



PRIMARY RESEARCH ARTICLE

Mating patterns influence vulnerability to the extinction vortex

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Abstract

Earth's biodiversity is undergoing mass extinction due to anthropogenic compounding of environmental, demographic and genetic stresses. These different stresses can trap populations within a reinforcing feedback loop known as the extinction vortex, in which synergistic pressures build upon one another through time, driving down population viability. Sexual selection, the widespread evolutionary force arising from competition, choice and reproductive variance within animal mating patterns could have vital consequences for population viability and the extinction vortex: (a) if sexual selection reinforces natural selection to fix 'good genes' and purge 'bad genes', then mating patterns encouraging competition and choice may help protect populations from extinction; (b) by contrast, if mating patterns create load through evolutionary or ecological conflict, then population viability could be further reduced by sexual selection. We test between these opposing theories using replicate populations of the model insect *Tribolium castaneum* exposed to over 10 years of experimental evolution under monogamous versus polyandrous mating patterns. After a 95-generation history of divergence in sexual selection, we compared fitness and extinction of monogamous versus polyandrous populations through an experimental extinction vortex comprising 15 generations of cycling environmental and genetic stresses. Results showed that lineages from monogamous evolutionary backgrounds, with limited opportunities for sexual selection, showed rapid declines in fitness and complete extinction through the vortex. By contrast, fitness of populations from the history of polyandry, with stronger opportunities for sexual selection, declined slowly, with 60% of populations surviving by the study end. The three vortex stresses of (a) nutritional deprivation, (b) thermal stress and (c) genetic bottlenecks had similar impacts on fitness declines and extinction risk, with an overall sigmoid decline in survival through time. We therefore reveal sexual selection as an important force behind lineages facing extinction threats, identifying the relevance of natural mating patterns for conservation management.

KEYWORDS

environmental stress, genic capture, inbreeding, monogamy, polyandry, sexual conflict, *Tribolium*

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1 | INTRODUCTION

The extinction vortex describes a theoretical scenario in which environmental, genetic and demographic forces interact through time to push a population towards extinction (Gilpin & Soulé, 1986). Importantly, the vortex occurs because these fundamental biotic and abiotic forces amplify one another, driving a reinforcing feedback loop which leads to a progressive loss of population viability (Figure 1). The extinction vortex has proven to be an informative model for conceptualizing the interacting forces behind the dynamics of biodiversity loss and lineage extinction (Brook, Sodhi, & Bradshaw, 2008; Fagan & Holmes, 2006; Höglund, 2009; Stephens, Sutherland, & Freckleton, 1999). The heart of a classic extinction vortex is driven by synergistic impacts of environmental stresses, reduced genetic diversity and smaller population size, with potential damage from stochastic catastrophic events also contributing as the population moves towards extinction. With the comprehensive Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services report (IPBES, 2019) recently estimating that one million species are currently suffering accelerating rates of extinction, many populations are now facing the extinction vortex.

A range of observational, comparative and experimental studies under both field and laboratory conditions have used aspects of the extinction vortex for understanding population viability, with ample evidence across a range of systems showing that individual or combined effects of environmental stress and genetics lead to reduced population size or even extinction (e.g. Brook et al., 2008; Fagan & Holmes, 2006; Frankham, Ballou, & Briscoe, 2002; IPBES, 2019). However, explicit experimental tests of the extinction vortex model to examine how a combination of environmental, demographic and genetic stresses impact on population viability across multiple generations have been lacking. Here, we apply such an approach by experimentally exposing small replicate populations of a model insect to multiple cycles of environmental, genetic and demographic

stress (Figure 2), and then measuring the consequences for population viability. We applied three conditions known to stress both natural populations and our experimental model, and which have topical relevance to conservation ecology and the extinction vortex. First, we restricted access to essential food resources by limiting dietary protein to a level which constrains adult reproduction and slows offspring development in our model system (Godwin, 2016). Second, we exposed reproducing adults to environmental warming through a 5 day heatwave, which we know reduces reproduction and survival (Sales, 2019; Sales et al., 2018). Third, we drove each population through a genetic bottleneck to increase the risks of inbreeding and fitness depression (Frankham et al., 2002; Keller & Waller, 2002; Lumley et al., 2015). At each generation, following exposure to one of these stressors, we measured the specific consequences for population fitness as the vortex progressed for 15 generations, scoring the number of offspring reproduced through each replicate experimental population, until five cycles of the three stressors (15 generations) down the vortex had completed (Figure 2).

On top of these explicit measures of population dynamics across replicated extinction vortices, we also investigated how mating pattern and opportunities for sexual selection influence vulnerability to the extinction vortex. Mating patterns show enormous variability across species and populations (Taylor, Price, & Wedell, 2014), with the adaptive significance of widespread polyandry (when females mate with multiple males and promote male-male competition and opportunities for choice and sexual selection) receiving considerable debate and remaining poorly understood (Slatyer, Mautz, Backwell, & Jennions, 2012). Sexual selection, when opportunities for competition and choice can generate more variance between individuals in reproductive success (Anderson, 1994; Darwin, 1874), could have profound consequence for populations facing stress and the extinction vortex, depending on (a) whether natural selection is reinforced and strengthened by sexual selection, or whether (b) there is evolutionary or ecological conflict

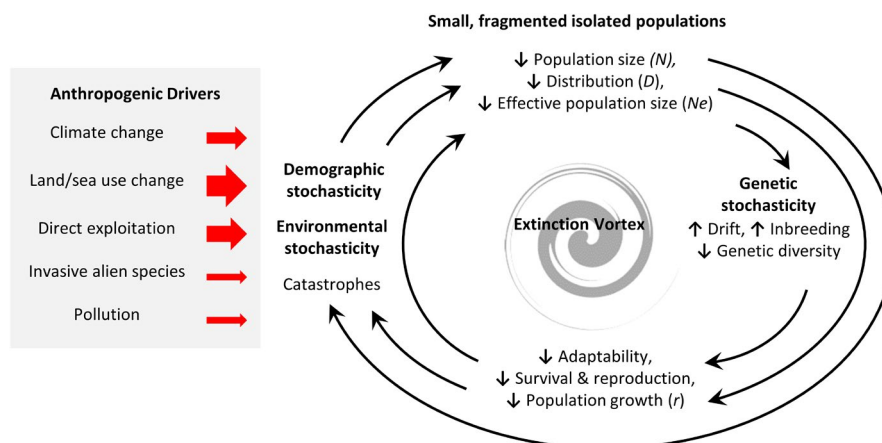


FIGURE 1 The extinction vortex. A feedback cycle through time that results in progressive loss of population viability and increased vulnerability to extinction. Environmental, genetic and demographic drivers (often with anthropogenic causes) interact synergistically to alter the structure and fitness of populations and increase vulnerability to future stochastic events. Width of block arrows from the anthropogenic drivers indicates the relative impact of each following IPBES (2019). Adapted from Gilpin and Soulé (1986) and Frankham et al. (2002)

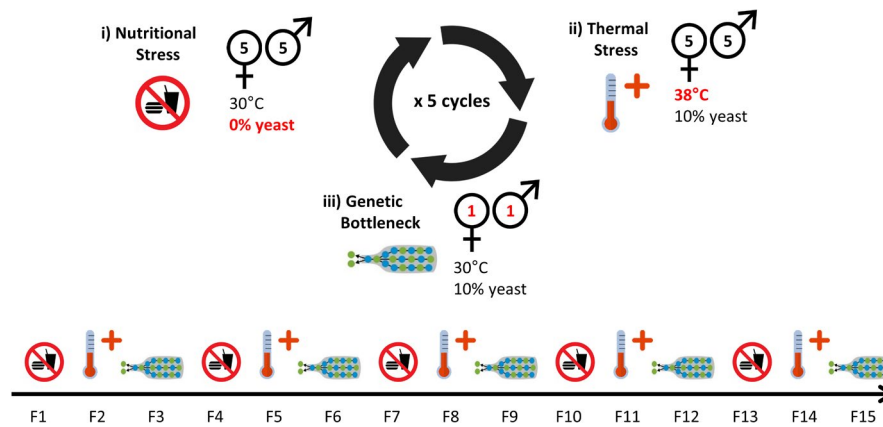


FIGURE 2 Extinction vortex experimental design. Replicate small populations were initiated following 95 generations of experimental evolution under contrasting strengths of sexual selection from Monogamy versus Polyandry regimes. All replicate populations experienced a three-generation cycle of constraining abiotic and/or biotic conditions created through: (i) nutritional stress, (ii) thermal stress, (iii) genetic stress. Stress manipulations are highlighted in red. The vortex was continued for five complete iterations of the triple-stress cycle (15 generations in total). At each generation, and for each replicate population ($n = 9$ replicates \times 3 independent lines = 27 populations for either sexual selection regime background), pupae were removed and sexed as required to initiate the next generation, with the remaining offspring left to develop to adult eclosion (~35 days), frozen and counted (together with the 5 + 5 or 2 + 2 adults successfully emerging from the removed pupae) as a measure of population fitness

and tension between forces of natural and sexual selection (Holman & Kokko, 2013; Kokko & Brooks, 2003).

At its most positive, sexual selection could be a key force for maintaining population genetic health, even possibly allowing the evolution and existence of complex multicellular sexual life (Agrawal, 2001; Kokko & Brooks, 2003; Lorch, Proulx, Rowe, & Day, 2003; Rowe & Houle, 1996; Siller, 2001; Whitlock & Agrawal, 2009) and new species (Janicke, Ritchie, Morrow, & Lucas, 2018). Genic Capture theory proposes that reproductive success in the face of competition and choice depends on an individual's wider condition which is contingent on genome-wide variation (Rowe & Houle, 1996; Tomkins, Radwan, Kotiaho, & Tregenza, 2004; Whitlock & Agrawal, 2009). Thus, sexual selection through Genic Capture will influence most loci across the genome, offering a clear mechanism for promoting wider genetic health. The burden of genetic load faces all living systems (Haldane, 1937; Muller, 1950), with widespread accumulation of mutations of small effect throughout the genome theoretically summing to an overall and significant fitness load (Charlesworth, Morgan, & Charlesworth, 1993; Haldane, 1937; Muller, 1950). Sexual selection could be an important force to reduce load through two simple, but connected, routes: (a) if mutations are more deleterious in males because of sexual selection (Agrawal, 2001) or (b) if load affects mating and fertilization success so that the average father carries less load than the average male (Siller, 2001), then intraspecific competition and choice should encourage greater reproductive success for individuals in a population that carry lower mutation load, purging it from the lineage (Whitlock & Agrawal, 2009). Thus, sexual selection could be an important force which promotes the genetic health of a population if reproduction in the face of competition is achieved by more individuals that have superior overall condition, strengthening a population's ability to resist the extinction vortex. There is mounting empirical evidence that polyandry and sexual

selection can indeed improve population fitness (Cally, Stuart-Fox, & Holman, 2019).

In contrast, sexual selection could be a negative force for living systems, because competition and choice might divert investment from the requirements of natural selection, pushing phenotypes away from 'survival' optima at the expense of succeeding in costly competitions for reproduction (Houle & Kondrashov, 2002; Kirkpatrick & Ryan, 1991; Kokko & Brooks, 2003; Lande, 1980). One theory behind the extinction of the Irish elk, for example, was that extreme sexual selection for enormous antlers accelerated its demise (Moen, Pastor, & Cohen, 1999). In addition to this tension, sexual conflict between divergent male and female reproductive optima could also create ecological and evolutionary fitness loads within a population (Arnqvist & Rowe, 2005; Kokko & Brooks, 2003; Parker, 1979). Thus, if evolutionary conflicts exist between natural and sexual selection, and/or between male and female sexual optima, increasing opportunities for reproductive competition and choice within a population could increase vulnerability to biotic and abiotic stresses arising from the extinction vortex.

To test whether mating pattern and sexual selection strengthen or weaken a population's ability to cope with the extinction vortex, we use an established model system in which we experimentally evolved replicate lines of the flour beetle *Tribolium castaneum* under strong versus weak sexual selection for over 10 years, and then assayed their responses to the extinction vortex. *T. castaneum* is a tropical beetle with a naturally promiscuous mating pattern (Fedina & Lewis, 2008; Sokoloff, 1972), so its ecology, biology and taxonomy are widely representative. To generate populations evolved under contrasting strengths of sexual selection, two mating pattern regimes were applied across 95 generations of experimental evolution: (a) an enforced monogamy regime, in which we altered the naturally promiscuous mating pattern and randomly paired one male and one

female for breeding, and competition or mate choice were removed; (b) a polyandry regime, in which female promiscuity was generated by allowing five males to compete for reproduction with a single female (see Demont et al., 2014; Lumley et al., 2015). All individuals originated from the same ancestral stock population, and all other variables (including effective population size and genetic diversity) had been equalized through experimental evolution (see full details in Godwin et al., 2017, 2018; Lumley et al., 2015), allowing us to test how mating pattern and sexual selection influence a population's ability to cope with the extinction vortex.

2 | MATERIALS AND METHODS

2.1 | Experimental evolution under varying mating pattern

Tribolium castaneum of the commonly used Georgia 1 (GA1) strain (Haliscak & Beeman, 1983), originating from the Beeman Lab (United States Department of Agriculture), were used to initiate divergent sexual selection regimes in 2005, which were subsequently maintained in conditions that specifically varied the mating system applied to the adult life stage. For full details, see Lumley et al. (2015). The regimes were maintained throughout under controlled abiotic conditions of 30°C and 60% humidity, with food medium consisting of 90% organic white flour, 10% brewer's yeast and a thin layer of oats to aid traction. An enforced Monogamy (one male to one female) regime was contrasted with a Polyandrous regime (five males to one female) which applied opportunities for sexual selection. Three independent lines within either regime were maintained, and within-line replication consisted of 20 monogamous pairs per line and 12 polyandrous groups per line, equalizing the theoretical effective population size ($N_e = 40$) between the regimes (Wright, 1931; Figure 3). Genetic testing using multiple microsatellites confirmed that neither

regime had experienced differential genetic bottlenecks throughout experimental evolution, with equal levels of heterozygosity in monogamous and polyandrous lines (Lumley et al., 2015).

For each line, at every generation, individuals sexed as pupae were used to create adult pairs or groups in fresh medium for 7 days of mating, fertilization and oviposition. Monogamous pairs were maintained and mated in containers containing 2 g flour medium, and polyandrous groups were maintained and mated in containers with 6 g flour medium, therefore allocating 1 g flour medium per adult throughout. After reproduction, adults were removed and eggs/larvae pooled from the multiple pairs or groups within each line, with the flour medium increased and equalized between regimes to 100 g and left to develop under standardized conditions until pupae were ready for the next generation (Godwin et al., 2018; Lumley et al., 2015).

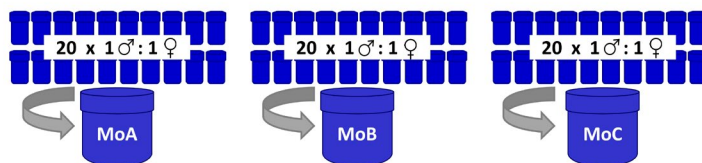
2.2 | The experimental extinction vortex

Vulnerability to an experimental extinction vortex was assayed between regimes and across the lines following 95 generations of experimental evolution under strong versus weak sexual selection. The reproductive output and extinction time of replicate small populations from monogamous and polyandrous regime backgrounds were tracked across 15 generations inside the vortex (Figure 2). Within each of the three independent lines in either sexual selection regime (Figure 3), we initiated nine replicate populations using non-sibling virgin pairs placed together for 7 days mating and oviposition (=9 populations \times 3 lines \times 2 sexual selection = 54 replicate populations to enter the vortex). Adults were then removed, and eggs/larvae left to develop to the pupal stage, at which point the required number of pupae to initiate the next generation was removed, and all remaining offspring left to develop to adult eclosion (~35 days) before being frozen and counted as a measure of baseline population

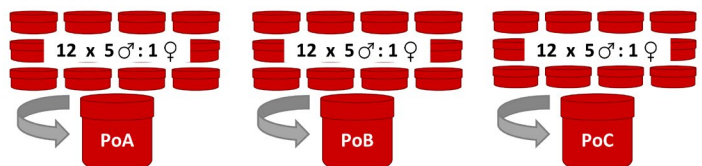
Manipulation of adult mating system:

- F_1 adults in pairs/groups for 7 days mating and oviposition
- Adults removed, **eggs/larvae pooled** and left ~21 days to develop
- Pupae sexed and maintained in single sex groups until reproductive maturation to create F_{i+1}

Monogamy (Mo)



Polyandry (Po)



Effective
population
size (N_e)

$$N_e = \frac{4N_m N_f}{N_m + N_f}$$

$$= 20 \left(\frac{4(1 \times 1)}{1 + 1} \right)$$

$$= 40$$

$$= 12 \left(\frac{4(5 \times 1)}{5 + 1} \right)$$

$$= 40$$

FIGURE 3 Experimental evolution of the strength of sexual selection under contrasting monogamous (blue) and polyandrous (red) adult mating patterns. Contrasting intensities of sexual selection were imposed upon each generation of adult reproduction (7 days mating and oviposition), while equalizing effective population size ($N_e = 40$) and allowing genetic mixing of juveniles within the independent lines

fitness. Control abiotic conditions to initiate the populations for the vortex experiment were maintained at 30°C, 60% humidity and a protein-enriched food medium consisting of 10% brewer's yeast, 90% organic white flour with a thin layer of organic oats to aid traction. For the subsequent 15 generations after initiation, all replicate populations experienced a three-generation extinction vortex cycle of abiotic and/or biotic stress conditions consisting of: (a) nutritional deprivation, (b) thermal stress and (c) a genetic bottleneck (see Figure 2). Within each cycle, the three stresses were maintained in a consistent nutritional-thermal-genetic stress cycle, so that lineages experienced the same number of episodes of different stress, and which meant that we could not analyse interaction effects of variation in the order of stresses, but did mean we could track the overall decline across each cycle, and compare the relative impact of either stressor more consistently.

1. Under *nutritional stress*, replicate small populations consisting of five adult males and five adult females ($N_e = 10$) experienced a protein-restricted food medium consisting of 0% brewer's yeast and 100% organic white flour and a thin layer of oats to aid traction. Temperature and humidity were maintained at control levels throughout (30°C and 60% RH). This level of protein restriction typically halves the fecundity of females and prolongs egg-to-eclosion development (Grazer, Demont, Michalczyk, Gage, & Martin, 2014). For each replicate population, five male and five female pupae from the previous generation were sexed and placed in single sex groups for 10 days to complete development and reach reproductive maturation. These adults were then placed together for 7 days of mating and oviposition, after which adults were removed and eggs/larvae left to develop to the pupal stage (18–24 days). Pupae required to initiate the next generation of the experimental extinction vortex were then isolated, and all remaining offspring left to develop to adult eclosion (~35 days), before being frozen and counted (together with the adults successfully emerging from the 5 + 5 removed pupae) as a measure of population fitness.
2. *Thermal stress* can constrain adult reproductive fitness through damage to male fertility, including in *T. castaneum* (Sales et al., 2018). Replicate small populations ($N_e = 10$) were exposed to a 38°C 5 day heatwave during the adult mating and oviposition stage. Humidity and the food medium were maintained at control levels. Within each population, five male and five female pupae were sexed and placed in single sex groups for 10 days to complete development and reach reproductive maturation. Adults were then placed together for 7 days of mating and oviposition, with the first 5 being maintained at 38°C, before being returned to 30°C for the remaining 2 days. Adults were then removed, and eggs/larvae left to develop to the pupal stage (18–24 days). Pupae required to initiate the next generation of the extinction vortex were then removed, and all remaining offspring left to develop to adult eclosion (~35 days), before being frozen and counted (together with the adults successfully emerging from the 5 + 5 removed pupae) as a measure of population fitness.

3. To create *genetic stress*, which is known to lead to inbreeding depression, including in *T. castaneum* (Michalczyk, Martin, Millard, Emerson, & Gage, 2010; Pray & Goodnight, 1995), we applied genetic bottlenecks through the vortex, by restricting the effective population size of each replicate to $N_e = 2$ (one male and one female adult). Control abiotic conditions were maintained throughout. To ensure that one male and one female adult successfully enclosed to enter the genetic bottleneck stage of the vortex, two male and two female pupae were sexed and placed in single sex groups for 10 days to complete development and reach reproductive maturation for this stage. A single adult male and female were then placed together in fresh control medium for 7 days of mating and oviposition (spare adults were discarded), then removed and eggs/larvae left to develop to pupal stage (18–24 days). Required pupae to initiate the next generation of the vortex were then removed, and all remaining offspring left to develop to adult eclosion (~35 days), before being frozen and counted (together with the adults successfully emerging from the 2 + 2 removed pupae) as a measure of population fitness.

As population fitness declined in later generations through the experimental extinction vortex, it was not always possible to isolate the required number of male and female pupae for the following generation, in which case as many pupae as were available were isolated. A population was considered extinct when the number of reproductively mature adults produced had declined to either one or zero, or if any remaining offspring were of the same sex.

2.3 | Baseline reproductive fitness

To gain insight into the relative impacts of applying nutritional, thermal and genetic stress within the vortex, reproductive output (offspring production over 7 days mating and oviposition) was measured for both sexual selection regime backgrounds in (a) small groups ($N_e = 10$) and (b) pairs ($N_e = 2$) under control conditions, as well as small groups under (c) nutritional stress and (d) thermal stress conditions, over a single generation. At F95 (a) and F100 (b–d) generations of experimental evolution, pupae from each independent line within either sexual selection regime were isolated in single sex groups to complete development and reach reproductive maturation. Adults were then randomly allocated to treatments (a–d; $n = 9$ per line per treatment), and placed together for 7 days mating and oviposition, then removed and eggs/larvae left to develop to adult eclosion (~35 days), before being frozen and counted as a further measure of baseline population fitness.

2.4 | Statistical analyses

All analyses were conducted in R V3.6.1 (R Core Team, 2019), with 'plyr' (Wickham, 2011), 'pastecs' (Grosjean, Ibanez, & Etienne, 2014), 'car' (Fox & Weisberg, 2011) and 'stats' (R Core Team, 2019) packages

used for data exploration, descriptive statistics and testing assumptions. Figures were created using 'ggplot2' (Wickham, 2009) and 'gridExtra' (Auguie & Antonov, 2017). Generalized linear mixed models (GLMMs) were constructed using the 'glmmTMB' package (Brooks et al., 2017), to fit zero-inflated models with Poisson or negative binomial distributions, which account for zeros and overdispersion in the data. Both Poisson and negative binomial distributions were tried, and the model with the lowest AIC was selected. Models were fitted by maximum likelihood, and likelihood ratio tests and AIC values were used to compare models with and without factors of interest (Crawley, 2013).

Time to extinction of populations from contrasting sexual selection backgrounds within the experimental extinction vortex were compared using the 'survival' package (Therneau, 2015). A parametric accelerated failure time (AFT) model with a lognormal error distribution, and right censoring to account for lineages which survived to the termination of the experiment, was fitted to the data. A Kaplan-Meier object was created with sexual selection (SS) background (monogamy vs. polyandry) as the fixed effect, and independent line (A, B, C) entered as a cluster indicator to account for the hierarchical design (Lumley et al., 2015; Therneau, 2015). Akaike's information criteria and visual interpretation of log-log plots were used to inform the choice of model and error distribution.

Population fitness, measured as the total number of offspring produced by all adults (nutritional stress and thermal stress: $N_e = 10$; genetic bottleneck: $N_e = 2$) following 7 days of mating and oviposition (averaged from $n = 9$ populations \times 3 independent lines per sexual selection regime per generation), was compared between the two SS regime backgrounds, across 15 experimental generations through the experimental extinction vortex. A zero-inflated negative binomial model was constructed, and the maximum model was fitted with SS regime (monogamy vs. polyandry) and generation (continuous variable: 1–15) entered as fixed effects. Generation was also entered as a random effect to account for temporal pseudoreplication (Bates, Mächler, Bolker, & Walker, 2015; Crawley, 2013), and independent line (A, B, C) nested within SS regime (monogamy vs. polyandry) as a random effect to account for the hierarchical design (Crawley, 2013).

Mating pattern influences on reproductive output were compared between sexual selection regimes for (a) small groups and (b) pairs, to gain insight into the experimental vortex treatments. Maximal models with Poisson distributions were fitted with SS regime (monogamy vs. polyandry) entered as a fixed effect, and independent line (A, B, C) nested within SS regime (monogamy vs. polyandry) as a random effect to account for the hierarchical design (Crawley, 2013).

Per female fitness was calculated as the total number of offspring produced by all adults (small groups: $N_e = 10$, pairs: $N_e = 2$) following 7 days of mating and oviposition (averaged from $n = 9$ populations \times 3 independent lines per SS regime per generation), divided by the number of adult breeding females (females = $N_e/2$). Per female fitness was compared between the two sexual selection backgrounds for each mating pattern across a single generation, by constructing a GLMM with a Poisson distribution. A maximal model

was fitted with sexual selection regime (monogamy vs. polyandry) and mating pattern (small groups vs. pairs) entered as fixed effects, and independent line (A, B, C) nested within SS regime (monogamy vs. polyandry) as a random effect to account for the hierarchical design (Crawley, 2013).

Relative population fitness was calculated as the mean population fitness per sexual selection regime per generation (averaged from $n = 9$ populations \times 3 independent lines per SS regime per generation), divided by the mean baseline population fitness for the relevant mating pattern (small populations vs. pairs) per SS regime ($n = 9$ replicates \times 3 independent lines per SS regime). Relative population fitness was used to compare the effects of nutritional, thermal and genetic stress within the experimental extinction vortex for populations from (a) monogamous and (b) polyandrous backgrounds. Zero-inflated Poisson models were constructed, and a maximum model fitted with stress (nutritional, thermal and genetic) entered as a fixed effect, and independent line (A, B, C) nested within cycle (1–5) to account for temporal pseudoreplication (Crawley, 2013).

3 | RESULTS

3.1 | Comparison of mating patterns and per female fitness

Under control abiotic conditions, the total reproductive output of small populations (five males and five females) did not differ significantly between those originating from monogamous and polyandrous sexual selection regimes (Poisson GLMM: $\chi^2_{(1)} = 2.54$, $p = .11$). A significant but small difference was found in the reproductive output of pairs (Poisson GLMM: $\chi^2_{(1)} = 3.81$, $p = .05$) with monogamous background showing higher reproductive output than polyandrous background under this mating system (Table 1). This difference could result from selection under monogamy encouraging the experimental evolution of adults that optimize reproduction as monogamous male–female pairs.

Calculation of per female offspring production (reproductive output/number of females) revealed significantly fewer offspring per female for small groups compared to pairs for both sexual selection backgrounds (Poisson GLMM: monogamy: $\chi^2_{(1)} = 221.09$, $p < .001$, polyandry $\chi^2_{(1)} = 64.74$, $p < .001$) which may have been caused by the quinone effect on group oviposition in *T. castaneum* (Khan et al., 2018) or cannibalism (Sokoloff, 1972). Thus, baseline fitness was equivalent for both mating regime backgrounds, and even slightly higher for monogamous pairs, before lines were assayed through the extinction vortex.

3.2 | Extinction

Following 95 generations of experimental evolution under weak versus strong sexual selection, our simulated extinction vortex assay revealed that populations from the monogamous background were

TABLE 1 Summary of population fitness values for contrasting histories of sexual selection (SS) under control conditions and over five cycles of three stresses across 15 generations of the experimental extinction vortex. Population fitness means are numbers of adult offspring produced by adult groups and pairs following exposure to nutritional, thermal or genetic stress. Nutritional and thermal stress population means are derived from offspring groups generated by up to five females and five males, while genetic stress population means are offspring groups generated by pairs containing one female and one male. Control values allow comparison of baseline fitness for monogamous and polyandrous groups or pairs without the application of stress within the vortex. Monogamous groups and pairs had slightly higher baseline fitness than those from polyandrous backgrounds (groups: $\chi^2_{(1)} = 2.54$, $p = .11$; pairs: $\chi^2_{(1)} = 3.81$, $p = .05$). In addition to the 15 population means and errors for each stress and generation (F1–F15) for monogamous and polyandrous backgrounds, average population fitness values for each of the five triple-stress cycles are included in the adjacent column

			Mean (\pm SE) population fitness				Outcome of zero-inflated negative binomial GLMM maximal model			
			Monogamy		Polyandry			Estimate (SE)	z	p
N _e = 10		Control	240 (\pm 12)		277 (\pm 23)		Intercept	5.40 (0.20)	27.01	<.001
N _e = 2		Control	80 (\pm 4)		73 (\pm 1)		SS regime	−0.45 (0.24)	−1.88	.06
1	F1	Nutritional	139 (\pm 17)	114 (\pm 11)	130 (\pm 5)	119 (\pm 7)	Generation	−0.26 (0.05)	−5.19	<.001
	F2	Thermal	151 (\pm 17)		163 (\pm 12)		SS*Generation	0.19 (0.06)	3.32	<.001
	F3	Genetic	53 (\pm 3)		66 (\pm 8)					
2	F4	Nutritional	101 (\pm 16)	54 (\pm 6)	120 (\pm 9)	92 (\pm 4)				
	F5	Thermal	40 (\pm 3)		120 (\pm 9)					
	F6	Genetic	23 (\pm 1)		39 (\pm 3)					
3	F7	Nutritional	22 (\pm 7)	16 (\pm 3)	92 (\pm 14)	75 (\pm 5)				
	F8	Thermal	19 (\pm 1)		97 (\pm 7)					
	F9	Genetic	7 (\pm 4)		35 (\pm 4)					
4	F10	Nutritional	3 (\pm 2)	1 (\pm 1)	64 (\pm 10)	50 (\pm 8)				
	F11	Thermal	1 (\pm 1)		64 (\pm 12)					
	F12	Genetic	1 (\pm 1)		23 (\pm 5)					
5	F13	Nutritional	2 (\pm 2)	1 (\pm 1)	53 (\pm 12)	41 (\pm 9)				
	F14	Thermal	0 (\pm 0)		53 (\pm 11)					
	F15	Genetic	0 (\pm 0)		17 (\pm 6)					

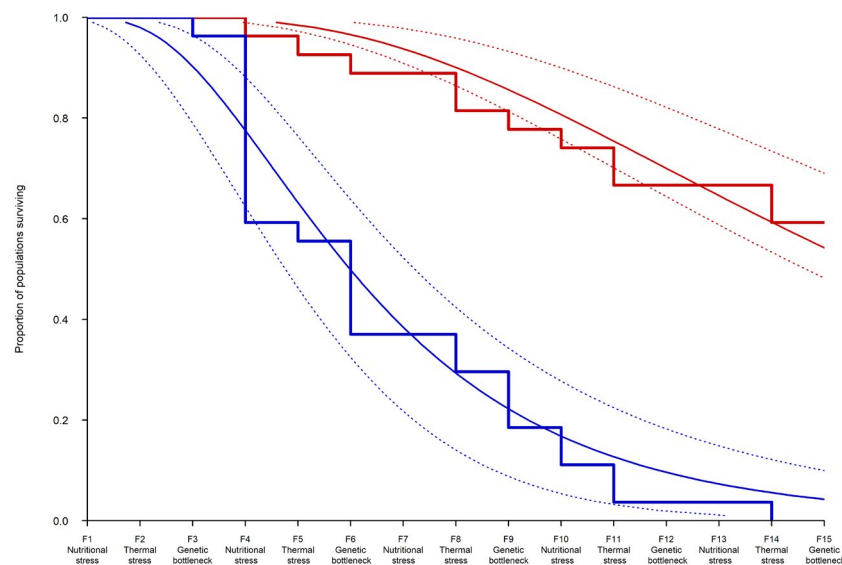


FIGURE 4 Time to death within an experimental extinction vortex of populations derived from experimentally evolved monogamous (blue) and polyandrous (red) sexual selection regimes. Data grouped by sexual selection regime ($n = 9$ replicate populations \times 3 independent lines per regime). Survival curves of raw data (thick stepped line) overlaid with AFT (lognormal error distribution) model fit (thin line) and 95% confidence intervals (dotted lines). A background of strong sexual selection under Polyandry significantly enhanced survival compared to a background of Monogamy ($z = 6.86$, $p < .001$), with the pattern to complete extinction following a sigmoid curve. See Figure 2 and Section 2 for details of the experimental extinction vortex

significantly more likely to go extinct than populations from the polyandrous regime ($z = -6.86, p < .001$, Figure 4). At the end of the experiment, after five cycles of three stress types across 15 generations, 100% of the 27 replicate populations from the monogamous background starting the vortex experiment had gone extinct, while 60% of the 27 polyandrous background populations were still surviving and reproducing. The AFT model predicted that polyandrous populations survived 2.65 times longer than monogamous populations, with the mean number of generations to extinction (accounting for censoring in the data) predicted as $16 (\pm 1 \text{ SE})$ for the polyandrous regime background, compared with only $6 (\pm 1 \text{ SE})$ for the monogamous background.

3.3 | Population fitness decline

Across 15 generations of the experimental extinction vortex, the decline in mean population fitness occurred more rapidly, and to a greater degree, in populations from a background of monogamy compared to those from polyandrous backgrounds (Table 1; Figure 5).

Fitness in small populations from the monogamous background declined rapidly to zero and 100% extinction. In contrast, small populations from the polyandrous background showed a more gradual fitness decline, losing ~30% fitness over each cycle of three stresses relative to the previous cycle (Figure 5b). At the termination of the experiment, extant populations maintained ~20% total reproductive fitness relative to total reproductive fitness under control conditions (Table 1).

Through the first complete cycle (generations 1–3) of the experimental extinction vortex, populations from both weak and strong sexual selection backgrounds showed a consistent response to nutritional, thermal and genetic stresses over consecutive generations. Overall, during the first cycle of the extinction vortex, mean population fitness of populations fell by 36% relative to mean population fitness under control conditions. However, during the second cycle of the vortex (generations 4–6), the response of populations from contrasting sexual selection backgrounds diverged. The fitness of populations from the monogamous background declined sharply in response to thermal stress (generation 5) and continued to decline throughout the remaining generations/cycles of the vortex until a

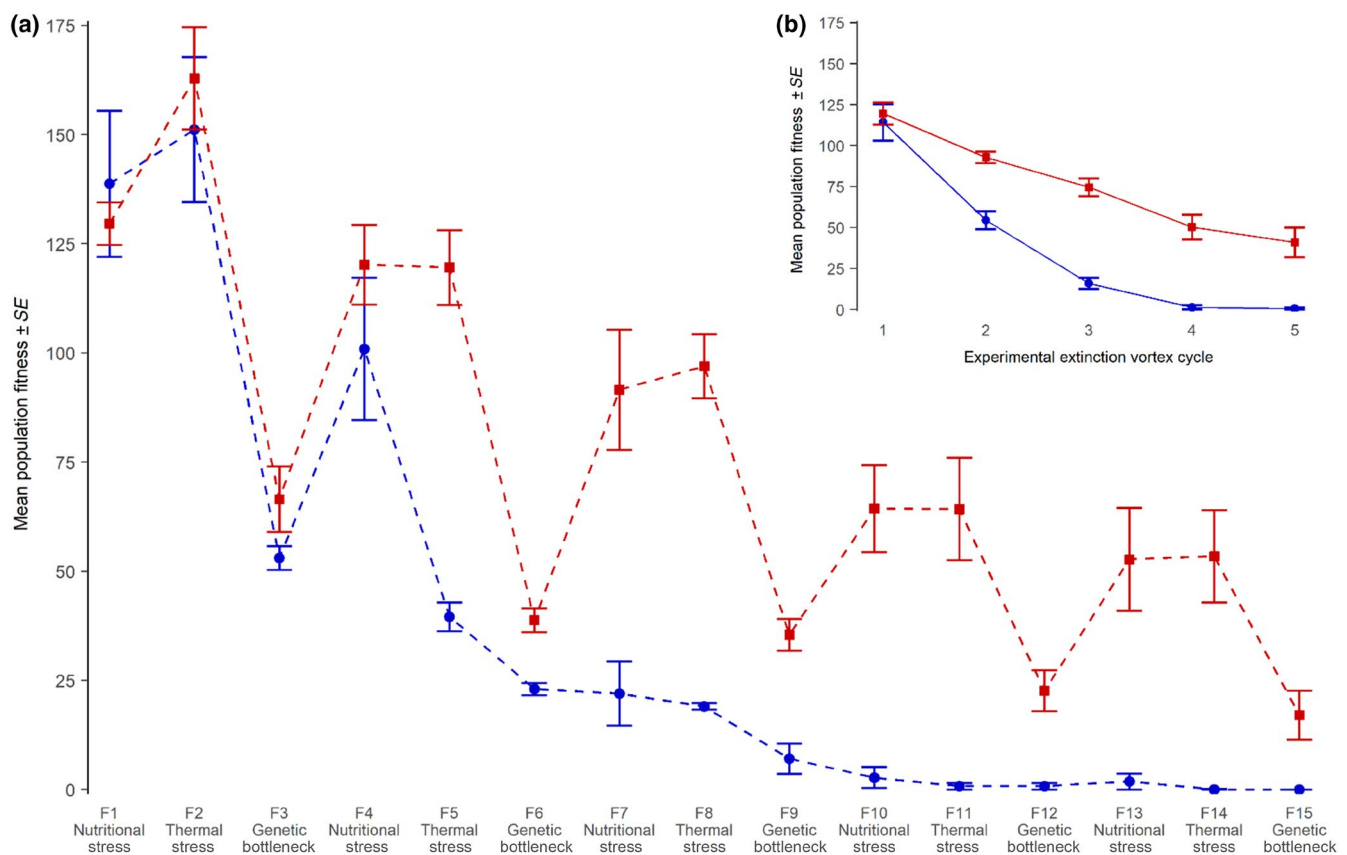


FIGURE 5 Total reproductive fitness of populations from experimentally evolved monogamous (blue circles) versus polyandrous (red squares) sexual selection backgrounds through 15 generations of an extinction vortex. (a) Data grouped by sexual selection background ($n = 9$ replicate populations \times 3 independent lines per regime). The total fitness of populations differs significantly between monogamous and polyandrous sexual selection regime (SS) backgrounds over generations (G) (SS*G: $z = 3.32, p < .001$). Note that total reproductive fitness will also depend on the number of breeding females within each population to reproduce the next experimental generation, which was (usually) $n = 5$ for the nutritional and thermal environmental stresses (to maintain small populations), but only $n = 1$ for the genetic stress (to create repeated bottlenecks). (b) (inset) Total reproductive fitness of populations averaged over each three-generation cycle of the experimental extinction vortex. See Figure 2 and Section 2 for details of the experimental extinction vortex

population went extinct. In contrast, the fitness of populations from the polyandrous background showed declines in total reproductive fitness during bottleneck events, followed by an incomplete recovery which created an overall gradual decline in fitness over five complete cycles of three stresses (Figure 5).

3.4 | Comparison of the relative effects of nutritional, thermal and genetic stress treatments

Within either sexual selection regime, there was no significant difference between the relative effects of nutritional, thermal and genetic stress on relative decline in population fitness (Figure 6; zero-inflated Poisson GLMM: monogamy: $\chi^2_{(1)} = 0.78$, $p = .67$, polyandry $\chi^2_{(1)} = 5.19$, $p = .07$).

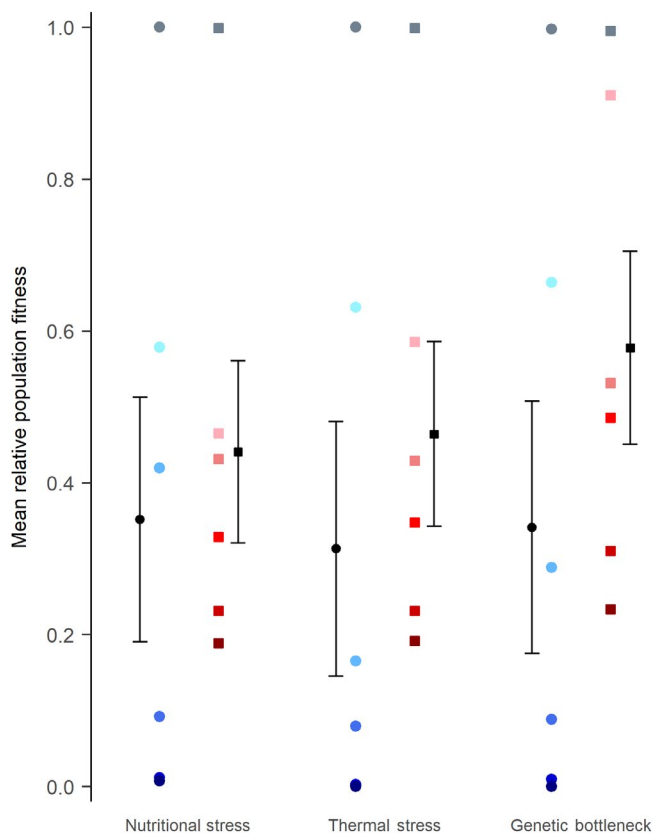


FIGURE 6 Mean relative fitness of populations from experimentally evolved monogamous (blue circles) versus polyandrous (red squares) sexual selection backgrounds under nutritional, thermal and genetic bottleneck stress within the experimental extinction vortex. Relative population fitness values for each stress regime are compared to their respective baseline stress-free fitness values for groups or pairs (see Section 2). Increasing colour saturation represents increasing iterations of the experimental extinction vortex cycle. Fitness relative to that in the absence of stress (grey). No significant difference between the stress treatments in mean \pm SE (black points) relative fitness of populations from either sexual selection background (monogamy: $\chi^2_{(1)} = 0.78$, $p = .67$, polyandry $\chi^2_{(1)} = 5.19$, $p = .07$), indicating similar responses to the three different stresses

4 | DISCUSSION

Following 95 generations of experimental evolution under strong versus weak sexual selection, our study clearly reveals that deprivation of opportunities for reproductive competition and choice through enforced monogamy had weakened the ability of populations to resist the extinction vortex. Replicate populations from the enforced monogamy sexual selection history showed steep fitness declines after the first cycle of three stressors, with all 27 replicate lineages going extinct by the 15th generation of the experimental vortex. By contrast, populations provided with opportunities for reproductive competition and choice under a history of polyandry (in which five males competed for reproduction with each female) were much more resilient to fitness decline, with 60% of the 27 replicate lineages beginning the experiment remaining alive at the 15th generation of the vortex.

Our experimental results, therefore, find no evidence that stronger sexual selection creates a negative fitness load within populations (Arbuthnott & Rundle, 2012; Arnqvist & Rowe, 2005; Houle & Kondrashov, 2002; Kirkpatrick & Ryan, 1991; Lande, 1980). Instead, we find experimental support for theoretical analyses that sexual selection can improve longer term population fitness (Agrawal, 2001; Kokko & Brooks, 2003; Siller, 2001; Tomkins et al., 2004; Whitlock & Agrawal, 2009). An increasing body of research, pioneered by Radwan's work in 2004 demonstrating that sexual selection could remove experimentally induced mutations from mite lineages (Radwan, 2004), has shown empirically that the forces of competition and choice within reproduction can provide important longer term benefits for population resilience (Almbro & Simmons, 2014; Baur & Berger, 2020; Dugand, Kennington, & Tomkins, 2018; Fricke & Arnqvist, 2007; Grieshop, Stångberg, Martinossi-Alilbert, Arnqvist, & Berger, 2016; Jacomb, Marsh, & Holman, 2016; Janicke et al., 2018; Jarzebowska & Radwan, 2010; Lumley et al., 2015; Parrett & Knell, 2018; Parrett, Mann, Chung, Slade, & Knell, 2019; Plesnar-Bielak, Skrzynecka, Prokop, & Radwan, 2012), including a recent meta-analysis (Cally et al., 2019). To complement this 'phenomics' evidence, recent work analysing genomic evolution in *D. melanogaster* following 14 generations of selection on male competitiveness has provided molecular genetic evidence for genome-wide purging of load from sexual selection (Dugand, Tomkins, & Kennington, 2019). Even more recently, experimental evolution with *C. maculatus* seed beetles showed that sexual selection on males can purge deleterious alleles but, interestingly, that socio-sexual activity by sexually selected males can also increase the number of de novo mutations that they transfer into a lineage (Baur & Berger, 2020; see also Power & Holman, 2015).

Previous work using the *Tribolium* system has revealed that experimental evolution under stronger sexual selection: (a) improves male reproductive competitiveness (Godwin et al., 2017), (b) enhances female ability to handle sexual conflict (Demont et al., 2014; Michalczyk et al., 2011), (c) strengthens a lineage's ability to cope with genetic stress from inbreeding (Lumley et al., 2015) and (d) creates populations that are generally superior across multiple life stages when faced with the broad challenges of invading into

conspecific competitors (Godwin et al., 2018). Here, we now demonstrate applied benefits of sexual selection for population and lineage fitness by revealing that an evolutionary history of enforced monogamy with low sexual selection weakens the ability of populations and lineages to cope with multiple interacting anthropogenic challenges through an extinction vortex.

It is relevant to clarify that the inferior performance of our monogamous background lineages through the vortex is not easily explained by differences in inbreeding under experimental evolution and is conservative to the possibility that sexual selection might have previously reduced genetic variation under polyandry, for four related reasons (details also in Lumley et al., 2015). First, the monogamous and polyandrous regimes have been carefully maintained throughout their 10 year existence using identical theoretical effective population sizes (see Section 2: each replicate line in the enforced monogamy regime is reproduced using $n = 20 \times 1\text{-male} + 1\text{-female}$ pairs, and each of the polyandrous lines reproduced using $n = 12 \times 5\text{-male} + 1\text{-female}$ groups, so N_e for both regimes = 40 [with all offspring being pooled and mixed each generation after reproduction by the separate pairs/groups]). Second, molecular genetic comparisons of more than 600 individuals between different sexual selection regimes using microsatellite markers showed that near-identical levels of heterozygosity existed in our monogamous and polyandrous lines after 6 years and 45 generations of experimental evolution. This period of selection provides ample opportunity for divergence in heterozygosity to have occurred between our regimes if the differences in sexual selection also increase inbreeding in the monogamous condition. Nothing has changed in the way we manage these lines, so we have no reason to expect this to have since diverged (Lumley et al., 2015). Third, the baseline fitness of our lines showed no difference between sexual selection regimes (Table 1), even through the first full cycle of the vortex experiment (Figure 5), providing no evidence that variation in prior levels of inbreeding has weakened monogamous lines before they are challenged by stress. This similar baseline fitness for monogamous and polyandrous regimes under benign conditions indicates that population benefits of sexual selection become more visible under the more challenging conditions within the extinction vortex, when genetic load influencing multiple small effects will be more likely to be exposed (Haldane, 1937). Finally, if differential inbreeding had occurred between our sexual selection lines, logic dictates that the polyandrous regime would have been more likely to experience reductions in genetic diversity, because competition and choice within each male group may have limited the reproductive or fertilization success of some males, potentially reducing N_e and encouraging genetic drift (Kokko & Brooks, 2003). By contrast, all 20 males in the enforced monogamy treatment were given the opportunity to reproduce without restrictive choice or competition. This reduction in genetic variation but improvement in fitness was recently demonstrated following experimental evolution under heightened sexual selection in *D. melanogaster* (Dugand et al., 2018, 2019), but our previous microsatellite assays showed monogamous and polyandrous lines to have near-identical heterozygosities after 45 generations of

experimental evolution. This similarity in heterozygosity suggests that polyandry might have enabled sexually selected choice in favour of males and/or sperm that was more genetically different to each female (Vega-Trejo, Head, Keogh, & Jennions, 2017), countering any loss of genetic variation or reduced N_e through skews in mate choice under polyandry. Alternatively, new research suggests that male competitive interactions could increase de novo mutations through spermatogenesis and the male germ line, enabling polyandry to recapture some genetic variation (Baur & Berger, 2020).

Our results, therefore, reveal that population vulnerability to the extinction vortex is amplified when the adult mating pattern has been deprived of opportunities for competition and choice, supporting the theory of Genic Capture within sexual selection (Lorch et al., 2003; Rowe & Houle, 1996; Tomkins et al., 2004; Whitlock & Agrawal, 2009). Genic capture is theorized to operate when reproductive success in the face of competition and choice is achieved by individuals in better condition. If overall condition is captured by genome-wide variation for a broad range of traits, sexual selection will theoretically act as an effective filter across the whole genome in synergy with natural selection to maintain or improve population-wide condition, and hence improved resilience in the face of stress. It was this reasoning that led Agrawal (2001) and Siller (2001) independently to theorize that the substantial costs of sexual reproduction and the production of males (which do not produce offspring) could be countered by sexual selection, because intraspecific reproductive competition and choice could enable an especially efficient and beneficial intraspecific purging of deleterious mutation load from the genome (Haldane, 1937; Whitlock & Agrawal, 2009). Our results support these ideas and also identify the potential importance of sexual selection in an applied context as a vital force for promoting the genetic health of a population through competitive selection of reproductive individuals that have superior overall condition, strengthening a population's ability to resist the extinction vortex. Importantly, when we examine the impact of each of the three vortex stresses on relative fitness declines compared with their stress-free respective baseline values, it is clear that each stress generates a similar overall impact on population fitness and extinction risk (Figure 6). (It is important to note here that population fitness values following nutritional and thermal stress are generated by groups of up to 5 + 5 females and males, whereas fitness following genetic stress is generated by pairs of 1 + 1 female and male, so we have calculated relative fitness values to the non-stressed baseline condition for comparison.) Our results for relative fitness declines following each of the three stresses presented in Figure 6, therefore, reveal equivalent and combined susceptibility to the environmental and genetic challenges that are increasing through the Anthropocene.

We designed our experimental vortex so that it challenged the viability of small populations of *T. castaneum* beetles through the application of environmental, demographic and genetic stresses that are relevant to natural populations today. Our 'nutritional' environmental stressor reduced protein levels in the larval and adult diet by removing yeast from the beetle fodder, forcing elevated competition

for food and constraining the availability of basic proteins for building and maintaining new life. The baseline impact of this nutritional stress at the start of the experiment almost halved overall reproductive fitness compared with non-stressed small populations (Table 1). Such a dietary challenge will be widely relevant to populations facing habitat loss and the disruption of food webs leading to rapid shifts in access to essential food sources and/or trophic position. Having suffered a generation of nutritional deprivation, our extinction vortex then introduced thermal stress by exposing small adult populations to a 38°C 5 day heatwave, reducing small population overall fitness levels by 40% relative to the baseline fitness shown by unstressed control groups (Table 1). Heatwaves and other extreme weather patterns are expected to increase in frequency, duration and intensity with climate change (Meehl & Tebaldi, 2004; Perkins, Alexander, & Nairn, 2012). Such extreme events will be stressful to evolutionarily mismatched populations, with heatwave conditions known to be especially damaging to reproductive fitness (Sales et al., 2018; Walsh et al., 2019). Finally, having exposed small populations to two relevant environmental stressors, we created genetic bottlenecks within each lineage by limiting reproduction between a single male and female. Although this is a relatively extreme bottleneck which we applied for experimental purposes, and therefore only directly relevant to captive and/or heavily reduced populations, natural populations suffering depletion and fragmentation are experiencing reductions in the spatial and temporal flow of genetic diversity, increasing risks of inbreeding (Keller & Waller, 2002). Genetic bottlenecks are essential drivers within the extinction vortex, because inbreeding usually reduces fitness, damaging a wide range of traits that are essential for population viability, with reproduction (Keller & Waller, 2002) and male competitiveness (Vega-Trejo et al., 2017) showing particular sensitivities, including in *T. castaneum* (Michalczyk et al., 2010; Pray & Goodnight, 1995). Inbreeding can also render populations more vulnerable to environmental stresses (Armbruster & Reed, 2005), and reduced genetic diversity will constrain a lineage's ability to adapt to change (Frankham et al., 2002). By comparison with our previous work measuring population fitness after 45 generations of experimental evolution with this system, we found that monogamous background lines went extinct after nine generations of continuous inbreeding, at which point one-third of the polyandrous background lines were still viable (Lumley et al., 2015). Here, in our vortex experiment started after 95 generations of experimental evolution, the monogamous background lines were extinct after five generations of inbreeding, but only when combined with 10 additional generations of environmental challenge from nutritional deprivation and thermal stress.

Our experiment identifies the extinction vortex to be an informative framework for studying how small populations decline towards extinction in the face of interactive stressors. Importantly, our results demonstrate the importance of mating patterns, adult sex ratios and reproduction for population viability, despite these often being neglected factors which can significantly underestimate natural extinction rates (Melbourne & Hastings, 2008). Two important general predictions arising from the vortex model have

received empirical support: first, that there should be a logarithmic scaling between time-to-extinction and population size within the vortex (Fagan & Holmes, 2006; Lande, 1993); and second, as the vortex progresses closer to extinction, rates of decline should increase (Fagan & Holmes, 2006; Gilpin & Soulé, 1986). Our experimental results do not support these predictions, with sigmoid rates of population declines evident through the vortex, and a flattening of fitness decreases as extinction approaches (Figure 4). Such a response could be explained by the actions of genetic purging through each population bottleneck (Crnokrak & Barrett, 2003), leaving small groups of individuals carrying reduced genetic load and therefore able to tolerate environmental stress further until extinction. Our fine levels of experimental control will enable more detailed measures of population decline than would be possible in the natural environment, so such a purging process may operate the wild but be hard to detect. In addition, the absence of complex ecological pressures and interactions within the natural environment, such as interspecific competition and predation, may also explain the continued and flattening of rates of mortality and reproductive output in our lab populations as lineages approach extinction.

Where practically possible, conservation managers are increasingly aware of the need to incorporate evolutionary principles into the management of vulnerable biodiversity (Avisé, 1989; Carroll et al., 2014; Frankham, 2015; Hoffmann & Sgrò, 2011; Ralls et al., 2017; Smith, Kinnison, Strauss, Fuller, & Carroll, 2014). Three main factors that influence the genetics of endangered populations are (a) selection, (b) variation and (c) gene flow (Carroll & Fox, 2008). Managers have frequently focused their attentions on promoting the latter two factors within depleted populations in order to minimize risks of inbreeding, while maximizing opportunities for adaptation. Although 'genetic rescue' has been successful for some vulnerable populations (Whiteley, Fitzpatrick, Funk, & Tallmon, 2015), recent analyses have identified that enhancing genetic variation and gene flow per se is not always the best solution for populations with depleted genetic variation (Bell et al., 2019). Here, we demonstrate the importance of mating pattern for declining populations facing environmental stress and extinction risk, even if sexual selection reduces effective population size and increases risks of inbreeding. Mating patterns enable competition and choice, and our results show that these evolved processes enable sexual selection of gene flow and variation that gives a declining population an improved ability to resist the stresses of the extinction vortex. The conservation of evolved mating patterns and opportunity for sexual selection has received some attention from conservation biologists, most notably for the management of captive populations (Chargé, Teplitsky, Sorci, & Low, 2014). However, such processes have also been considered in the wild, with concerns about the longer term impacts of endocrine-disrupting chemicals being a relevant example (Shenoy & Crowley, 2011). In addition, reduced population sizes, especially in conjunction with size-selective harvesting such as in fisheries (Hutchings, 2009), can cause evolutionary responses that will erode opportunities for female choice and male-male competition among

mature adults, and hence weaken opportunities for sexual selection. Atlantic cod and other commercially important fish species, for example, have complex mating patterns that become disrupted when abundance declines, and both direct fertility and indirect genetic and fecundity effects may weaken the resilience of such populations even further (Rowe & Hutchings, 2003). Although the conservation of mating patterns that enable reproductive competition and choice may be of secondary importance for biodiversity issues that often require reactive approaches, our findings do reveal that population viability in the face of modern environmental and genetic stresses can be strengthened by opportunities for sexual selection.

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CONFLICT OF INTEREST

The authors declare no competing interest.

ETHICS

This study was approved by, and followed strict guidelines to, the University of East Anglia's Animal Welfare and Ethical Review Board.

DATA AVAILABILITY STATEMENT

The data used in this study are available on Dryad (<https://doi.org/10.5061/dryad.nzs7h44nz>) or upon request from the authors.

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