of entire populations is increased because cost of developing and carrying heavy weapons by males increase their mortality under environmental challenge (Moen et al., 1999: Kokko & Brooks, 2003). Increasing temperature did not disproportionately affect survival of males in FT populations. Instead, in both FT and ST populations, females survived better than males in early generations, but in generations 3 and 4 the differences between the sexes disappeared, suggesting that female survival was more negatively affected by increasing temperature compared to males (Fig. S3). Our results support earlier suggestions that that because of their widespread condition-dependence, elaborate sexually selected traits should not compromise population fitness because most males not express these costly traits when environment deteriorates (Kokko & Brooks, 2003). This was indeed the case in the present study, as proportion of fighters decreased across generations with increasing temperature in FT populations, with proportion of fighters already down to 75,7% at the first step of temperature increase (Figure S2). This decrease can be explained by condition-dependence weapon expression (Radwan, 1995; Smallegange, 2011; Plesnar-Bielak et al., 2018), and, additionally by selection against 'fighter genes' under increased temperature (Plesnar-Bielak et al., 2013). Irrespective of the cause, suppression of weapon expression with increasing thermal stress did not prevent extinctions. Indeed, most of extinctions occurred at generation four, when only a minority (25%) of males expressed the costly weapon. Thus, our results demonstrate that evolution of costly, sexually selected traits may affect the risk of extinction even when the expression of such traits is reduced due to their condition-dependence.

Thus overall, survival cost of developing and maintaining elaborated sexual traits by males does not appear to be a reason for increased extinction of FT populations. Another reason for elevated extinction risk of fighter populations could be differences in effective population sizes (Ne), which might occur if reproductive success among fighter males is more biased compared to scrambler males. Parrett et al. (in prep) have estimated Ne for populations fixed for scrambler and fighter morph at 37% and 46% of the census population size, based on SNPs frequency changes between generations. This implies that for our populations of 50 individuals, Ne would be 18.5 and 23.0, respectively, and the resulting increase in inbreeding over four generation, assuming first generation was outbred, 0.08 and 0.10. A difference in inbreeding of the order of 2% is unlikely to explain a significant proportion of the difference in fitness and extinction risk between our treatments. Yet another possible reason is increased sexual antagonism associated with male weapon, which in the bulb mite was reported to be genetically correlated with decreased female fecundity and survival (Plesnar-Bielak et al., 2014; Lukasiewicz et al., 2020). Therefore, sexually antagonistic, pleiotropic effects of male weapon on female fitness may have contributed to increased extinction risk under genetic or environmental stress. The role of ontogenetic conflict in extinction was implied in the study of bean beetles, where inbred lines associated with high male fitness, but low female fitness, suffered increased extinction risk under inbreeding (Grieshop et al., 2017). However, that study did not eliminate the possibility that high-male-fitness inbred lines carried higher load of deleterious recessives. In case of our study, such explanation could be ruled out by significantly lower inbreeding depression we recorded in our fighter lines after four generations of inbreeding (Lukasiewicz et al., 2020). The same study confirmed that gender load was present, manifested as decreased fecundity in outbred females descended from F-lines compared to those derived from S-lines. This gender load may have interacted with environmental stress, thus increasing extinction rate, as earlier suggested by Grieshop et al. (2017) for genetic stress. Finally, F populations might have failed to adapt to increasing temperature if deleterious variants removed from F populations via enhanced "good genes" selection (Lukasiewicz et al., 2020) were rendered adaptive under increased temperature (Jensen, 2014). Further work is needed to discriminate between these alternatives.

It has been suggested that the increase in sexually selected dimorphism may increase adaptive potential of populations by helping to maintain genetic variance (Radwan et al., 2015) or by increasing environmental scope (Bonduriansky, 2011; De Lisle & Rowe, 2015). Our results suggest otherwise, but the outcome may be context-dependent and affected by e.g. the rate of environmental deterioration and population size. Large populations can better preserve genetic variation under negative pleiotropy than small populations (Connallon & Clark, 2012), and thus large populations of sexually dimorphic species may be able to use sexually antagonistic variation to respond to environmental changes. Furthermore, selection is more effective in larger populations, and 'good genes' effects may prevail over negative pleiotropic effects (Martinez-Ruiz & Knell, 2017). Further work is required to elucidate the role of costly, sexually selected trait on extinction

at various demographic and environmental scenarios.

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Fig. 1. The effect of treatment, i.e. control vs. gradual temperature increase (GTI) and generation on proportion of individuals which survived till the end of a given generation. The box encloses the inter-quartile range (IQR, values between the first and third quartiles of the data), horizontal bar within the box indicates the median, and whiskers 1.5x IQR.

Fig. 2. Proportions of populations enriched for both fighter and scrambler genes (F populations and S populations, respectively) that survived throughout 4 generations in control and gradual temperature increase (GTI) treatment.

Fig. 3. Schematic representation of short and long-term effects of the sexual selection on population fitness. Within any population at a given time, natural selection will favour the fittest individuals (grey areas within gaussian distribution of fitness values), a process that can be further enhanced by good genes sexual selection (black areas). Thus, sexual selection would increase population fitness. However, increasing investment in sexually selected traits may also have negative impact on population fitness, e.g. due to their sexually antagonistic effects on female fitness. As sexually selected traits evolve to be more and more elaborated, this negative impact may outweigh the positive good genes effects. Consequently, the relationship between the investment in sexually selected traits, and population fitness can become negative in the long term (red line). Such relationship may be detected e.g. in comparative analyses across species, despite positive relationship between elaboration of sexual traits and fitness detected within each species.

Table 1. Results of the beta-binomial GLMM, testing the effect of population type (FT vs. ST, i.e. enriched for fighter vs. scrambler-associated genes respectively) and generation on proportion of individuals that survived till the end of a given generation in gradual temperature increase treatment.

Fixed effects											
Intercept											
Population type	- ST										
Generation											
Population type	* Generatio	n									
Random effect											
Line											
Replicate											
Abbreviations: a	oef. Estimat	e coefficient.	s.e.	Standard error	Std.	Dev.	Standard	deviation; p-va	alue $<$	0.05 h	ighlighted in







