Evolution, 2024, **78(5)**, 951–963
https://doi.org/10.1093/evolut/qpae031
Advance access publication 28 February 2024
Original Article

Sexual selection and mate limitation shape evolution of species' range limits

Maximilian Tschol[1], Jane M. Reid[1,2], Greta Bocedi[1]

[1]School of Biological Sciences, University of Aberdeen, Aberdeen, United Kingdom
[2]Centre for Biodiversity Dynamics, Institutt for Biologi, NTNU, Trondheim, Norway

Corresponding author: School of Biological Sciences, University of Aberdeen, Zoology Building, Tillydrone Avenue, Aberdeen AB24 2TZ, United Kingdom. Email: tschol.maximilian@gmail.com

Abstract

Understanding what processes shape the formation of species' geographic range limits is one central objective linking ecology and evolutionary biology. One potentially key process is sexual selection; yet, theory examining how sexual selection could shape eco-evolutionary dynamics in marginal populations is still lacking. In species with separate sexes, range limits could be shaped by limitations in encountering mates at low densities. Sexual selection could therefore modulate mate limitation and resulting extinction–colonization dynamics at range margins, through evolution of mate encounter ability and/or mate competition traits, and their demographic consequences. We use a spatially explicit eco-genetic model to reveal how different forms of sexual selection can variably affect emerging range limits. Larger ranges emerged when sexual selection acted exclusively on traits increasing mate encounter probability, thus reducing female's mate limitation toward the range margins. In contrast, sexual selection via mate competition narrowed range limits due to increased trait-dependent mortality in males and elevated mate limitation for females. When mate encounter coevolved with mate competition, their combined effects on range limits depended on the mating system (polygyny vs. monogamy). Our results demonstrate that evolution of species' ranges may be importantly shaped by feedbacks between sexual selection and spatial population demography and dynamics.

Keywords: sexual selection, range limits, evolution, mate limitation, sexual traits, intraspecific interactions

Introduction

Understanding how abiotic and biotic conditions affect eco-evolutionary dynamics of species' range limits is a central aim linking ecology and evolutionary biology. Yet, while interactions among species are increasingly well considered (Alexander et al., 2022; Case et al., 2005; Paquette & Hargreaves, 2021; Price & Kirkpatrick, 2009; Svenning et al., 2014), similar focus on the evolutionary impacts of intraspecific interactions on species' range limits is surprisingly scarce (Holt et al., 2004).

For species with separate sexes, multifaceted effects of mating and mate choice, which fundamentally underpin reproduction and hence population growth, could substantially shape range limits. For example, difficulty of encountering mates could restrict range expansion given low population densities at range margins (Holt et al., 2004; Keitt et al., 2001). Furthermore, the dynamics of mate encounter will depend on the mating system and adult sex ratio (ASR; Bessa-Gomes et al., 2004; Shaw et al., 2018). Meanwhile, the degree to which mating interactions generate competition for fertilization determines how sexual selection shapes the evolution of sexual traits (Kokko et al., 2012), and resulting trait-dependent costs and benefits could, in turn, affect spatial population dynamics and even drive "evolutionary suicide" (Kokko & Brooks, 2003). However, despite such expectations, the degrees to which different combinations of sexual selection and mating system affect the eco-evolutionary dynamics of species' range limits, acting through population-level consequences of evolving sexual traits and consequent sex-specific life-history trade-offs, remains almost entirely unexplored, both theoretically and empirically.

Species' distributions can be rationalized from a meta-population perspective (Carter & Prince, 1981; Lennon et al., 1997), where range limits reflect a balance between local extinction and colonization (Holt & Keitt, 2000). Evolutionary explanations for observed limits often focus on why local population growth rates decline and ultimately turn negative at range edges as a consequence of increasing maladaptation along a spatial abiotic gradient (Kirkpatrick & Barton, 1997; Polechová, 2018; Polechová & Barton, 2015). Interactions among species may then generate range limits that are narrower than any focal species' abiotic niche (Alexander et al., 2022; Case et al., 2005). Additionally, the small population sizes expected at species' niche margins may shape range limits through demographic Allee effects (i.e., decreased fitness components and hence population growth rate due to small population size; Holt et al., 2004; Keitt et al., 2001; Stephens et al., 1999). Indeed, mate limitation arising from difficulty of finding mates at low densities is the most commonly reported component Allee effect (Gascoigne et al., 2009) and may therefore shape range limits in sexually reproducing species with separate sexes. Empirically linking the mate-finding component to the demographic Allee effect, as well

Received September 23, 2023; revisions received January 11, 2024; accepted February 27, 2024

Associate Editor: Yvonne Willi; Handling Editor: Tim Connallon

as distinguishing different Allee components and demographic stochasticity, remains challenging (Gascoigne et al., 2009). However, theoretical studies have proven invaluable in examining how variable aspects of mating and mate choice affect the Allee effect and its consequences for population extinction and colonization (Berec, 2018; Berec et al., 2018). Understanding range limit formation therefore requires theory that examines the evolutionary dynamics that modulate mate limitation, encompassing the form of operation of sexual selection and resulting consequences for mate finding in the context of low range-edge population densities (Figure 1).

In many species, males compete indirectly or directly at different stages to successfully reproduce (Murphy, 1998; Shuster & Wade, 2003), and resulting sexual selection drives evolution of male traits that enhance mating success (Figure 1A; Andersson, 1994; Rico-Guevara & Hurme, 2019; Wiens & Tuschhoff, 2020). Males may often be selected for increased mate searching or mate attraction (i.e., mate encounter traits; Fromhage et al., 2016; Kokko et al., 2012). Additionally, males may directly compete for access to females via male combat or courtship, causing evolution of elaborate male weapons or displays (Hunt et al., 2009; Kokko et al., 2006; Moore et al., 2022; Rico-Guevara & Hurme, 2019). Population-level consequences of evolving sexually selected traits could then modulate mate-finding Allee effects and resulting extinction–colonization dynamics at range margins in several ways (Figure 1).

First, evolving male mate encounter traits could mitigate female mate limitation by increasing females' probability of mating at least once, thereby promoting successful population establishment and persistence at low densities (Figure 1B; Berec, 2018; Berec et al., 2018). Second, expressing sexually selected traits may often impose a cost comprising increased male mortality (Andersson, 1994; Kotiaho, 2001; Promislow, 1992; Somjee, 2021; Székely et al., 2014). Resulting female-biased ASR could then feed back to increase female mate limitation (Figure 1C and D). Effects of female-biased ASR on mate-finding Allee effects will also be modulated by the mating system, with polygyny increasing population persistence and establishment success compared to monogamy, because females are less likely to remain unmated when males mate multiply (Figure 1E; Bessa-Gomes et al., 2004; Shaw et al., 2018). Additionally, female-biased ASR could result in increased population growth rate (Bessa-Gomes et al., 2004). However, positive effects of polygyny and female-biased ASR are predicted to be highly nonlinear, and populations may rapidly go extinct given extremely biased ASR (Bessa-Gomes et al., 2004; Shaw et al., 2018). The net consequences of sexual selection for mate-finding Allee effects and population growth will thus depend on how resulting mate encounter probability and ASR interact with the mating system to jointly determine mate availability and successful female reproduction.

Predicting how evolving sexual traits will ultimately shape range limits via mate limitation will be further complicated because changes in both mate encounter

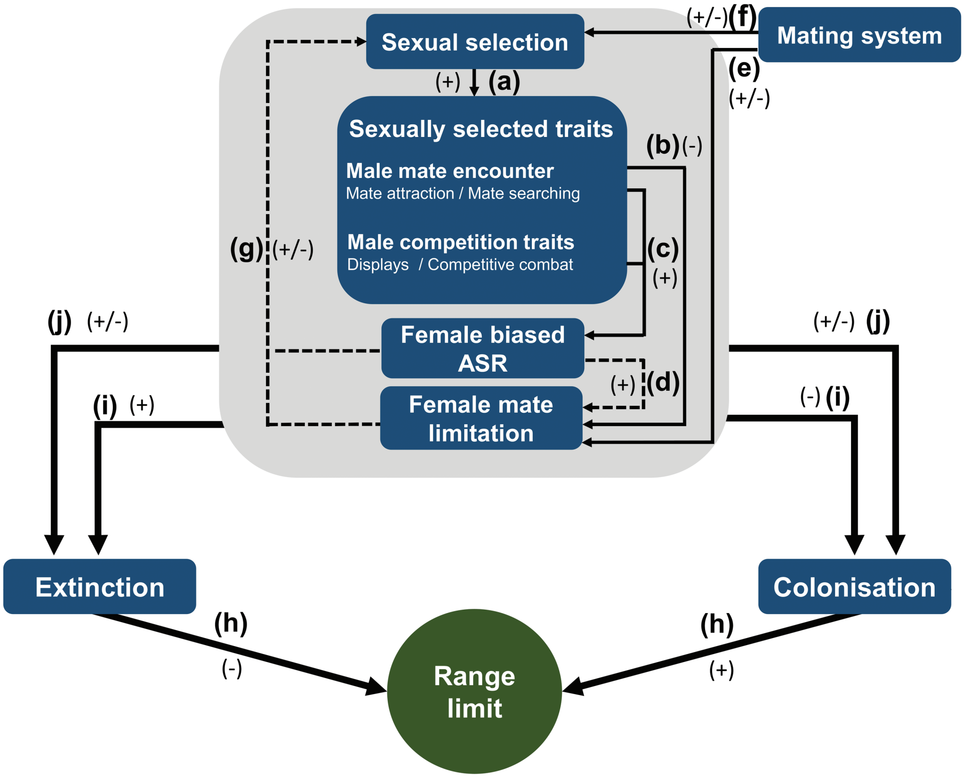

Figure 1. Conceptual representation of potential effects of sexual selection on range limit formation. (A) Sexual selection drives evolution of male mate encounter or competition traits. (B) Evolving mate encounter trait reduces mate limitation for females, and (C) viability costs of sexually selected traits affect adult sex ratio (ASR) via trait-dependent mortality in males. (D) Female-biased ASR affects mate limitation in females, (E) depending on the mating system. (F) Mating system also affects sexual selection by modulating the potential for competition among males. (G) ASR and mate limitation feedback to sexual selection. (H) Range limits emerge from the balance between extinction and colonization at the range margins, which, in turn, depends on how population persistence and establishment are affected by (I) mate limitation in females and (J) the magnitude of female bias in the ASR. Dashed arrows indicate emerging feedbacks; plus and minus symbols denote positive or negative effects, respectively.

probability and ASR could feed back on the strength of sexual selection itself (Figure 1F and G; Klug et al., 2019; Kokko & Rankin, 2006; Liker et al., 2021). Mate choice models show that the strength of sexual selection depends on the number of potential mates a female samples (Benton & Evans, 1998; Muniz & Machado, 2018) and predict positive density dependence in sexual selection when females sample all available mates (Kokko & Rankin, 2006; Watts et al., 2022). Decreasing population density toward range margins may therefore weaken sexual selection on male competition traits due to low mate availability. However, coevolving male mate encounter traits may act to increase the strength of sexual selection on male competition traits, and resulting exaggeration of competition traits may then promote evolutionary suicide of small marginal populations (Kokko et al., 2002; Martínez-Ruiz & Knell, 2017; Tschol et al., 2022). Net population-level consequences of combinations of evolving sexual traits will therefore be complex and will likely depend on the strength of sexual selection and to what extent mating success is determined by mate encounter and/or competition traits. But, no theory yet exists on the consequences of sexual selection for emerging range limits.

We built and analyzed a genetically and spatially explicit individual-based model to reveal the variable effects of sexual selection on range limits when the population-level consequences of evolving sexually selected traits feed back to shape mate availability throughout a species' range. Specifically, our model jointly considers the (co)evolution of sexually selected traits and the dynamics of mate encounter within a metapopulation context, where range limits emerge from extinction–colonization dynamics. We test (a) whether evolution of a male mate encounter trait can alleviate mate limitation at low population densities thereby extending a species' range limits despite trait-dependent mortality costs; (b) how the evolution of a male competition trait affects range limits when male mate encounter cannot evolve; and (c) how coevolution of male mate encounter and competition traits alters range limits compared to when these traits evolve alone. We thereby show how multifaceted eco-evolutionary interactions involving sexual selection, mating system, and population dynamics can yield range limits across environmental gradients.

Methods

We model a dioecious species inhabiting a one-dimensional array (i.e., line) of patches along a linear environmental gradient in carrying capacity (K), where patch K_x at spatial position x is given by:

$$K_x = \max(K_c - bx,\ 0) \tag{1}$$

where b is the slope of the environmental gradient and K_c is the maximum K at the range core. This gradient represents a species abiotic niche. The area A of each patch is assumed to be the same, effectively creating a density gradient following the gradient in K, given an emerging gradient in population size. Generations are nonoverlapping. Within each subpopulation, individuals follow a lifecycle of offspring dispersal, viability selection, and density-dependent survival, followed by mating and reproduction before all adults die. The C++ source code is available via the URL in the *Data availability* statement. All model variables and simulation parameters are summarized in Supplementary Table S1.

Genetic architecture

We model two traits expressed by males: a mate encounter trait (E) and a competition trait (C). Each trait has a diploid autosomal additive genetic architecture comprising $L = 200$ unlinked loci with a continuous distribution of allelic values at each locus (Kimura, 1965) and no pleiotropy. Initial allele values are independently sampled from normal distributions with means u_{E_0}, u_{C_0} and variances $\sigma^2_{E_0}, \sigma^2_{C_0}$ for the mate encounter and competition traits, respectively. Alleles mutate with probability $\mu =\ 0.0001$/diploid locus/generation. Mutational effects are drawn from a normal distribution with mean zero and mutational variance, σ^2_m, and added to the current allelic value. Individual's genotypic values for each trait (gE, gC) are given by the sum of the two L allelic values. Phenotypic values correspond to genotypic values within the range 0–30, effectively assuming no environmental variance (e.g., Bocedi & Reid, 2015). The lower limit means that male traits cannot be negative, while the upper limit avoids numerical error due to the potential for runaway evolution imposed by our mate competition function (see Equation 3).

Mate finding and reproduction

At each generation, males search for or attract females within the same patch, where the probability of male i to encounter any female is:

$$p_i = \min\left(\frac{1}{A} + \frac{E_i}{A}, 1\right) \tag{2}$$

here $1/A$ represents the baseline probability of encountering a female randomly given the patch area, simply conceptualizing the expectation that, given a certain population size, the encounter probability will decrease with increasing patch area A. The term E_i/A describes a male's mate encounter probability determined by its phenotype E_i. This formulation means that the phenotypic effect is additive on the baseline, all scaled by A. Conceptually, this may arise if the encounter trait allows males to actively search for females or advertise their presence over a proportion of area A. For each male, females then draw a random number q_i from the uniform distribution $U[0, 1]$, and males enter the female's encounter list of *Nmales* when $p_i > q_i$. Males may enter multiple females' lists under polygyny, while already mated males are not available for mating under monogamy. Males may further compete for mating when several males are on a female's encounter list, where a male's probability of mating with a female (m_i) is determined by his competition trait C phenotype relative to the phenotypes of the N_{males} on the list, such that:

$$m_i = \frac{\left(e^{c_i}\right)^{\alpha}}{\sum_{k=1}^{Nmales}\left(e^{c_k}\right)^{\alpha}}, \tag{3}$$

here α determines to what degree mating success is skewed toward males with relatively higher values of C (Bocedi & Reid, 2015; Lande, 1981; Martinossi-Allibert et al., 2019) and thus controls the strength of competition and the potential reproductive benefits arising from sexual selection. With $\alpha = 0$, a male's mating probability is independent of C, while $\alpha > 0$ introduces increasingly strong competition. Conceptually, competition may arise from male–male combat, where it is assumed that larger trait values defeat smaller trait values or, alternatively, represent open-ended directional female preference for increasing male display, where α represents the preference strength (Bocedi & Reid, 2015; Lande, 1981). Each female mates once and the number of offspring is drawn from the Poisson distribution Pois (R), with mean fecundity R. We assume a primary sex ratio of 1:1.

Dispersal and survival

Offspring disperse to a different patch with probability d. Dispersers consequently move randomly toward either side of their home patch, with dispersal distance sampled from a negative exponential $Exp\left(\frac{1}{\lambda}\right)$, with mean distance λ ($\lambda = 1$ patch). If the destination falls outside the landscape at either end, distance is resampled (Supporting Information S2). After dispersal, male offspring experience viability selection where male i's viability v_i (i.e., survival probability) results from selection on each phenotypic trait:

$$v_i = \prod_{t}^{2} e^{\frac{-(z_t-\theta_t)^2}{2\omega_t^2}}, \tag{4}$$

where t denotes the traits E and C, z_t the trait phenotypic value, θ_t the trait's naturally selected optimum, and ω_t^2 the strength of selection, where increasing values indicate weaker selection (acting equally in all subpopulations). Depending on the choice of θ_t, viability selection is directional given $\theta_t \leq 0$, or stabilizing given $\theta_t > 0$, the latter representing sexual traits that exhibit some level of ecological pleiotropy. After viability selection, all remaining offspring reach adulthood with density-dependent survival probability δ according to local carrying capacity K_x:

$$\delta = min\left(\frac{K_x}{N_{offs}}, 1\right), \tag{5}$$

where N_{offs} is the total number of offspring in the subpopulation.

Simulation experiments

We set an array of 100 patches with area $A = 10$, environmental gradient $b = 1$, and $K_c = 100$. This parameterization defines a hard abiotic range limit at the end of the array (i.e., $K_x = 0$, given $x = 100$, Equation 1). We ran simulations to test impacts of sexual selection on the extent of biotic ranges arising within the abiotic limit when (a) only the mate encounter trait E evolves; (b) only the competition trait C evolves; and (c) both traits evolve jointly. For evolving traits, we initialized each simulation by sampling individual's alleles such that the trait's genotypic distributions had means $u_{C_0}, u_{E_0} = 0$ and variances $\sigma^2_{E_0}, \sigma^2_{C_0} = 0.25$, with allelic values of nonevolving traits set to zero. In all simulations, we set the naturally selected optimums of both traits $\theta_t = 0$, resulting in directional selection against positive values of E and C, thus always imposing a viability cost on males. We ran different simulation sets, varying the strength of selection on each trait ($\omega_t^2 = 25,\ 100,\ \ 1 \times 10^6$); the strength of male competition α, and thus the potential for sexual selection on C ($\alpha = 0.5,\ 1$); and the dispersal probability ($d = 0.001,\ 0.01,\ 0.1$), since the emerging range limit should be sensitive to dispersal determining recolonization at the range edge. We present results for $d = 0.1$ (Supporting Information S3 and S4 show results for lower d).

To determine whether sexual selection and consequent trait evolution extends or contracts the range limit within the spatial context of our model, we simulated two nonevolutionary "control" scenarios without sexual selection. Here, gE and gC are prevented from evolving away from 0, meaning that mating is functionally random with respect to the two traits. First, in an "area-dependent encounter" control scenario (*AE-control*), we assumed males only encounter females with baseline probability determined by the patch area (i.e., male's encounter probability solely given by $\frac{1}{A}$). This can be conceptualized as the species' range limit that would emerge in the absence of sexual selection but given limitations in spatially locating mates as well as limitations imposed by the mating system. Second, in a "mating-system-dependent encounter" control scenario (*ME-control*), males can in principle encounter all females in the patch (i.e., encounter is independent of area), but mate availability still depends on the mating system, representing a scenario where there are no limitations in spatially locating potential mates, but females might be limited by the number of unpaired males given monogamy. Thus, the *ME-control* represents the best-case scenario for encountering mates under a particular mating system, while mate encounter in the *AE-control* may be more difficult due to the additional challenge of spatially locating mates. All simulations were run for 120,000 generations for traits to reach equilibrium and replicated 30 times.

To quantify emerging range limits, we discarded the first 100,000 generations and thereafter extracted subpopulation sizes at 500 generation intervals (i.e., 40 data points per simulation). We then calculated median subpopulation sizes N_{med} across the last 20,000 generations. The subpopulation with the lowest spatial position x and $N_{med} = 0$ was recorded as the range limit. This measure accounts for variation in the range limit due to extinction and recolonization. To link emerging range limits to trait evolution and population-level consequences of evolving traits, we calculated the genotypic mean gC and gE across all adults in each subpopulation, the ASR (number of males divided by total individuals), and the proportion of unmated females. Because both trait means reached equilibrium after 100,000 generations (Supporting Information S5), we averaged genotypic means (i.e., subpopulation means), ASR, and proportion of unmated females across the last 20,000 generations. We present spatial grand means of genotypic trait values (i.e., global means) and ASR for the entire meta-population, alongside some representative examples of emerging trait clines. Comprehensive information on spatial trait variation across the range is in Supporting Information S6.

Results

Range limits when only mate encounter trait E evolves

Sexual selection via evolving mate encounter trait E extended the range limit compared to when sexual selection was absent, given the area-dependent encounter control scenario (*AE-control*, Figure 2A). Lower trait-dependent costs generally caused extended range limits, and low costs ($\omega_E^2 = 1 \times 10^6$)led to similar range limits as with the mating-system-dependent encounter control scenario (*ME-control*, Figure 2A). The difference between *AE-control* and *ME-control* represents range contraction due to spatial limitations in finding mates at low density. Hence, sexual selection on mate encounter caused range extension by alleviating limitations in mate finding, even when E was costly to males. Range limits were further affected by the mating system. Polygyny slightly but consistently extended the range limit in comparison to monogamy for simulations with and without sexual selection (Figure 2A).

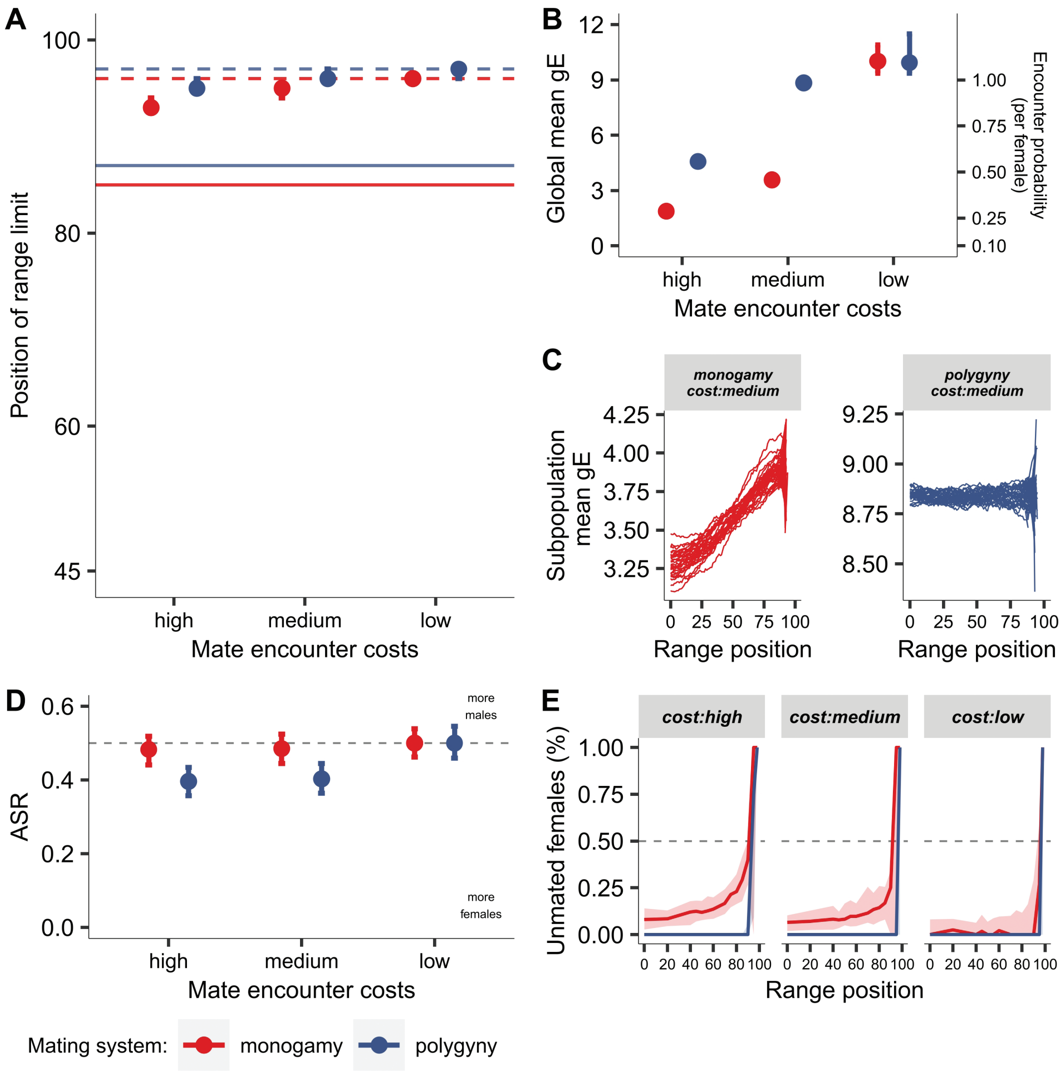

Figure 2. Effect of mate encounter (*E*) evolution on range limits and population-level consequences for different trait-dependent costs (high: $\omega_t^2 = 25$; medium: $\omega_t^2 = 100$; low: $\omega_t^2 = 1 \times 10^6$). (A) Emerging range limits; for comparison, the median range limit of nonevolutionary control scenarios without sexual selection is indicated with lines (solid lines: "area-dependent" encounter *AE-control*; dashed lines: "mating-system-dependent" encounter *ME-control*); (B) global mean mate encounter trait *gE* and corresponding female mate encounter probability (right axis); (C) subpopulation *gE* across range; (D) mean adult sex ratio (ASR); and (E) proportion of unmated females across the range. Colors indicate different mating systems. Dots and thick lines indicate medians and bars, and shaded regions indicate the 95% central intervals across 30 replicates. For visual aid, dashed lines indicate an equal sex ratio in (D) and 50% unmated females in (E).

These extended range limits were underpinned by evolution of higher global mean *gE* under polygyny and lower costs (Figure 2B). Consequently, at low cost, males found all females within their patch regardless of the mating system (Figure 2B). Subpopulation mean *gE* increased toward the range margins under monogamy (Figure 2C; Supplementary Figure S10A and B), but did not show spatial variation under polygyny (Figure 2C; Supplementary Figure S10D and F). Increasing the cost of *E* (decreasing ω_E^2) skewed the ASR toward females, particularly under polygyny (Figure 2D). Yet, no female remained unmated under polygyny except at the extreme range edge (Figure 2E). Under monogamy, the percentage of unmated females remained low in most of the range, but increased toward the range margins for medium and high costs (Figure 2E). Thus, while the probability that a given male encountered a given female decreased with higher costs of *E* (Figure 2B), the overall probability for a given female to encounter no males at all remained low across large parts of the range for all costs and both mating systems (Figure 2E).

Range limits when only mate competition trait C evolves

In contrast to evolution of *E*, sexual selection via evolution of the competition trait *C* often resulted in contracted range limits compared to the control scenario *AE-control*, except when costs of C were low ($\omega_C^2 = 1 \times 10^6$) or when the potential for competition was limited by monogamy (Figure 3A). Range limits were then similar to, but not larger than, *AE-control*. At medium ($\omega_C^2 = 100$) and high ($\omega_C^2 = 25$) costs, polygyny led to substantial range contractions, of magnitudes depending on the competition parameter α. Specifically, stronger competition ($\alpha = 1$) led to contracted range limits. The effect of polygyny on range limits therefore depended on the mechanism that caused sexual selection (compare mate encounter in Figure 2 vs. competition in Figure 3).

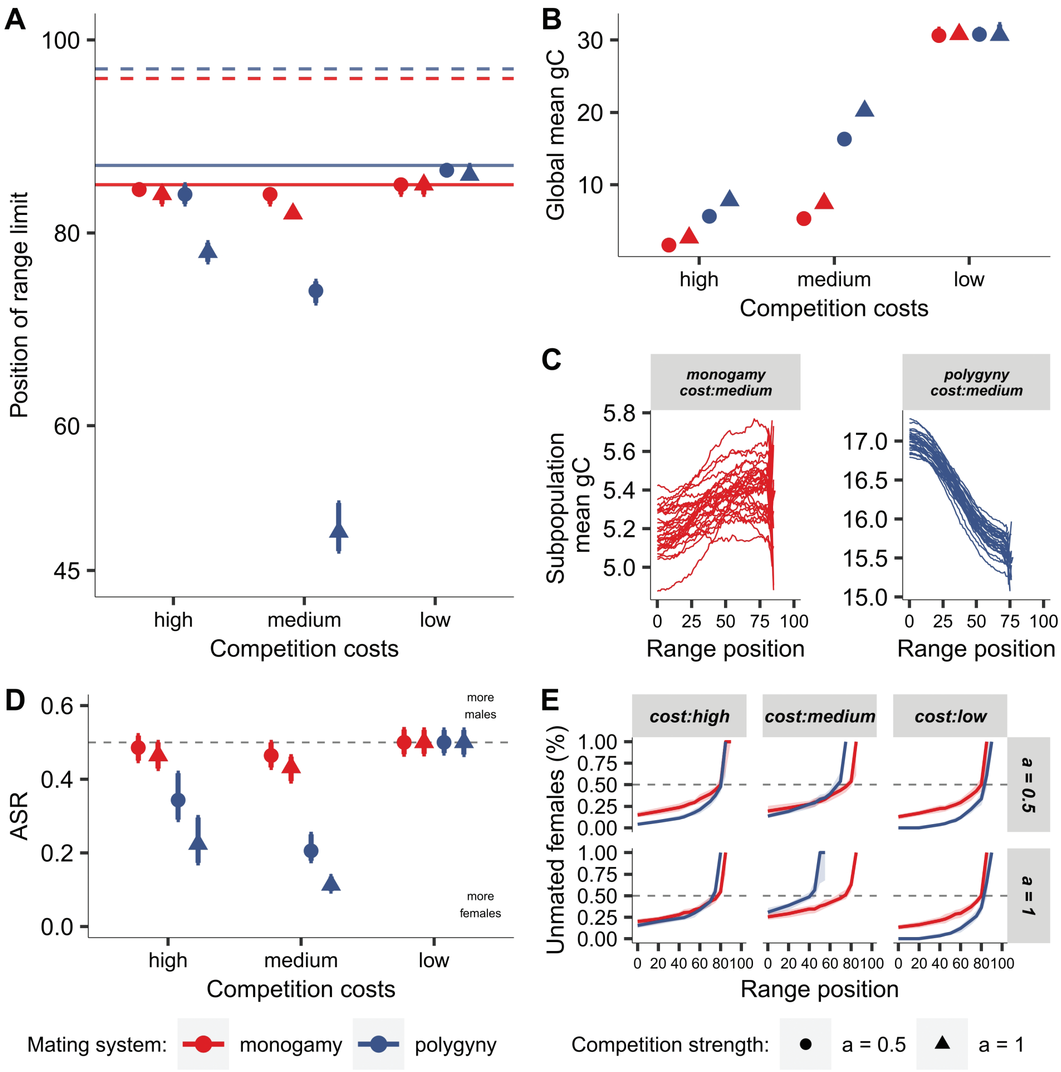

Figure 3. Effect of mate competition (C) evolution on range limits and population-level consequences for different trait-dependent costs (high: $\omega_t^2 = 25$; medium: $\omega_t^2 = 100$; low : $\omega_t^2 = 1 \times 10^6$). (A) Emerging range limits; for comparison, solid lines: "area-dependent" encounter *AE-control*; dashed lines: "mating-system-dependent" encounter *ME-control*; (B) global mean mate competition trait gC; (C) subpopulation gC across range; (D) mean adult sex ratio (ASR); and (E) proportion of unmated females across the range. Shapes represent different strengths of competition (dot: $\alpha = 0.5$; triangle: $\alpha = 1$). Dots/triangles and thick lines indicate medians and bars, and shaded regions indicate the 95% central intervals across 30 replicates. For visual aid, dashed lines indicate an equal sex ratio in (D) and 50% unmated females in (E).

The contracted range limits arising from sexual selection via competition (Figure 3A) resulted from costs of the evolving C. Global mean gC evolved to higher levels with lower costs, stronger competition ($\alpha = 1$), and polygyny (Figure 3B). At low cost, global mean gC reached the imposed numerical limit of 30, indicating that evolution would have proceeded to higher values if not bounded (Figure 3B). Under monogamy and medium to high trait cost, subpopulation mean gC slightly increased toward the range margin, indicating negative density dependence of sexual selection manifesting at low population density (Figure 3C; Supplementary Figure S11A and B). In contrast, under polygyny and medium to high costs, subpopulation mean gC decreased toward the range margin (Figure 3C; Supplementary Figure S11D and E), indicating positive density dependence in sexual selection caused by fewer competitors at low population density. Thus, differences in the density dependence of sexual selection were induced by the mating system across the range.

The fact that C and its effect on competition could increase indefinitely in our model, while the effect of E on mate finding was functionally bounded, meant that costly exaggeration of C caused the ASR to become more female biased when C was evolving compared to when mate encounter E was evolving (Figure 2D vs. Figure 3D). This female bias was particularly extreme with polygyny and strong competition (Figure 3D). The proportion of unmated females increased toward the range margin for all costs and strengths of competition (Figure 3E), indicating increased mate-finding difficulty for females when population density decreased. At low cost, polygyny caused fewer females to remain unmated compared to monogamy (Figure 3E). However, this pattern switched for scenarios where polygyny led to extremely female-biased ASR, particularly with medium costs and strong competition, showing how the balance between the evolving competition trait and its demographic consequences is modulated by the mating system.

Range limits when mate encounter E and competition trait C jointly evolve under monogamy

The effect of joint evolution of *E* and *C* on emerging range limits depended on the mating system (Figure 4 vs. Figure 5). Under monogamy, joint evolution generated similar range limits as when *E* evolved alone and extended the range limit compared to when only *C* evolved or without sexual selection under the area-dependent encounter control scenario *AE-control* (Figure 4A). Generally, range limits extended with decreasing costs of *E*, while increasing costs of *C* only slightly contracted the range limit at higher costs of *E*.

Global mean *gE* and *gC* generally evolved to similar levels with joint evolution as when they evolved alone (Figure 4B and C). They also showed similar clines across the range, namely increasing trait values toward the range margin at high and medium costs (Supplementary Figure S12A–C, Supplementary Figure S13A–C). Furthermore, the ASR became slightly female-biased when costs of both traits were medium to high, similar to the scenarios with single evolving traits (Figure 4D). The proportion of unmated females at low costs of *C* was similar to that when *E* evolved alone but increased at higher costs of *C* (Figure 4E). Nevertheless, joint evolution alleviated mate limitation across most parts of the range, and fewer females remained unmated compared to when only *C* evolved, particularly toward the range margins (Figure 4E).

Range limits when mate encounter E and competition trait C jointly evolve under polygyny

Given joint evolution and polygyny, range limits under polygyny were predominantly affected by costs of *C* (Figure 5A). At low costs of *C*, range limits were similar to when only *E* evolved and even slightly exceeded those emerging given the mating-system-dependent encounter control scenario *ME-control* at low costs of *E*. In contrast, medium and high

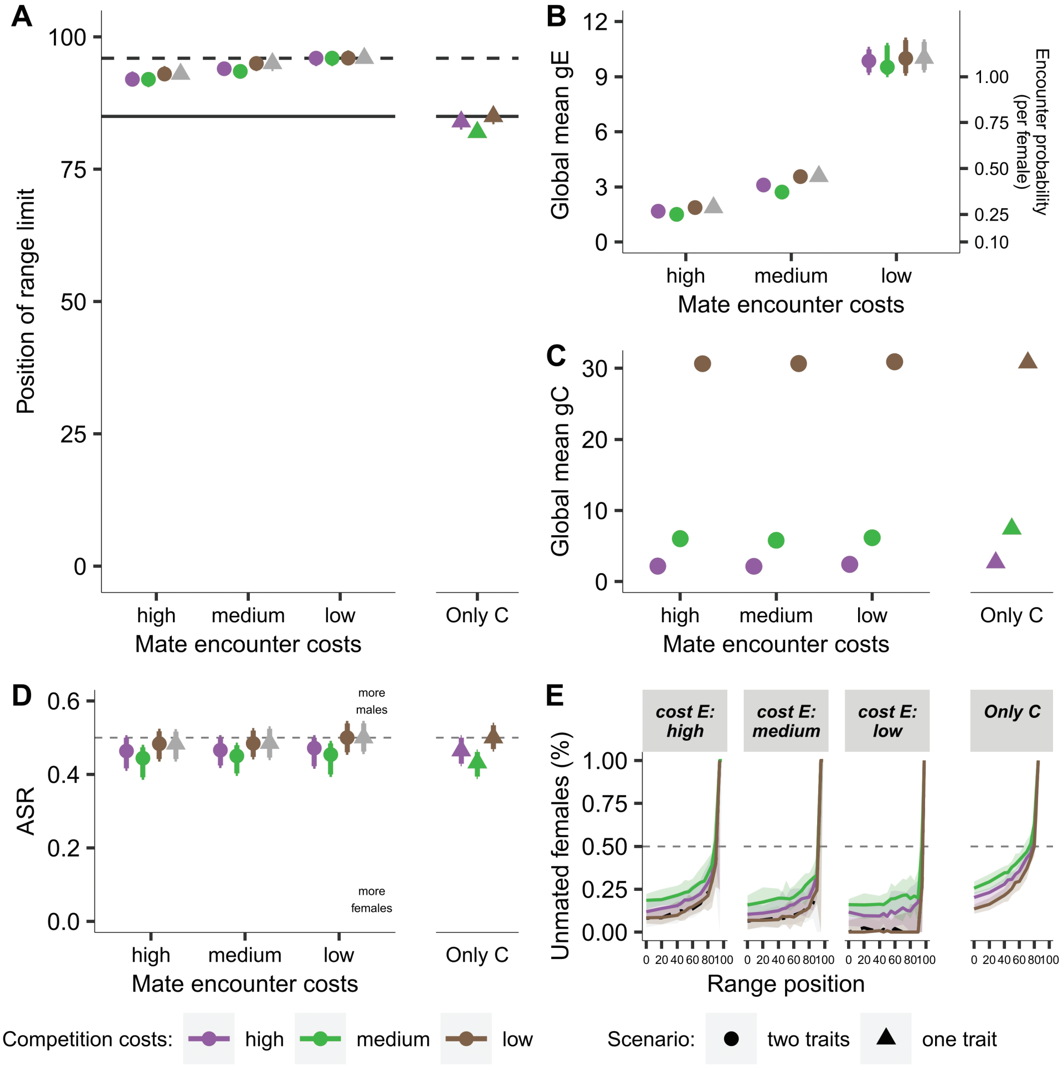

Figure 4. Joint evolution of mate encounter trait *E* with competition trait *C* under monogamy for different trait-dependent costs of mate encounter (high: $\omega_E^2 = 25$; medium: $\omega_E^2 = 100$; low: $\omega_E^2 = 1 \times 10^6$) and competition (high, $\omega_C^2 = 25$; medium, $\omega_C^2 = 100$; low, $\omega_C^2 = 1 \times 10^6$). (A) Emerging range limits; for comparison, solid lines: "area-dependent" encounter *AE-control*; dashed lines: "mating-system-dependent" encounter *ME-control*; (B) global mean mate encounter trait *gE* and corresponding encounter probability; (C) global mean competition trait *gC*; (D) mean adult sex ratio (ASR); (E) proportion of unmated females across the range. Dots represent coevolutionary simulations, and triangles represent single trait evolution for comparison (gray: *E* or on x-axis: *C*). Dots/triangles and lines indicate the medians, while bars and shaded regions indicate the 95% central interval across 30 replicates. For visual aid, dashed lines indicate an equal sex ratio in (D) and 50% unmated females in (E). Other parameters: $\alpha = 1$.

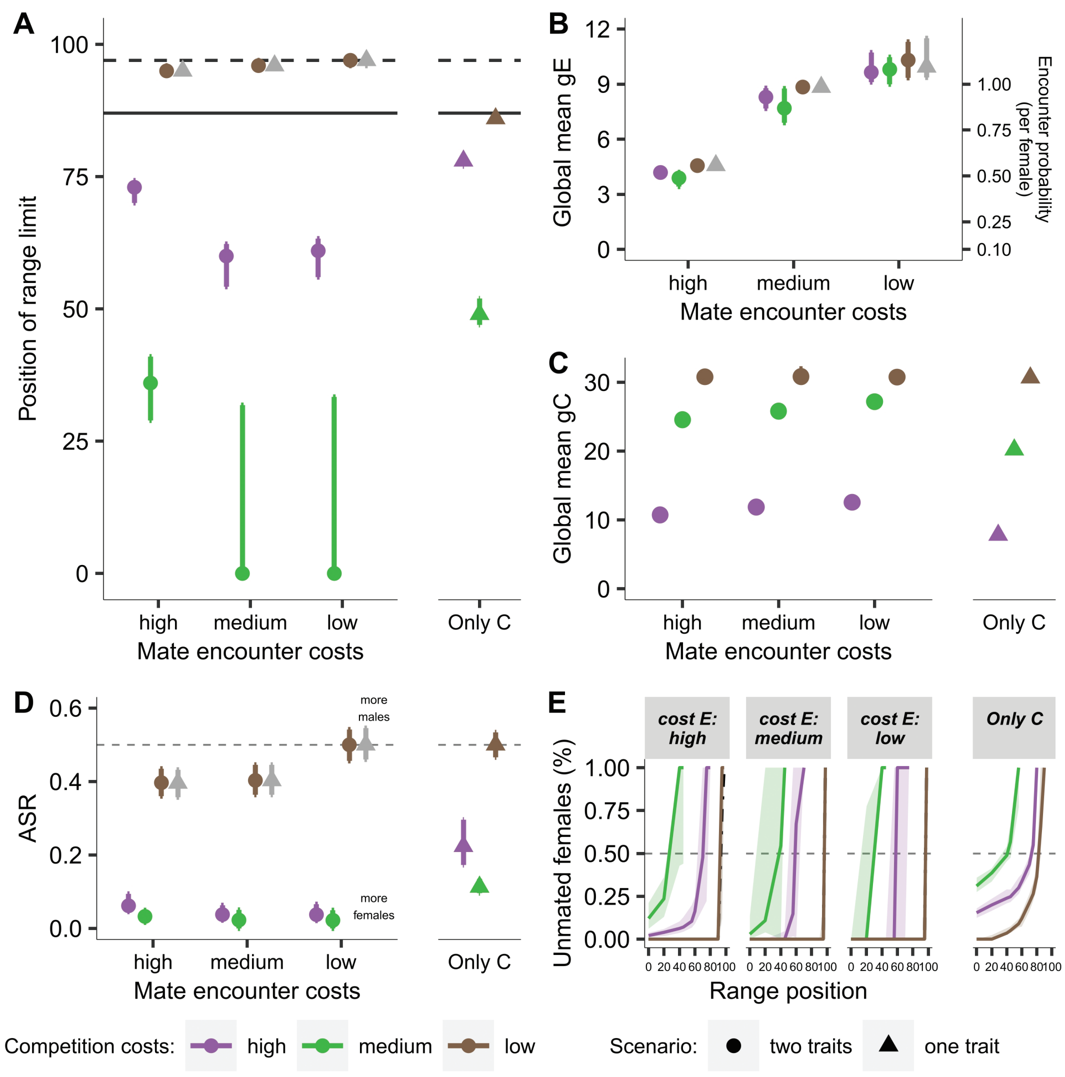

Figure 5. Joint evolution of mate encounter trait *E* with competition trait *C* under polygyny for different trait-dependent costs of mate encounter (high: $\omega_E^2 = 25$; medium: $\omega_E^2 = 100$; low: $\omega_E^2 = 1 \times 10^6$) and of competition (high, $\omega_C^2 = 25$; medium, $\omega_C^2 = 100$; low, $\omega_C^2 = 1 \times 10^6$). (A) Emerging range limits; for comparison, solid lines: "area-dependent" encounter *AE-control*; dashed lines: "mating-system-dependent" encounter *ME-control*; (B) global mean mate encounter trait *gE* and corresponding encounter probability; (C) global mean competition trait *gC*; (D) mean adult sex ratio (ASR); (E) proportion of unmated females across the range. Dots represent coevolutionary simulations and triangles single trait evolution for comparison (gray: *E* or on x-axis: *C*). Dots/triangles and lines indicate the medians, while bars and shaded regions indicate the 95% central interval across 30 replicates. For visual aid, dashed lines indicate an equal sex ratio in (D) and 50% unmated females in (E). Other parameters: $\alpha = 1$.

costs of *C* markedly contracted the range limit, generally causing much narrower ranges than when *C* evolved alone. The magnitude of range reduction also depended on the costs of *E*, with decreasing costs contracting range limits and causing frequent collapse of the entire range (i.e., global extinction) for medium and low costs of *E*. Hence, when both traits evolved, decreasing costs of *E* had opposite effects on range limits under polygyny compared to monogamy (Figure 4A vs. Figure 5A).

Under polygyny, evolved global mean *gE* closely matched that arising when *E* evolved alone for all costs (Figure 5B). In contrast, global mean *gC* evolved to higher values than when *C* evolved alone. This indicates that the higher number of encountered females following evolution of higher *E* increased the strength of sexual selection on *C* (Figure 5C), especially under higher costs of competition and lower costs of mate encounter (i.e., more females encountered). Additionally, joint evolution changed the trait cline in subpopulation mean *gC* under polygyny and medium costs (Supplementary Figure S13E), which remained constant across the range instead of decreasing toward the margin as with single trait evolution (Supplementary Figure S11E). Joint evolution led to generally higher global mean *gC*, causing an extremely female-biased ASR with medium to high costs of *C* (Figure 5D). Despite this female bias, joint evolution of *C* and *E* under polygyny almost completely alleviated mate limitation across most parts of the range when costs of *E* were low, except for the very range edge. Furthermore, toward the range core, the proportion of unmated females was markedly reduced at high costs of *E* and compared to when only *C* evolved (Figure 5E). Thus, coevolving mate encounter *E* reduced the average proportion of unmated females across the last 20,000 generations. However, the extreme range contraction and collapse observed with increasing costs of *C* indicate that the extremely female-biased ASR also elevated vulnerability to extinction despite high mate encounter probability.

Effects of dispersal on emerging range limits

Range limits contracted with lower dispersal probability ($d = 0.001$, 0.01) for all evolutionary and nonevolutionary scenarios (Supporting Information S3). Hence, as expected, lower *d* reduced capacity for recolonization at the range margins. The effect of trait evolution on range limits remained qualitatively similar at lower *d* when only mate encounter *E* evolved and under monogamy when only competition trait C evolved. However, range limits markedly contracted at lower *d* when *C* evolved under polygyny, and the range completely collapsed when competition was strong and costs of *C* medium, which is when sexual selection was strongest. Additionally, joint evolution of *E* and *C* resulted in range collapse for a wider set of trait costs under lower *d* (Supporting Information S3), further indicating that evolutionary scenarios characterized by extremely female-biased ASR required relatively higher dispersal to buffer against the increased extinction risk.

Discussion

Our model reveals how sexual selection can affect species' range limits via the population-level consequences of evolving sexually selected traits, once population densities become low enough for mate limitation (and resulting component Allee effects) to impact extinction and colonization dynamics. Furthermore, the effects of sexual selection on range limits were highly dependent on the interactions between the mechanism (and hence form) of sexual selection, the overall mating system (monogamy vs. polygyny), and population density.

Range limits extended with sexual selection on a mate encounter trait, enhancing male efficiency at finding potential mates and thereby reducing mate limitation toward the range margins. Conversely, range limits contracted with sexual selection on a competition trait. Here, trait-dependent mortality increased in males, causing female-biased ASRs, and thereby increasing female mate limitation. Furthermore, when both traits coevolved, their combined effects on range limits depended on the mating system. Extended range limits under monogamy indicated that evolution of increased mate encounter compensated for evolution of the costly competition trait, particularly since competition is generally low under monogamy. However, under polygyny, sexual selection caused exaggerated evolution of the costly competition trait, generating highly female-biased ASRs. This increased the chance of evolutionary suicide for subpopulations, despite high mate encounter trait values among surviving males, ultimately causing range contraction or collapse.

Nonevolutionary models examining the consequences of mating system on mate-finding Allee effects predict polygyny to increase population establishment (Shaw et al., 2018) and prolong population persistence (Bessa-Gomes et al., 2004). Indeed, our nonevolutionary simulations without sexual selection (*AE*-control and *ME*-control scenarios) also generated extended range limits under polygyny. Our results thus emphasize that efforts to quantify the effects of the mating system on the evolution of range limits should explicitly consider eco-evolutionary dynamics arising from specific forms of sexual selection at the range margins, and the consequences for spatial population dynamics.

Forms of sexual selection

The functional relationships built into our current model imply that the marginal benefits of mate encounter become zero once all females within a patch can be encountered, beyond which there is no directional selection that could further increase the encounter trait E. Conversely, sexual selection arising from male competition or female choice depends on the relative difference between a male's and his competitors' values of the competition trait C, implying continued directional sexual selection. This difference in assumed functional relationships between male traits and mating success underpins the qualitatively different evolutionary trajectories of E and C and resulting range limits. At low costs, evolution of mate encounter proceeded until males encountered all females within the patch, but costs readily limited mate encounter evolution and did not produce strong trait-dependent male mortality. Hence, given our model assumptions, sexual selection on mate encounter did not produce ongoing evolution and was generally rather weak, likely because all encountered males had the same chances of successful mating. In contrast, the competition trait was under stronger directional sexual selection, depending on the strength of competition, causing ongoing exaggeration of the trait at low costs and driving increased male mortality at higher costs.

Our formulation of mate competition may particularly apply to traits used as weapons in male–male combat (Emlen, 2008; Rico-Guevara & Hurme, 2019), but may equally describe systems where females choose the most preferred male among a group of potential mates, such as in several lekking species (Jennions & Petrie, 1997). Nevertheless, different ways of modeling male competition or mate choice would likely change the trait's evolutionary trajectory. For instance, females may only be choosy until a fixed threshold is met (Jennions & Petrie, 1997), causing the marginal benefits of increasing competition trait values to diminish at some point, weakening the overall strength of sexual selection and yielding trajectories similar to how mate encounter is formulated in our current model. Nevertheless, in agreement with several other models of sexual selection that incorporate the demographic consequences of costly male traits, our model shows that ASR can become strongly female biased due to strong sexual selection, causing evolutionary suicide through increased male mortality (Kokko et al., 2002; Martínez-Ruiz & Knell, 2017; Tanaka, 1996; Tschol et al., 2022). Recently, Berec et al. (2018) modeled the evolution of a male mate-finding trait determining the probability of mate encounter, but female mating decision was additionally weighted by male phenotypes, effectively assuming that mate encounter and mate competition were mediated via the same trait. This created runaway selection of the male mate-finding trait and caused population extinction (Berec et al., 2018). Similarly, our results under joint trait evolution show that, given our assumed functional relationships between male traits and mating success, the negative population-level consequences of exaggerated sexual traits can outweigh any benefits accrued by decreasing mate limitation in the population.

Demographic stochasticity and density dependence of sexual selection

In our model, biotic range limits emerged from interactions between the mating system and sexual trait evolution shaping both the deterministic and stochastic components underlying population demography and dynamics (e.g., means and variances, respectively, underlying the probability distributions of male survival or male mate finding). While reductions in the deterministic growth rate, due to the exaggeration of costly traits, are a key driver for population extinction, demographic stochasticity has the potential to contribute to emerging range limits. We modeled an abiotic gradient in carrying capacity and hence local population sizes, where the risk of population extinction due to demographic stochasticity will generally increase in smaller populations toward the range margins (Gilpin, 1992; Lande et al., 2003). The overall magnitude and impact of demographic stochasticity will further depend, among other things, on combinations of the mating system and the ASR (Lee et al., 2011). Particularly, polygyny and a female-biased ASR may result in high demographic stochasticity, as successful mating of many females depends on a small number of males, where any random events that limit the mating ability of single males will have proportionally large effects on the population growth rate (Lee et al., 2011). The high probability of population extinction, and thus large range contractions, observed in our coevolutionary simulations under polygyny may thus stem from a low deterministic growth rate combined with substantial demographic stochasticity. While our current simulations do not explicitly distinguish the effects of deterministic and stochastic components on demography, future analysis of the evolutionary dynamics of demographic stochasticity would prove useful in understanding the complex relationship between different factors affecting population extinction and establishment.

Our results concur with recent work examining the effects of mating system and mate encounter on the density dependence of sexual selection (Berec et al., 2018; Watts et al., 2022). We show that the emergence of density-dependent sexual selection was determined by the combination of mating system and the mechanism of sexual selection. Under monogamy, both the encounter and competition traits increased toward the range margins, indicating negative density-dependent sexual selection arising from the benefits of securing a mating with rarely encountered females at low population densities. In contrast, polygyny caused generally higher investment in both traits throughout the range, frequently leading the competition trait to decrease toward the range margins, likely because of reduced scope for competition at lower population densities, and resulting positive density-dependent sexual selection. These results indicate that sexual selection across the range may importantly contribute to spatial patterns of sex-specific selection (De Lisle et al., 2018), causing the strength of overall selection to increase or decrease toward the range margins depending on the type of trait under selection and the mating system. Furthermore, the evolutionary history of sexual selection and range position might affect population responses to rapidly occurring human-induced abundance changes (Berec et al., 2018). For example, our results suggest that in monogamous species, marginal populations with an evolutionary history of sexual selection on mate encounter traits might better cope with the effects of habitat fragmentation in comparison to core populations. Similarly, polygynous species where sexual selection occurs via mate competition or mate choice may be more vulnerable to fragmentation when they occur at the core of a range, due to larger investment in costly competition traits.

Alignment of natural and sexual selection

Our current parameterizations assume that sexual selection pushes traits away from their naturally selected optima of zero. However, natural and sexual selection might align for some parts of the underlying genetic variation when sexually selected traits exhibit condition dependence (Rowe & Houle, 1996; Whitlock & Agrawal, 2009). Stronger sexual selection may then reduce genome-wide genetic load (Agrawal, 2001; Siller, 2001; Whitlock, 2000) by reducing accumulation and fixation of deleterious mutations in marginal populations (Henry et al., 2015; but see Tschol et al., 2023). Sex ratio biases caused by trait-dependent costs would then likely be weakened, and range contraction or collapse observed in some of our simulated scenarios could be halted or even reversed. Polygyny, by facilitating sexual selection, could then extend the range limits compared to monogamy. Additionally, sexual selection could further extend range limits by promoting local adaptation (Lorch et al., 2003). In contrast, increased mate encounter could decrease population fitness when there is sexual conflict over mating rate, and females are harmed during copulation or competitive interactions among males (Andersson, 1994; Arnqvist & Rowe, 2005). The effects of sexual selection on emerging range limits thus likely depend on genetic architecture, the level of condition and/or environmental dependence, and the potential for sexual conflict over mating, alongside the functional relationship between trait values and reproductive success.

Effects of dispersal

Lower dispersal probability contracted range limits. However, the magnitude of range contraction depended on the mechanism of sexual selection, the mating system, and trait costs. Particularly, higher dispersal probabilities buffered against range contractions when sexual selection drove evolution of exaggerated competition traits and extremely female-biased sex ratios. Such stabilizing effects of dispersal on metapopulations also arose in models studying range evolution emerging from limits to local adaptation (Polechová, 2018). Hence, our results predict that relatively philopatric species with elaborate but costly mate choice or male combat could be more likely to exhibit abrupt range limits. While we modeled dispersal as a nonevolving trait, selection toward the range margins may lead to increased or decreased dispersal depending on the degree of habitat availability (Travis & Dytham, 1999) and the type of gradient in habitat quality (Dytham, 2009). Dispersal may be selected against closer to the margins when habitat suitability changes abruptly (Dytham, 2009; Travis & Dytham, 1999), further contracting range limits of species with elaborate and costly competition traits. In contrast, our model assumed a linear gradient of decreasing habitat quality, where dispersal may increase closer to the range margins (Dytham, 2009). Additionally, free habitat patches resulting from evolutionary suicide of populations exhibiting elaborate sexually selected traits could also select for increased dispersal (Shaw & Kokko, 2015), such as otherwise expected under conditions of habitat turnover (Dytham, 2009), thus extending range limits under highly dynamic extinctions and recolonizations. The interplay between dispersal evolution and sexually selected traits will likely be complex and sexual selection may often be a prominent driver of dispersal-related traits itself (Li &

Kokko, 2019). Future work on range limits could therefore explicitly consider multiple traits determining mating success and their joint evolution with dispersal.

Implications

Our results suggest that considering sexual selection, and its feedback with population and range dynamics, can contribute to understanding global patterns of species' distributions. Species' range sizes tend to be smaller at lower latitudes (Rapoport, 1982; Stevens, 1989), which could partly reflect stronger sexual selection in the tropics. For example, experimental work comparing the strength of sexual selection in different populations of the freshwater fish, *Oryzias latipes*, demonstrated stronger sexual selection at lower latitudes (Fujimoto et al., 2015; Sasaki & Yamahira, 2016). Furthermore, both interpopulation and phylogenetic comparative studies among vertebrate and invertebrate species also suggest stronger sexual selection in the tropics compared to temperate regions, based on indirect measures such as degree of sexual dimorphism or mating system characteristics (Blanckenhorn et al., 2006; Dale et al., 2015; Matsumura et al., 2023; Murray et al., 2021; Sumarto et al., 2020; but see Cardillo, 2002). Yet, while stronger sexual selection might regularly occur in the tropics (Macedo & Machado, 2013), only a single comparative study has considered a direct link between sexual selection and range size. Cally et al. (2021) used phylogenetic path analysis to investigate drivers of speciation in birds and found no effect of sexual selection on range size. However, given that our model predicts contrasting effects on range limits under different mechanisms of sexual selection, we advocate for further comparative studies that explicitly investigate the complex and potentially contrasting effects of sexual selection on range size. More generally, our work emphasizes that better evolutionary understanding of species' ranges will require linking the causes and consequences of sexual selection and other sources of intraspecific selection to the spatial population dynamics across species' ranges.

Supplementary material

Supplementary material is available online at *Evolution*.

Data availability

Software code is publicly available via a Zenodo repository at https://doi.org/10.5281/zenodo.8335029. Simulation output is available via a Dryad repository at https://doi.org/10.5061/dryad.2547d7wzz, and processing and data visualizing scripts are available via https://zenodo.org/records/10702090.

Author contributions

M.T.: Conceptualization; Formal analysis; Investigation; Methodology; Software; Validation; Visualization; Writing—original draft; Writing—review & editing. G.B.: Conceptualization; Funding acquisition; Investigation; Methodology; Software; Supervision; Validation; Writing—review & editing. J.M.R.: Conceptualization; Funding acquisition; Investigation; Methodology; Supervision; Validation; Writing—review & editing.

Funding

M.T. and G.B. were funded by the Royal Society through G.B.'s University Research Fellowship (UF160614) and Research Fellows Enhancement Award (RGF\EA\180184). J.M.R. was supported by Research Council of Norway (SFF-III, project 223257) and NTNU.

Conflict of interest: The authors declare no conflict of interest.

Acknowledgments

We thank Luke Holman and Natalie Pilakouta for insightful comments that improved the manuscript draft. Simulations were performed using the Maxwell Computing Cluster at the University of Aberdeen.

References

Agrawal, A. F. (2001). Sexual selection and the maintenance of sexual reproduction. *Nature*, *411*(6838), 692–695. https://doi.org/10.1038/35079590

Alexander, J. M., Atwater, D. Z., Colautti, R. I., & Hargreaves, A. L. (2022). Effects of species interactions on the potential for evolution at species' range limits. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, *377*, 0020. https://doi.org/10.1098/rstb.2021.0020

Andersson, M. B. (1994). *Sexual selection*. Princeton University Press.

Arnqvist, G., & Rowe, L. (2005). *Sexual conflict. Monographs in behavior and ecology*. Princeton University Press.

Benton, T. G., & Evans, M. R. (1998). Measuring mate choice using correlation: The effect of female sampling behaviour. *Behavioral Ecology and Sociobiology*, *44*(2), 91–98. https://doi.org/10.1007/s002650050520

Berec, L. (2018). Mate search and mate-finding Allee effect: On modeling mating in sex-structured population models. *Theoretical Ecology*, *11*(2), 225–244. https://doi.org/10.1007/s12080-017-0361-0

Berec, L., Kramer, A. M., Bernhauerová, V., & Drake, J. M. (2018). Density-dependent selection on mate search and evolution of Allee effects. *The Journal of Animal Ecology*, *87*(1), 24–35. https://doi.org/10.1111/1365-2656.12662

Bessa-Gomes, C., Legendre, S., & Clobert, J. (2004). Allee effects, mating systems and the extinction risk in populations with two sexes. *Ecology Letters*, *7*, 802–812. https://doi.org/10.1111/j.1461-0248.2004.00632.x

Blanckenhorn, W. U., Stillwell, R. C., Young, K. A., Fox, C. W., & Ashton, K. G. (2006). When Rensch meets Bergman: Does sexual size dimorphism change systematically with latitude? *Evolution*, *60*(10), 2004–2011. https://doi.org/10.1111/j.0014-3820.2006.tb01838.x

Bocedi, G., & Reid, J. M. (2015). Evolution of female multiple mating: A quantitative model of the "sexually selected sperm" hypothesis. *Evolution*, *69*(1), 39–58. https://doi.org/10.1111/evo.12550

Cally, J. G., Stuart-Fox, D., Holman, L., Dale, J., & Medina, I. (2021). Male-biased sexual selection, but not sexual dichromatism, predicts speciation in birds. *Evolution*, *75*(4), 931–944. https://doi.org/10.1111/evo.14183

Cardillo, M. (2002). The life-history basis of latitudinal diversity gradients: How do species traits vary from the poles to the equator? *Journal of Animal Ecology*, *71*, 79–87. https://doi.org/10.1046/j.0021-8790.2001.00577.x

Carter, R. N., & Prince, S. D. (1981). Epidemic models used to explain biogeographical distribution limits. *Nature*, *293*(5834), 644–645. https://doi.org/10.1038/293644a0

Case, T. J., Holt, R. D., McPeek, M. A., & Keitt, T. H. (2005). The community context of species' borders: Ecological and evolutionary perspectives. *Oikos*, *108*(1), 28–46. https://doi.org/10.1111/j.0030-1299.2005.13148.x

Dale, J., Dey, C. J., Delhey, K., Kempenaers, B., & Valcu, M. (2015). The effects of life history and sexual selection on male and female plumage colouration. *Nature*, *527*(7578), 367–370. https://doi.org/10.1038/nature15509

De Lisle, S. P., Goedert, D., Reedy, A. M., & Svensson, E. I. (2018). Climatic factors and species range position predict sexually antagonistic selection across taxa. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, *373*(1757), 20170415. https://doi.org/10.1098/rstb.2017.0415

Dytham, C. (2009). Evolved dispersal strategies at range margins. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, *276*(1661), 1407–1413. https://doi.org/10.1098/rspb.2008.1535

Emlen, D. (2008). The evolution of animal weapons. *Annual Review of Ecology, Evolution, and Systematics*, *39*(1), 387–413. https://doi.org/10.1146/annurev.ecolsys.39.110707.173502

Fromhage, L., Jennions, M., & Kokko, H. (2016). The evolution of sex roles in mate searching. *Evolution*, *70*(3), 617–624. https://doi.org/10.1111/evo.12874

Fujimoto, S., Miyake, T., & Yamahira, K. (2015). Latitudinal variation in male competitiveness and female choosiness in a fish: Are sexual selection pressures stronger at lower latitudes? *Evolutionary Biology*, *42*(1), 75–87. https://doi.org/10.1007/s11692-014-9300-9

Gascoigne, J., Berec, L., Gregory, S., & Courchamp, F. (2009). Dangerously few liaisons: A review of mate-finding Allee effects. *Population Ecology*, *51*(3), 355–372. https://doi.org/10.1007/s10144-009-0146-4

Gilpin, M. (1992). Demographic stochasticity: A Markovian approach. *Journal of Theoretical Biology*, *154*(1), 1–8. https://doi.org/10.1016/s0022-5193(05)80183-3

Henry, R. C., Bartoń, K. A., & Travis, J. M. J. (2015). Mutation accumulation and the formation of range limits. *Biology Letters*, *11*(1), 20140871. https://doi.org/10.1098/rsbl.2014.0871

Holt, R. D., & Keitt, T. H. (2000). Alternative causes for range limits: A metapopulation perspective. *Ecology Letters*, *3*(1), 41–47. https://doi.org/10.1046/j.1461-0248.2000.00116.x

Holt, R. D., Knight, T. M., & Barfield, M. (2004). Allee effects, immigration, and the evolution of species' niches. *The American Naturalist*, *163*(2), 253–262. https://doi.org/10.1086/381408

Hunt, J., Breuker, C. J., Sadowski, J. A., & Moore, A. J. (2009). Male-male competition, female mate choice and their interaction: Determining total sexual selection. *Journal of Evolutionary Biology*, *22*(1), 13–26. https://doi.org/10.1111/j.1420-9101.2008.01633.x

Jennions, M. D., & Petrie, M. (1997). Variation in mate choice and mating preferences: A review of causes and consequences. *Biological Reviews of the Cambridge Philosophical Society*, *72*(2), 283–327. https://doi.org/10.1017/s0006323196005014

Keitt, T. H., Lewis, M. A., & Holt, R. D. (2001). Allee effects, invasion pinning, and species' borders. *The American Naturalist*, *157*(2), 203–216. https://doi.org/10.1086/318633

Kimura, M. (1965). A stochastic model concerning the maintenance of genetic variability in quantitative characters. *Proceedings of the National Academy of Sciences of the United States of America*, *54*(3), 731–736. https://doi.org/10.1073/pnas.54.3.731

Kirkpatrick, M., & Barton, N. H. (1997). Evolution of a species' range. *The American Naturalist*, *150*(1), 1–23. https://doi.org/10.1086/286054

Klug, H., Langley, C., & Reyes, E. (2019). 2022 Cascading effects of pre-adult survival on sexual selection. *Royal Society Open Science*, *9*, 73. https://doi.org/10.1098/rsos.211973

Kokko, H., & Brooks, R. (2003). Sexy to die for? Sexual selection and the risk of extinction. *Annales Zoologici Fennici*, *40*, 207–219.

Kokko, H., Brooks, R., McNamara, J. M., & Houston, A. I. (2002). The sexual selection continuum. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, *269*(1498), 1331–1340. https://doi.org/10.1098/rspb.2002.2020

Kokko, H., Jennions, M. D., & Brooks, R. (2006). Unifying and testing models of sexual selection. *Annual Review of Ecology, Evolution, and Systematics*, *37*(1), 43–66. https://doi.org/10.1146/annurev.ecolsys.37.091305.110259

Kokko, H., Klug, H., & Jennions, M. D. (2012). Unifying cornerstones of sexual selection: Operational sex ratio, Bateman gradient and the scope for competitive investment. *Ecology Letters*, *15*(11), 1340–1351. https://doi.org/10.1111/j.1461-0248.2012.01859.x

Kokko, H., & Rankin, D. J. (2006). Lonely hearts or sex in the city? Density-dependent effects in mating systems. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, *361*(1466), 319–334. https://doi.org/10.1098/rstb.2005.1784

Kotiaho, J. S. (2001). Costs of sexual traits: A mismatch between theoretical considerations and empirical evidence. *Biological Reviews of the Cambridge Philosophical Society*, *76*(3), 365–376. https://doi.org/10.1017/s1464793101005711

Lande, R. (1981). Models of speciation by sexual selection on polygenic traits. *Proceedings of the National Academy of Sciences of the United States of America*, *78*(6), 3721–3725. https://doi.org/10.1073/pnas.78.6.3721

Lande, R., Engen, S., & Saether, B.-E. (2003). *Stochastic population dynamics in ecology and conservation*. Oxford University Press.

Lee, A. M., Saether, B. -E., & Engen, S. (2011). Demographic stochasticity, Allee effects, and extinction: The influence of mating system and sex ratio. *The American Naturalist*, *177*(3), 301–313. https://doi.org/10.1086/658344

Lennon, J. J., Turner, J. R. G., & Connell, D. (1997). A metapopulation model of species boundaries. *Oikos*, *78*(3), 486. https://doi.org/10.2307/3545610

Li, X. -Y., & Kokko, H. (2019). Sex-biased dispersal: A review of the theory. *Biological Reviews of the Cambridge Philosophical Society*, *94*(2), 721–736. https://doi.org/10.1111/brv.12475

Liker, A., Bókony, V., Pipoly, I., Lemaître, J. -F., Gaillard, J. -M., Székely, T., & Freckleton, R. P. (2021). Evolution of large males is associated with female-skewed adult sex ratios in amniotes. *Evolution*, *75*(7), 1636–1649. https://doi.org/10.1111/evo.14273

Lorch, P. D., Proulx, S. R., Rowe, L., & Day, T. (2003). Condition-dependent sexual selection can accelerate adaptation. *Evolutionary Ecology Research*, *5*, 867–881.

Macedo, R. H., & Machado, G. (2013). *Sexual selection: Perspectives and models from the Neotropics* (R. H. Macedo & G. Machado, Eds.). Academic Press.

Martínez-Ruiz, C., & Knell, R. J. (2017). Sexual selection can both increase and decrease extinction probability: Reconciling demographic and evolutionary factors. *The Journal of Animal Ecology*, *86*(1), 117–127. https://doi.org/10.1111/1365-2656.12601

Martinossi-Allibert, I., Rueffler, C., Arnqvist, G., & Berger, D. (2019). The efficacy of sexual selection under environmental change. *Proceedings of the Royal Society B: Biological Sciences*, *286*, 20182313. https://doi.org/10.1098/rspb.2018.2313

Matsumura, K., Wakabayashi, K., Kawakami, R., & Miyatake, T. (2023). Latitudinal cline in reproductive traits in the red flour beetle *Tribolium castaneum*. *Behavioral Ecology and Sociobiology*, *77*(7), 77. https://doi.org/10.1007/s00265-023-03359-x

Moore, A. J., McGlothlin, J. W., & Wolf, J. B. (2022). Runaway evolution from male-male competition. *Ecology Letters*, *25*(2), 295–306. https://doi.org/10.1111/ele.13921

Muniz, D. G., & Machado, G. (2018). Mate sampling influences the intensity of sexual selection and the evolution of costly sexual ornaments. *Journal of Theoretical Biology*, *447*, 74–83. https://doi.org/10.1016/j.jtbi.2018.03.026

Murphy, C. G. (1998). Interaction-independent sexual selection and the mechanisms of sexual selection. *Evolution*, *52*(1), 8–18. https://doi.org/10.1111/j.1558-5646.1998.tb05133.x

Murray, C. M., McMahan, C. D., Litmer, A. R., Goessling, J. M., & Siegel, D. (2021). Latitudinal gradients in sexual dimorphism: Alternative hypotheses for variation in male traits. *Ecology and Evolution*, *11*(23), 17519–17526. https://doi.org/10.1002/ece3.8386

Paquette, A., & Hargreaves, A. L. (2021). Biotic interactions are more often important at species' warm versus cool range edges. *Ecology Letters*, *24*(11), 2427–2438. https://doi.org/10.1111/ele.13864

Polechová, J. (2018). Is the sky the limit? On the expansion threshold of a species' range. *PLoS Biology*, *16*(6), e2005372. https://doi.org/10.1371/journal.pbio.2005372

Polechová, J., & Barton, N. H. (2015). Limits to adaptation along environmental gradients. *Proceedings of the National Academy of Sciences of the United States of America*, *112*(20), 6401–6406. https://doi.org/10.1073/pnas.1421515112

Price, T. D., & Kirkpatrick, M. (2009). Evolutionarily stable range limits set by interspecific competition. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, *276*(1661), 1429–1434. https://doi.org/10.1098/rspb.2008.1199

Promislow, D. E. (1992). Costs of sexual selection in natural populations of mammals. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, *247*, 203–210. https://doi.org/10.1098/rspb.1992.0030

Rapoport, E. H. (1982). *Areography: Geographical strategies of species* (The Fundación Bariloche series; E. H. Rapoport, Ed.; B. Drausal, Trans.). Fundación Bariloche by Pergamon Press.

Rico-Guevara, A., & Hurme, K. J. (2019). Intrasexually selected weapons. *Biological Reviews of the Cambridge Philosophical Society*, *94*(1), 60–101. https://doi.org/10.1111/brv.12436

Rowe, L., & Houle, D. (1996). The lek paradox and the capture of genetic variance by condition dependent traits. *Proceedings of the Royal Society of London, Series B: Biological Series*, *263*, 1415–1421. https://doi.org/10.1098/rspb.1996.0207

Sasaki, T., & Yamahira, K. (2016). Variation in male courtship activeness between latitudinal populations of Northern medaka. *Ichthyological Research*, *63*(2), 302–306. https://doi.org/10.1007/s10228-015-0484-5

Shaw, A. K., & Kokko, H. (2015). Dispersal evolution in the presence of Allee effects can speed up or slow down invasions. *The American Naturalist*, *185*(5), 631–639. https://doi.org/10.1086/680511

Shaw, A. K., Kokko, H., & Neubert, M. G. (2018). Sex difference and Allee effects shape the dynamics of sex-structured invasions. *The Journal of Animal Ecology*, *87*(1), 36–46. https://doi.org/10.1111/1365-2656.12658

Shuster, S. M., & Wade, M. J. (2003). *Mating systems and strategies. Monographs in behavior and ecology*. Princeton University Press.

Siller, S. (2001). Sexual selection and the maintenance of sex. *Nature*, *411*(6838), 689–692. https://doi.org/10.1038/35079578

Somjee, U. (2021). Positive allometry of sexually selected traits: Do metabolic maintenance costs play an important role? *BioEssays*, *43*(6), e2000183. https://doi.org/10.1002/bies.202000183

Stephens, P. A., Sutherland, W. J., & Freckleton, R. P. (1999). What is the Allee effect? *Oikos*, *87*(1), 185. https://doi.org/10.2307/3547011

Stevens, G. C. (1989). The latitudinal gradient in geographical range: How so many species coexist in the tropics. *The American Naturalist*, *133*(2), 240–256. https://doi.org/10.1086/284913

Sumarto, B. K. A., Kobayashi, H., Kakioka, R., Tanaka, R., Maeda, K., Tran, H. D., Koizumi, N., Morioka, S., Bounsong, V., Watanabe, K., Musikasinthorn, P., Tun, S., Yun, L. K. C., Anoop, V. K., Raghavan, R., Masengi, K. W. A., Fujimoto, S., & Yamahira, K. (2020). Latitudinal variation in sexual dimorphism in a freshwater fish group. *Biological Journal of the Linnean Society*, *131*(4), 898–908. https://doi.org/10.1093/biolinnean/blaa166

Svenning, J. -C., Gravel, D., Holt, R. D., Schurr, F. M., Thuiller, W., Münkemüller, T., Schiffers, K. H., Dullinger, S., Edwards, T. C., Hickler, T., Higgins, S. I., Nabel, J. E. M. S., Pagel, J., & Normand, S. (2014). The influence of interspecific interactions on species range expansion rates. *Ecography*, *37*(12), 1198–1209. https://doi.org/10.1111/j.1600-0587.2013.00574.x

Székely, T., Liker, A., Freckleton, R. P., Fichtel, C., & Kappeler, P. M. (2014). Sex-biased survival predicts adult sex ratio variation in wild birds. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, *281*, 0342. https://doi.org/10.1098/rspb.2014.0342

Tanaka, Y. (1996). Sexual selection enhances population extinction in a changing environment. *Journal of Theoretical Biology*, *180*(3), 197–206. https://doi.org/10.1006/jtbi.1996.0096

Travis, J. M. J., & Dytham, C. (1999). Habitat persistence, habitat availability and the evolution of dispersal. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, *266*(1420), 723–728. https://doi.org/10.1098/rspb.1999.0696

Tschol, M., Reid, J. M., & Bocedi, G. (2022). Strong spatial population structure shapes the temporal coevolutionary dynamics of costly female preference and male display. *Evolution*, *76*(3), 636–648. https://doi.org/10.1111/evo.14426

Tschol, M., Reid, J. M., & Bocedi, G. (2023). Environmental variance in male mating success modulates the positive versus negative impacts of sexual selection on genetic load. *Journal of Evolutionary Biology*, *36*(9), 1242–1254. https://doi.org/10.1111/jeb.14202

Watts, J. C., Hebets, E. A., & Tenhumberg, B. (2022). Mate sampling behavior determines the density dependence of sexual selection. *The American Naturalist*, *200*(4), 467–485. https://doi.org/10.1086/720716

Whitlock, M. C. (2000). Fixation of new alleles and the extinction of small populations: Drift load, beneficial alleles, and sexual selection. *Evolution*, *54*(6), 1855–1861. https://doi.org/10.1111/j.0014-3820.2000.tb01232.x

Whitlock, M. C., & Agrawal, A. F. (2009). Purging the genome with sexual selection: Reducing mutation load through selection on males. *Evolution*, *63*(3), 569–582. https://doi.org/10.1111/j.1558-5646.2008.00558.x

Wiens, J. J., & Tuschhoff, E. (2020). Songs versus colours versus horns: What explains the diversity of sexually selected traits? *Biological Reviews of the Cambridge Philosophical Society*, *95*(4), 847–864. https://doi.org/10.1111/brv.12593