

Sexual dimorphism driven by intersexual resource competition: Why is it rare, and where to look for it?

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Abstract

1. Sexes often differ more obviously in secondary sexual characteristics than in traits that appear naturally selected, despite conceivable benefits to intersexual niche partitioning. Genetic constraints may play a role in limiting sex-specific niche evolution; however, it is not clear why this limit should apply to naturally selected traits more than those under sexual selection; the latter routinely produces dimorphism. We ask whether ecological factors and/or features of the mating system limit dimorphism in resource use, or conversely, what conditions are the most permissible ones for sexual niche differences.
2. The scale of mating competition and spatial variation in resource availability can help predict sexually dimorphic niches or the lack thereof. We investigate why and when dimorphism might fail to evolve even if genetic covariation between the sexes posed no constraint.
3. Our analytical model incorporates the first aspect of spatial interactions (scale of mating competition). It is followed by simulations that explore broader conditions, including multiple resources with habitat heterogeneity, genetic correlations and non-Gaussian resource-use efficiency functions.
4. We recover earlier known conditions for favourable conditions for the evolution of niche partitioning between sexes, such as narrow individual niche and low degrees of genetic constraint. We also show spatial considerations to alter this picture. Sexual niche divergence occurs more readily when local mating groups are small and different resources occur reliably across habitats. Polygyny (medium-sized or large mating groups) can diminish the prospects for dimorphism even if no genetic constraints are present. Habitat heterogeneity typically also disfavours niche dimorphism but can also lead to polymorphism within a sex, if it is beneficial to specialize to be very competitive in one habitat, even at a cost to performance in the other.
5. Sexual conflict is usually used to explain dimorphic traits or behaviours. Our models highlight that introducing conflict (achieved by switching from monogamy to polygamy) can also be responsible for sexual monomorphism. Under monogamy, males benefit from specializing to consume other resources than what feeds the

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female best. Polygyny makes males disregard this female benefit, and both sexes compete for the most profitable resource, leading to overlapping niches.

KEYWORDS

bet-hedging, ecological character displacement, intersexual resource competition, mating system, niche partitioning, polymorphism, sexual dimorphism

1 | INTRODUCTION

Sexual dimorphism is widespread in animals: male and female animals can differ in size, colouration, ornaments and behaviour (Hedrick & Temeles, 1989; Karp et al., 2017; Ralls, 1977; Shine, 1989). While the causal role of sexual selection in driving sexual dimorphism is undisputed with abundant examples (Fairbairn et al., 2007; Székely et al., 2000), natural selection is less often evoked to explain sexually dimorphic traits. A typical model of niche evolution, for example, will not distinguish the sexes at all (original research: Ackermann & Doebeli, 2004; Bourne et al., 2014; Büchi & Vuilleumier, 2012; Débarre & Gandon, 2010; Qiao et al., 2016; Ravné et al., 2009; Vasconcelos & Rueffler, 2020; reviews: Holt, 2009; Morris, 2011) while a model of sexual selection that did not permit traits to become sexually dimorphic is nearly inconceivable.

Does the above difference between the conceived importance of natural and sexual selection on the evolution of sexual dimorphism reflect a mere difference in modelling tradition, or is the impression that the two sexes rarely differ in their niches a true reflection of reality? Most species indeed appear to use, broadly speaking, the same ecological niche, but here 'broad' has to be interpreted in the sense that a detailed look may reveal differences. For example, in cormorants (Quintana et al., 2011) and albatrosses (Patrick & Weimerskirch, 2014), both sexes are predators of fish, but males and females differ in foraging areas. The most obvious explanations for significant niche overlap between the sexes are that (a) since the environment is shared by both sexes at least at birth and at mating, this limits the possibility for utilizing dramatically different habitats at other times, which results in the absence of sexually divergent selection on traits that are relevant for niche evolution, (b) the two sexes share most parts of the genome; therefore, a similar phenotype is logically the default (and can prevent sexually dimorphic niches from evolving; Slatkin, 1984).

There are at least two reasons, one based on eco-evolutionary and the other on 'evo-devo' (developmental) considerations, why it would be unsatisfactory to leave the issue at that. We describe the eco-evolutionary reason first. Although shared environments (due to species range being identical for males and females) and genetic constraints combine to a null hypothesis of little or no sexual dimorphism in niche use, this null expectation also has to be pitted against a counterargument that would appear to predict the opposite. In an interspecific context, niche diversification is a very powerful mechanism to reduce resource competition (it is one of the classic principles in evolutionary ecology; MacArthur & Levins, 1967). If coexistence of different species is clearly helped by divergence to

utilize different resource, why should males and females of a single species not be observed to do the same? Slatkin (1984) was the first to highlight the analogy between interspecific and intersexual competition. His modelling was inspired by Lotka–Volterra competition between two species, but the 'species' were now males and females, which adds the possibility of genetic correlations between them. Genetic correlations only sometimes affected his model results, and he generally concluded that it is an open question whether competition for a limiting resource can account for observed sexual dimorphism.

Later work has added the possibility for the population to specialize instead of, or in addition to, becoming sexually dimorphic. The question is now rephrased as whether sex differences could, in some sense, substitute for evolutionary branching of a single population to yield two species (Van Dooren et al., 2004). Due to a focus on speciation, the emergence of assortative mating is of key interest in these models, as assortativeness keeps incipient species separated and allows them to evolve towards different resource peaks (Dieckmann & Doebeli, 1999; Geritz & Kisdi, 2000). Sexual dimorphism and adaptive speciation indeed appear to offer two alternative solutions to the same adaptive problem (Bolnick & Doebeli, 2003). They may also co-occur rather than one completely pre-empting the need for the other (Cooper et al., 2011; De Lisle & Rowe, 2017).

We now turn to the other, developmental, reason to not rely on the genetic constraint argument as a blanket explanation for absent or mild niche dimorphism. Constraints might impact any trait, but they sometimes do and sometimes do not appear to prevent the generation of very different phenotypes from a single gene pool. Any metamorphosing species is able to build very different bodies sequentially during ontogeny. More pertinently for the current context, no one expresses surprise at sexual dimorphism evolving when sexual selection is the underlying causality (despite intralocus sexual conflict having the potential to persist for very long; Ruzicka et al., 2019). This suggests that the difference between the typical outcome of natural selection (modest sexual dimorphism) and sexual selection (obvious sexual dimorphism) is real. Indeed, a recent review was able to find only few very clear examples of sexual dimorphism *caused by* intersexual resource competition (De Lisle, 2019).

As pointed out in De Lisle (2019) and Shine (1989), even in species with evident sexual differences in trophic morphology (which often implies ecological niche divergence; Fryxell et al., 2019), the observed sexual dimorphism is not necessarily causally attributable to intersexual resource competition. For example, body size generally impacts diet in fishes, but sexual size dimorphism is often easier to relate to sexual selection (Fleming & Gross, 1994)

or different sex roles in reproduction, such as mouthbrooding impacting the morphology of the mouth region (Ronco et al., 2019). Niche divergence may thus have evolved as a consequence of sexual selection, or could reflect feedback between sexual selection and resource competition (see Krüger et al., 2014 for a pinniped example).

Beyond a relative dearth of research effort and methodological difficulties in detecting sexual dimorphism driven by resource competition (De Lisle, 2019), we still lack a clear explanation for its relative rarity. Instead of continuing on the trajectory of speciation versus sexual dimorphism (with the complication of assortative mating), we here return to Shine's (1989) approach of a single-species setting, for it allows us to highlight, and model, two spatial aspects of intersexual resource competition that are missing from the theoretical base so far. The first spatial aspect reflects the scale of local versus global mating competition in the population, and we show it to modulate the extent to which sexual conflict prevails or is resolved. In an extremely local case, reproduction happens in monogamous pairs, there is little conflict, and reproductive output of the pair is maximized if resources are shared in a manner that maximally benefits female fecundity. When the male competes with many others over a large number of females (a more global setting), such a resolution of conflict becomes unlikely, and we show increasing conflict to lead to less dimorphism—a perhaps surprising outcome, given that sexual conflict is usually seen as a force promoting dimorphism. The second factor relates to the necessity that the two sexes have to meet (at least during some part of their life cycle) for sexual reproduction to occur. If sexes are highly divergent in their resource requirements, it is plausible that spatial variation in resource availability creates sites where only one sex can thrive. As this could make extensive sexual dimorphism suboptimal, we consider spatial variation in the availability of distinct resource types, to ask to what extent this limits the evolution of sexual dimorphism.

2 | METHODS AND RESULTS

We use two mathematical models to study the evolution of sexual dimorphism under intersexual resource competition. Our first analytical model includes one aspect of space (the population is split into mating groups of finite size) but does not consider habitat heterogeneity. To guarantee analytical tractability, we assume that the resource replenishment rate, trait distribution within each sex and the resource-use efficiency functions are all Gaussian. Doing so allows the subsequent analysis to take the advantage of a convolution of two Gaussian functions again being a Gaussian function. These convenient properties, however, are associated with an inherent danger of producing structurally unstable results (Gyllenberg & Meszena, 2005; Hernandez-Garcıa et al., 2009). To mitigate this and to relax the assumption of no spatial variability in resources, we also built a second, individual-based simulation model.

In both models, a continuous variable x describes a property (e.g. seed size) of each resource item arranged along a one-dimensional

axis. We consider the replenishment rate of resources explicitly and assume that the replenishment rate differs from resources of different x . In the simulation model, the resource replenishment rate can also differ between sites. Consumers (males and females) possess a trait z , such as body size or bill size, that gives them different efficiencies at extracting energy from resources of different x values. Without loss of generality, we assume that efficiency is maximized when $z = x$.

2.1 | The analytical model

Here we only present the most essential parts of the model: the incorporation of different spatial scales at which males and females interact (i.e. group size), and the interdependency of female and male fitness. The detailed description and analysis of the full model is presented in Appendix A.

We model a population of individuals competing for resources and reproduction opportunities in groups of size $2M$, with equal numbers of males and females (thus $M = 1$ implies monogamy). Resource of size x is replenished at a rate

$$r(x) = \frac{1}{\sigma_r \sqrt{2\pi}} \text{Exp} \left(\frac{-|x - \mu_r|^{2+\epsilon_r}}{2\sigma_r^{2+\epsilon_r}} \right), \quad (1)$$

which is a normal distribution with mean μ_r and variance σ_r^2 when the shape parameter $\epsilon_r = 0$. The shape of the distribution is more peaked or flat around $x = \mu_r$ when ϵ_r takes other values. The amount of resources each individual can obtain from the environment determines their condition. The efficiency γ of consuming resources of different sizes depends on the match between an individual's trait z and the size of resource item x following Equation (2), where g_0 is a species-wide constant, σ_γ represents the niche width of each individual, with larger values implying a broader niche, and ϵ_γ adjusts how quickly the resource consuming efficiency decreases within the individual niche as x and z deviate from each other.

$$\gamma(z, x) = g_0 \text{Exp} \left(\frac{-|z - x|^{2+\epsilon_\gamma}}{2\sigma_\gamma^{2+\epsilon_\gamma}} \right). \quad (2)$$

Males compete for fertilizations within the local group such that their condition relative to the local competitors determines paternity. Female reproduction, on the other hand, depends on their absolute condition (while being based on local resource availability): we assume that offspring production is condition-dependent and that the offspring join a global pool. The scale of competition thus combines local and global aspects for females. Note that since resource use is local for both sexes, a male whose trait value is suboptimal for the purpose of acquiring resources might nevertheless enjoy a fitness advantage, if there is a causal link between resources left by this male and the condition of females who produce offspring sired by him. However, this advantage may not be realized if his suboptimal condition means meagre siring prospects in the presence of other local males.

We are interested in the fitness of a female/male mutant with trait value deviating from the other females/males in the population. Assuming that mutants are rare, we consider three different types of local groups: (a) with one single female mutant (and $M - 1$ wild-type females as well as M wild-type males); (b) with one single male mutant (and $M - 1$ wild-type males as well as M wild-type females) and (c) with only wild-type individuals (M of each sex). We use sub- and superscripts to denote the condition of different individuals in different groups: the female-mutant group has individuals with condition c_{Gf}^{fMut} , c_{Gf}^{fWT} and c_{Gf}^{mWT} indicating the female mutant, a wild-type female of which there are zero or more, and a wild-type male of which there are one or more, respectively; the male-mutant group consists of individuals with condition c_{Gm}^{mMut} , c_{Gm}^{mWT} and c_{Gm}^{fWT} (one mutant male, zero or more wild-type males, one or more wild-type females); and groups without mutants, the number of wild-type males and females are equal, with condition values given by c_{G0}^{mWT} and c_{G0}^{fWT} , respectively.

Condition of every individual type is determined through local competition (see Appendix A for details). Females use their condition to produce young, and fitness has to be evaluated globally because offspring produced compete in the entire global population. Thus, the fitness of a female mutant, W_f^{Mut} , contrasts her offspring production with that of an average female in groups without mutants (since these females greatly outnumber the focal females' direct competitors in the same local patch). The relationship between condition and offspring production may be nonlinear. The formulation

$$W_f^{Mut} = \frac{(c_{Gf}^{fMut})^\beta}{(c_{G0}^{fWT})^\beta} = \left(\frac{c_{Gf}^{fMut}}{c_{G0}^{fWT}} \right)^\beta, \quad (3)$$

captures these effects, with parameter β determining how strongly the fecundity of females depends on their relative condition. The limit $\beta \rightarrow \infty$ describes a (biologically unlikely) 'winner takes all' situation, where a single female of higher than average condition mothers all offspring in the next generation; when $\beta = 1$, offspring production is proportional to condition; $\beta < 1$ predicts offspring production to be a decelerating function of condition, and finally, $\beta = 0$ assumes that all females have equal fecundity despite their different condition.

The fitness of a mutant male obeys a more complicated equation because the offspring production of a male depends both on his competitiveness relative to other local males and also on the productivity of local females (Equation 1). We model the fitness of a male mutant as

$$W_m^{Mut} = \begin{cases} \left(\frac{c_{Gm}^{mMut}}{c_{Gm}^{mWT}} \right)^\alpha \left(\frac{c_{Gm}^{fWT}}{c_{G0}^{fWT}} \right)^\beta & \text{if } M > 1 \\ \left(\frac{c_{Gm}^{fWT}}{c_{G0}^{fWT}} \right)^\beta & \text{if } M = 1 \end{cases}, \quad (4)$$

where α denotes the intensity of local mating competition on males. Note that in the case of monogamy, there is no competition between males; thus, the term with the α disappears and male fitness equals his female partner's fitness. Following Rankin et al. (2011), the exponents

α and β (in their model, u) reflect the extent to which a locally (for males) or globally (for females) superior individual enjoys disproportionately high fitness. Typically, $\alpha > \beta > 0$, if sexual selection acting on males is strong, but the model allows us to examine alternative choices too.

The coevolution of male and female traits can be tracked by comparing the fitness of a male/female mutant with an average wild-type individual of the same sex. If a male mutant with a positive trait deviation δ has higher fitness than an average male in the population, the mean trait of males will increase in the next generation, following the dynamics of mean trait values of males (μ_m) and females (μ_f) as

$$\begin{aligned} \mu_m(t+1) &= \mu_m(t) + \frac{h}{2} \frac{\partial W_m^{Mut}(\delta, \alpha, \beta, \mu_f(t), \mu_m(t))}{\partial \delta}, \\ \mu_f(t+1) &= \mu_f(t) + \frac{h}{2} \frac{\partial W_f^{Mut}(\delta, \beta, \mu_f(t), \mu_m(t))}{\partial \delta}, \end{aligned} \quad (5)$$

where the constant $0 < h \ll 1$ controls the speed of trait evolution in response to selection, and the division by two considers that the trait is expressed either in males or females (half of the population). Assuming that ecological process (i.e. resource replenishment and consumption dynamics) happen at much faster time-scales than evolutionary processes (i.e. the evolution of male and female traits) so that the resource distribution is always at equilibrium, we can study the evolutionary dynamics in Equation (5) numerically.

2.2 | Results of the analytical model

First, our basic model can recover the results of pre-existing theory. We show that when the fitness of males and females is independent from each other in panmictic populations, the condition for sexual dimorphism to evolve is $\sigma_y^2 + \sigma_z^2 < \sigma_r^2$, where σ_y represents the niche width of each individual, σ_z^2 stands for the variance of trait distribution within the same sex and σ_r^2 stands for the variance of resource size distribution in the environment (Appendices A.1 and A.2). This result can be further reduced to Slatkin's (1984) classic result by setting the individual trait variance within each sex, σ_z^2 , to zero.

More importantly, we show that by considering limited spatial scale of interactions in local groups and the interdependence of fitness between males and females, the parameter range where sexual dimorphism evolves can become broader (Figure 1b) than under panmixia (Figure 1a).

Under monogamy ($M = 1$), local mating competition for males vanishes and a male's fitness depends solely on the reproductive success of his female. This leads to a particularly interesting coevolutionary pattern of the male and female traits, which we call 'the gentlemanly solution' (Figure 1c). Here, after an initial divergence of both male and female traits, the female trait evolves back to the resource replenishment centre while the male trait continues to move away further at a decreasing rate (in real biological systems, the deviation will cease when genetic variation runs out or viability selection sets a lower limit to male condition). Varying the intensity of female fecundity competition, β , only changes the speed of coevolution and has no influence on

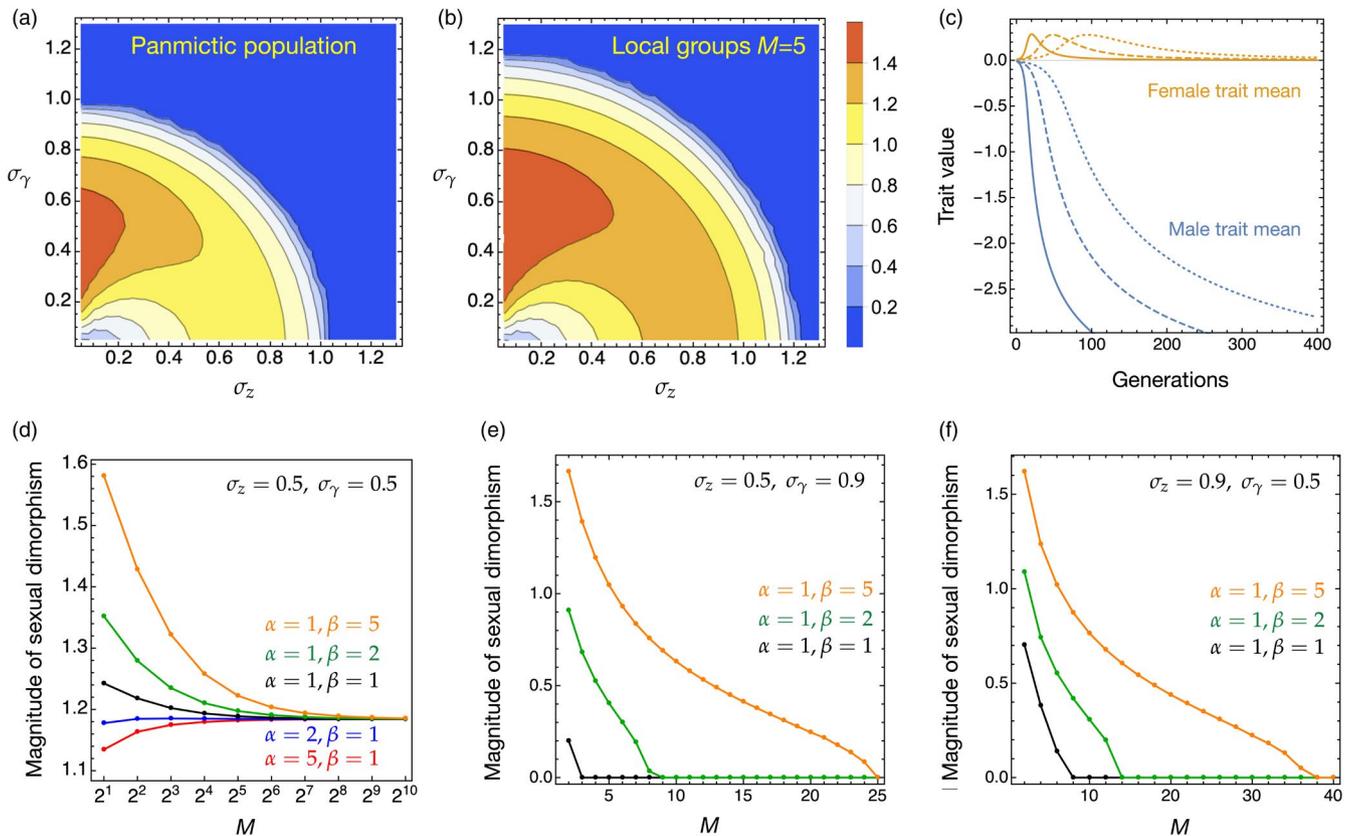


FIGURE 1 (a) Heatmaps of the equilibrium magnitude of dimorphism at different combinations of σ_z and σ_γ values, in a large panmictic population; (b) Heatmaps of the equilibrium magnitude of dimorphism in a population with small local interaction groups ($M = 5$). The colour scales are consistent in panels (a) and (b). The other parameters are $\mu_r = 0$, $\sigma_r = 1$, $\alpha = 1$ and $\beta = 5$. The value of g_0 does not matter (because it does not differ between individuals and thus cancels out when computing fitness). (c) Coevolutionary trajectories of the female and male trait mean under monogamy, where the dotted, dashed and solid lines correspond to $\beta = 1$, $\beta = 2$ and $\beta = 5$, respectively. The other parameters are $\sigma_z = \sigma_\gamma = 0.5$; the intensity of male mate competition α does not matter; (d) Effect of varying α , β and M on the magnitude of sexual dimorphism at equilibrium in groups where $M > 1$, when both σ_z and σ_γ are small. Note the log scale on the x-axis. (e, f) Effect of varying β and M on the magnitude of sexual dimorphism at equilibrium in groups where $M > 1$, when either σ_z or σ_γ is large. The numerical simulations are computed with an initial (at $t = 1$) small perturbation making the mean trait values of males and females deviate slightly from each other: $\mu_m = -0.01$ and $\mu_f = 0.01$. All other simulation parameters follow those in panel (c)

the long-term evolutionary outcome (Figure 1c, compare the trajectories of different line types).

In larger local groups ($M > 1$), the magnitude of sexual dimorphism (defined as the difference between the male and female trait mean) at equilibrium increases with the intensity of selection on females (Figure 1d, compare curves where $\alpha = 1$ but β varies) while it decreases with the intensity of selection on males (Figure 1d, compare curves where $\beta = 1$ but α varies). Dimorphism is generally more evident in small mating groups when α is not too large. Increasing group sizes lead to either modest dimorphism (if individual niches are narrow and within-sex individual trait variations are small, Figure 1d) or make dimorphism vanish completely (if individual niches are broader, Figure 1e; or within-sex trait variations are larger, Figure 1f). As group size increases, whether sexual dimorphism can evolve, and the magnitude of sexual dimorphism at evolutionary equilibrium approach the same results as under panmixia.

The analytical model provides useful insights on the evolution of sexual dimorphism affected by the different spatial scales of competition within and between sexes. However, it still has some limitations

(e.g. the assumption of Gaussian functions may cause structural instability of our results). Therefore, we use individual-based simulations to overcome several limitations of the analytical model.

2.3 | The individual-based simulation model

In the individual-based simulations, we relax a broad range of assumptions that may limit the generality of our analytical model. The resource replenishment rate and the resource consuming efficiency functions are no more limited to Gaussian functions. The trait distribution within each sex can evolve freely (e.g. the evolution of within-sex trait polymorphism is now possible), and we also consider the effect of genetic constraints. Furthermore, we now include more than one type of resources, which permits us to explore the option where not all resources are present in all habitat patches. For more details, please see Appendix B for a full description of the model, and the MATLAB script with detailed annotation in the Electronic Supplementary Materials.

2.4 | Results of the individual-based simulation model

2.4.1 | Effect of niche width σ_γ concurs with Slatkin (1984) and our analytical results

In the simplest case where a single type of resource is present in all habitat patches with the same Gaussian-shaped distribution, our simulations (Figure 2a, upper right subpanels) recover a baseline message of our analytical model and Slatkin's (1984) result: a broad individual niche width σ_γ tends to prevent the evolution of sexual

dimorphism. Note that to aid visual comparison of male and female trait distributions at evolutionary equilibrium, our plots use a time axis that runs from left to right for males but from right to left for females, allowing the evolved trait distribution of both sexes to align next to each other in the middle.

When each individual is able to utilize a wide niche (e.g. bills are omnicompetent tools for extracting food of different sizes), sexual dimorphism does not evolve even in the absence of any genetic constraint (Appendix C provides a more detailed analysis of the effect of genetic constraint). Conversely, when the individual niche width is narrower than the resource replenishment distribution (e.g. all bill

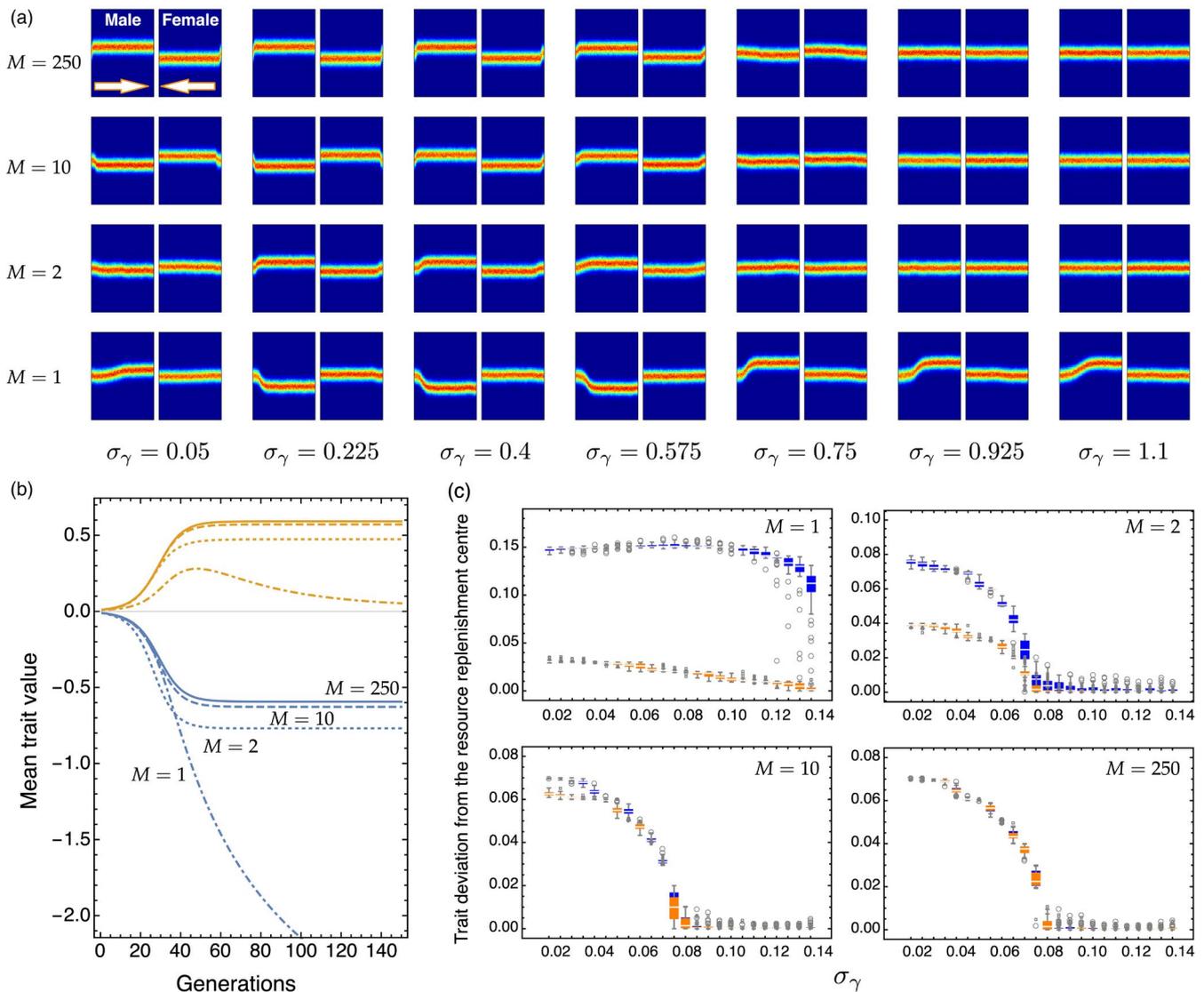


FIGURE 2 (a) The evolutionary trajectories of males and females at different combinations of mating group size ($2M$) and individual niche width (σ_γ). Under each combination, there are two panels. The y-axis represents the trait value, ranging from 0 to 1, and the x-axis represents time, running from generation 0 to 500 for males (left panel in each case) and 500 to 0 for females (right panel in each case), as indicated by the white arrows in the first subplot. In all simulations, the mutation rate at each locus is set to 0.01. (b) Evolutionary trajectories of male (blue) and female (orange) trait mean as M varies. The other parameters are $\mu_r = 0, \sigma_r = 1, \alpha = \beta = 1, \sigma_z = \sigma_\gamma = 0.5$; the initial trait mean of males and females are $\mu_m = -0.01$ and $\mu_f = 0.01$. (c) Sex-specific deviation of trait mean from the resource replenishment centre (blue: males, orange: females, each box plot represents 40 independent simulations). All simulations start from no sexual dimorphism between the sexes and run for 500 generations (sufficient for reaching evolutionary equilibrium). In all cases, $\mu_r = 0.5, \sigma_r = 0.1, \alpha = \beta = 1, S = 5,000$ and $\epsilon_r = \epsilon_\gamma = 0$; the trait distribution of each sex can freely evolve

sizes are specialized tools for particular sized seeds), resource items that are replenished at lower rates become more abundant—due to underutilization causing their accumulation—than the most rapidly replenished ones. This promotes the evolution of sexual dimorphism across a wide range of group sizes (Figure 2a, panels in the left columns).

2.4.2 | Effect of group size on the 'gentlemanliness' of males

While our simulation results regarding niche width (σ_y) qualitatively concur with the analytical results, the results regarding interacting group size differ somewhat, especially under monogamy ($M = 1$). In contrast to the analytical result where the female trait evolves back to the resource replenishment centre after a transient deviation while the male trait evolves away from the resource centre indefinitely, the mutation-selection balance in the simulations kept the trait deviation between the two sexes finite at an evolutionary equilibrium (Figure 2a, last row). However, the analytical model (Figure 2b) and the simulations (Figure 2c) agree on the general pattern that the 'gentlemanliness' of males decreases as group size increases. At small group sizes, males deviate more from the resource replenishment centre (marked by the grey line at zero) than do females (Figure 2b). This asymmetry decreases as M increases, and in sufficiently large groups (e.g. $M = 250$) the trait means of males and females stabilize equidistantly from the resource replenishment centre. Our simulations confirmed that the 'gentlemanliness' dwindles rapidly as M increases (Figure 2a,c) and is replaced either with sexual monomorphic resource use (if individual niches are broad) or both sexes deviating equally much from the resource replenishment centre (if individuals necessarily specialize as their niches are narrow). In groups of small to intermediate sizes (Figure 2c, $M = 2$ and $M = 10$), 'gentlemanliness' evolves more easily when the niche width of individual resource use is relatively narrow (i.e. small σ_y). Note that the direction in which males deviate away from the resource replenishment centre is random, as either displacement direction leaves resources for females.

2.4.3 | Effect of multiple resources and their spatial variation

The individual-based simulations up to now assumed a unimodal distribution of resource sizes. Reality may offer more complex cases of resource availabilities, for example, multiple types of resources, each with their own size distribution, and perhaps not all resource types present in all habitats. To return to our seed example, a consumer might utilize seeds of multiple tree species, in which case evolutionary processes can differ depending on whether all patches offer seeds of different types with identical replenishment rates, or if the resource mosaic shows significant inter-patch variation (some

resource types may be completely lacking in some patches). If every patch has more than one resource type, the equilibrium resource distribution can be much more complex with multiple local peaks.

When two different types of resources are present in the environment, and the replenishment rate of each follows a normal distribution, we find the intuitive result that the resulting multimodal resource distribution can favour sexual dimorphism (Figure 3). In this sense, we recover the results of Cooper et al. (2011) which was set in a multidimensional resource world. Our unidimensional world allows us to conveniently adjust how much the resource types are different from each other (e.g. in size), and we find that sexual dimorphism is more likely to evolve and reach a high magnitude at equilibrium, when the distributions of different resource types become more different from each other (Figure 3a). Note that in Figure 3a the niche width σ_y is chosen to be so large that sexual dimorphism cannot evolve if only one type of resource is present in the environment except under monogamy (leftmost column).

Although the above suggests that feeding on different resources is an effective way of reducing intersexual competition, it clearly also implicates the risk that on some sites only one type of the resources is present. If this happens, one of the sexes becomes locally maladapted. Taking a two-resource case that leads to clear dimorphism as a baseline (rightmost column, Figure 3b), we can examine the effect of reducing p , the proportion of patches that offer both resources. Under polygyny ($M > 1$), this hampers the evolution of sexual dimorphism, though dimorphism does not disappear immediately as soon as $p < 1$. Again, monogamy ($M = 1$) is an exception: other values feature symmetrical dimorphism, but under monogamy, males evolve to step away from the resource replenishment centre (the 'gentlemanly' solution), whereas females stay there. Females thus achieve moderate resource-use efficiency even if some sites offer resources that peak to the left or to the right of the global mean. This type of conservative bet-hedging appears to win over specializing in any of the two types of resources; note that no singular specialist strategy can avoid, in the worst case ($p = 0$), a 50% risk of being maladapted.

2.4.4 | Effect of spatial variation of resources under strong selection

Above, we already highlighted conservative bet-hedging (Starrfelt & Kokko, 2012), which in our current context means staying in a generalist state despite the environment sometimes offering more resources to the 'left' or to the 'right' of what the individual can best use. Another type of bet-hedging is diversified resource use: polymorphism in the resource-use trait such that an individual will do well in one habitat but very poorly in another. In our model, an example of this outcome is found—in a sexually dimorphic manner, with males hedging more strongly than females—when mating groups are of moderate size or large, intrasexual competition is relatively strong for both sexes, competition between males is stronger than that between females, and not all habitats offer all resources (Figure 4).

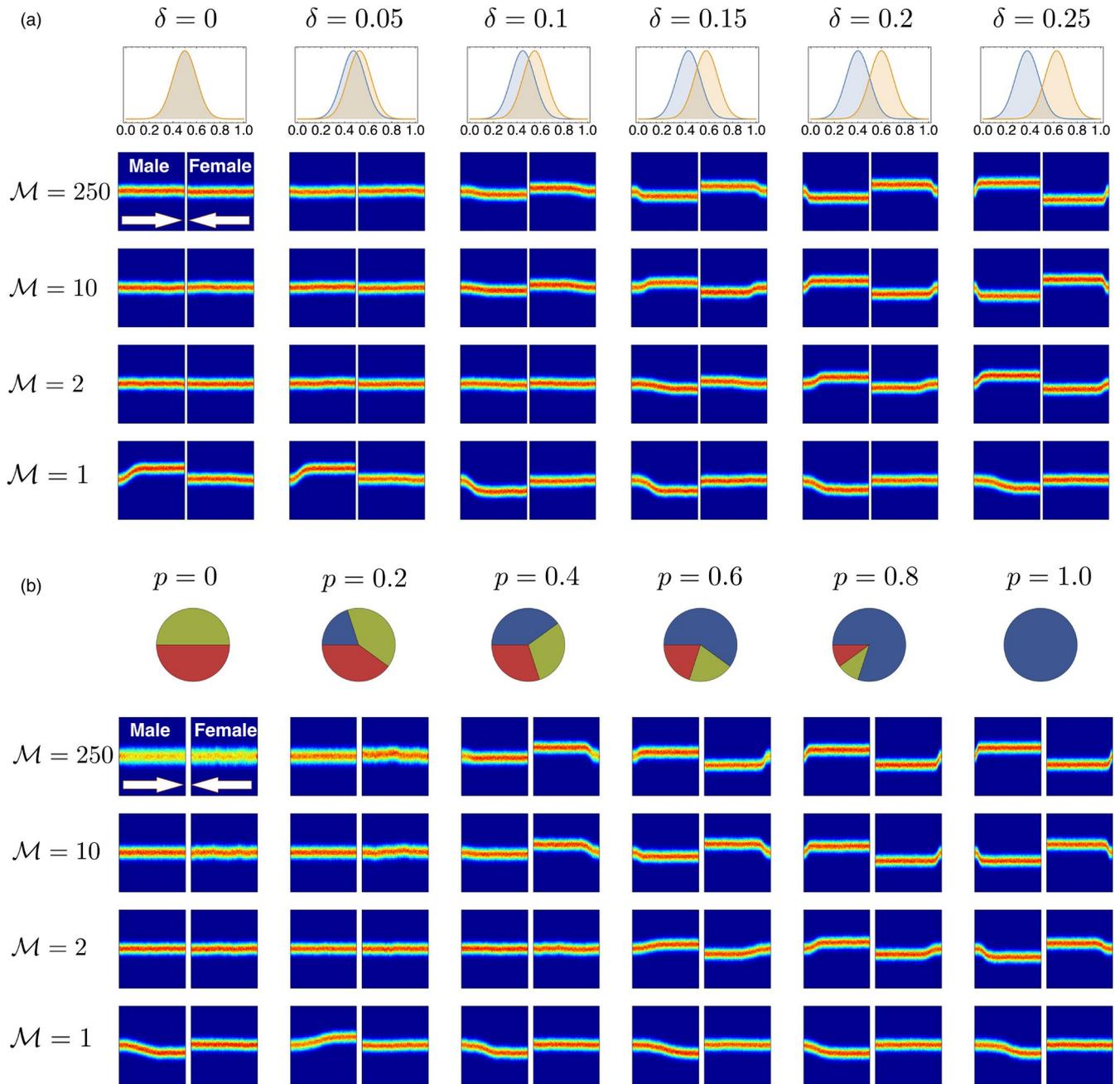


FIGURE 3 The evolutionary trajectories of males and females when two different types of resources are present in the environment. (a) Both resource types are present in all habitats, but with different distances (δ) between the replenishment centres. The niche width of both males and female are relatively large ($\sigma_y = 0.08$). (b) Both types of resources are present in p proportion of the habitats with $\delta = 0.25$ (thus the rightmost columns of both panels are simulated under identical conditions). In a proportion of $(1 - p)/2$ habitats only the smaller resource, and in the rest of habitats only the larger one is present. The pie chart on the top of each column shows the relative abundance of each habitat type (blue: both resources are present). The arrangement of male and female traits onto panels, the axes in each of the panels and the simulation parameters are all as in Figure 2a except for different values of δ and p

Under these conditions, strong sexual selection implies that the system is close to a 'winner takes all' scenario, and when most habitats do not offer both resources, only those males have good success who gamble by specializing in performing well in one of the habitats. Trying to hedge one's bets conservatively, by hoping for relatively adequate condition with a phenotype that does moderately well in both habitats, does not translate into moderate success when out-competed by specialists. In other words, with sufficiently high α , it

is better to be highly competitive in 50% of habitats and lose thoroughly in the rest of them, than to fall behind the best competitors in all habitats. Note that we do not assume any form of habitat choice. At least some offspring of a specialist will land in suitable habitats, and this is the fitness-gaining subset of the population. In Appendix D, we show additional cases where polymorphism evolves in only one of the sexes while the other sex remains a generalist, and a case where the female trait evolves to oscillate instead of producing stable

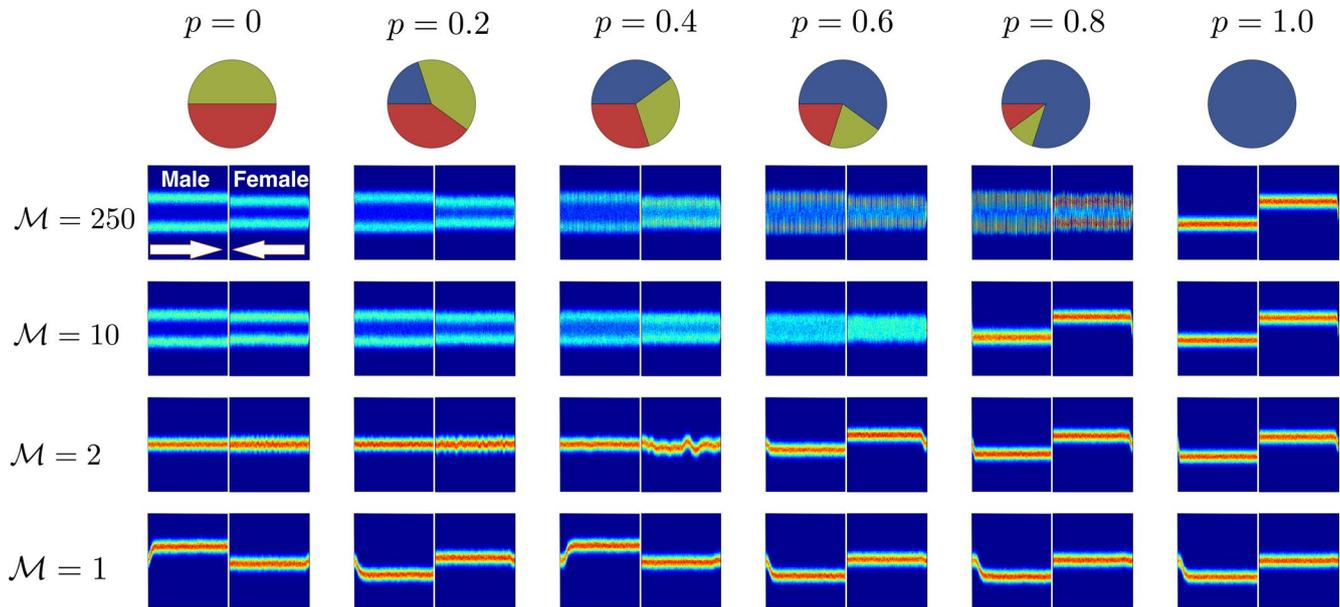


FIGURE 4 The evolutionary trajectories of the two sexes when two different types of resources are present in the environment, with distance $\delta = 0.25$ between the replenishment rate distribution centres. The arrangement of male and female traits onto panels, the axes in each of the panels and all simulation parameters are identical to those in Figure 2a except for the values of δ and p , and both sexes experience stronger intrasexual competition ($\alpha = 5$, $\beta = 2$)

polymorphism while the male trait stays in the centre of resource replenishment centre, due to different softness of selection between the two sexes. These results extend and complement those of Cooper et al. (2011), in which disruptive selection operated on two independent trait dimensions, implying that all habitats necessarily offering both dimensions.

2.4.5 | Additional results: Effect of genetic constraints and non-Gaussian functions

Genetic constraints generally increase the trait variance within each sex, reduce the parameter ranges where sexual dimorphism can evolve and decrease the magnitude of sexual dimorphism at equilibrium. They can, however, extend the parameter range where intrasexual polymorphism evolves, when spatial variation of resource distribution is present and males are under strong mating competition. More details are provided in Appendix C.

In the individual-based simulations, we also studied scenarios where the resource replenishment rate and resource-use efficiency are non-Gaussian functions. Relaxing these assumptions keeps the general findings intact, but the parameter ranges that permit the evolution of sexual dimorphism are affected by the shape of the functions. More detailed results are presented in Appendix E.

3 | DISCUSSION

Our models shed new light on why it is easier to identify sexual dimorphic traits caused by sexual selection than those caused by

resource competition (De Lisle, 2019). Earlier work on this topic considered genetic correlations (Slatkin, 1984); our results recover similar effects. Even so, genetic constraints do not suffice as an a priori explanation for the rarity of sexual dimorphism caused by resource competition, since they clearly do not prevent dimorphism to evolve when sexual selection is the direct cause (e.g. weaponry, ornaments). We show that conditions are rather stringent for resource competition alone to drive the evolution of sexual dimorphism, even at the absence of any genetic constraint. Furthermore, we identify the conditions favourable for the evolution of ecological sexual dimorphism, including narrow individual niche width of resource use, relatively small scale of interaction (ideally monogamous pairs in an exclusive territory) over an extended period of time, low degrees of intralocus sexual conflict and reliable co-presence of different types of resources.

Shine (1989) and De Lisle (2019) compiled useful lists of tentative cases of ecological character displacement across a variety of taxa. Since the latter work is up to date and nevertheless relatively brief, it appears that there is not sufficiently much systematic empirical and/or phylogenetic work available that would allow us to test our model predictions. Instead, we will now consider a few case studies in detail.

The conditions that our models highlight agree thought-provokingly well with a case study (Aplin & Cockburn, 2012) based on field observations of sooty oystercatchers *Haematopus fuliginosus*. Sooty oystercatchers are monogamous with year-round territoriality and biparental care of offspring, allowing us to interpret M as being very low. Adult females have on average 19% longer bills than males (male: 73.4 ± 3.3 mm; female: 87.1 ± 3.9 mm), contrasting with a heavier body mass of 2% (male: 806.7 ± 62.2 g; female:

826.7 ± 61.3 g; Hansen et al., 2009). Overlap in resource use between males and females was only 36%, with shorter-billed males taking relatively larger and thick-shelled molluscs, such as cockles and mussels, while females with longer and more fragile bills taking, for example, jellyfish and soft-bodied polychaetes. Several types of prey were eaten exclusively by one sex, and the shared prey were eaten in different portions (Aplin & Cockburn, 2012).

Although collecting field data is lamentably impossible for the now extinct *Huia heteralocha acutirostris*, it deserves some discussion as offering the world's most dramatic example of sexually dimorphic bills. The species was endemic to the North Island of New Zealand, with 60% longer (and curved) bills in females than in males (Burton, 1974)—causing the initial misclassification of females and males as different species. The idea that *Huia* dimorphism resulted from natural selection to reduce intersexual competition for food has a long history (Burton, 1974; Moorhouse, 1996; Rand, 1952; Selander, 1966, 1972). In this case, females have been shown to evolve a novel bill type (Moorhouse, 1996) while males differ little from related sister species. This, together with past observations suggesting monogamous year-round territoriality (Selander, 1966), provides at least some, though ambiguous, support for our model, in the sense of an evolutionary innovation (the long curved bill being used to probe decaying wood for grubs) evolving in females with the males not following suit, leaving the fruits of female labour to her alone (Buller and Keulemans (1888), cited in Moorhouse (1996), noted that the female did not appear to share grubs with the male).

Although differences in the size and shape of bird bills might provide the most straightforward examples of sexual dimorphism in resource use, ecological niche divergence between the sexes can be expressed in numerous traits. Among those, (micro-)habitat divergence and difference in foraging techniques appear relatively well studied. In Scopoli's shearwaters *Calonectris diomedea*, males follow fishing vessels more than do females, leading to a more variable diet (fishery discards) (Zango et al., 2020). In *Anolis* lizards, males generally perch higher in the tree than females (Shine, 1989), and their larger and wider heads are often associated with a greater proportion of larger prey items in the diet (Preest, 1994; Schoener, 1967). In green woodhoopoes, males prefer techniques such as bark scaling and end probing, while females spend more time pecking (Radford & du Pleissis, 2003). In the green woodhoopoe and a number of woodpecker species, sexual dimorphism in bill morphology, microhabitat separation and divergence in foraging technique often co-occur. For example, in the aforementioned green woodhoopoe, the bills of adult males were 35.5% longer than those of females (male: 62.6 ± 3.3 mm; female: 46.2 ± 2.0 mm), making them a more suitable device for probing than pecking. In the Middle Spotted Woodpecker, males have 4.4% longer bills than females, foraging more often in oaks (females foraged more often in conifers), and used different techniques (e.g. more searching and less gleaning) than females during the breeding period (Pasinelli, 2000). In the Magellanic Woodpecker, adult males have bills 12.4% longer than those of female, foraging on larger substrates (e.g. trunks) at intermediate heights (5–10 m) while females foraged higher within the crown (>15 m) on smaller substrates (e.g.

branches) (Chazarreta et al., 2012). Interestingly, in this species, sexual niche overlap is found to be greater in winter when resource is scarcer and competition resultantly stronger than in summer (Duron et al., 2018).

Our model predicts that sexual dimorphism evolves more easily when resources remain underutilized to the left and right of the resource replenishment peak. Although we did not develop multi-species models, it is easy to form a verbal prediction: underutilized resources will no longer be available if another species specializes in using them. As a consequence, we predict sexual niche dimorphism to be less prevalent if there are competing species in the environment. For example, in blue tits, bill dimorphism only occurred in locations where no other co-occurring members of the same genus (Martin & Pitocchelli, 1991), and in great tits, sexual dimorphism in bill morphology is only significant in populations with only one congener, but not in populations with three congeners (Ebenman, 1986).

In this light, it is interesting to ask whether islands, with their reduced number of competing consumer species, might provide optimal environments for the evolution of intersexual niche differences. Despite intriguing known cases such as sexual differentiated niches in the island-related adaptive radiation of *Anolis* lizards (Butler et al., 2007), and a general view that sexual size dimorphism (that may also associate with resource use) on islands is stronger than on the mainland [Meiri et al. (2014) and references therein], the general answer is not obvious (Meiri et al., 2014; Pincheira-Donoso et al., 2018; Siliceo-Cantero et al., 2016). Pincheira-Donoso et al. (2018), by studying community assemblage of *Liolaenus* lizards in the Chilean side of the Andes, found support for the idea that sexes (via dimorphism) and species are alternative ways to 'fill' a niche space. The evidence consists of a negative correlation across assemblage between dimorphism and species richness after controlling for phylogeny, and of within-assemblage negative correlations between the residual proportions of variance in body size explained by partitioning among species versus sexes. In a worldwide comparative study of island-dwelling mammals and lizards, however, Meiri et al. (2014) did not find a link between the number of competing species and sexual size dimorphism, suggesting that either the effect is truly absent or that the number of species present is a poor proxy for the strength of competitive interactions. Our models suggest two more possible reasons: island may imply fewer competitors but also a more limited range of resources in the first place, which might, as a net effect, lead to little or no net effect on dimorphism; or individuals may diversify along the resource axis with no clear sex biases (data from lizards; Costa et al., 2008).

The large multitude of factors operating in natural populations can also point out limitations of our model: our desire to keep the model general led us to focus solely on female condition as a determinant of reproductive success, ignoring interactions such as those provided by, for example, biparental feeding of young. This, under monogamy, might select for maximal efficiency of the breeding pair as a whole, rather than the male keeping female condition as intact as possible (our 'gentlemanly' solution). In several bird species, males may preclude females from the preferred foraging microhabitat (the

opposite of being 'gentlemanly') during the non-breeding season, but they also provide significant amount of food to the offspring once acting as one part of a pair. For example, in the green woodhoo-poe, males delivered significantly heavier prey than females (male: 0.47 ± 0.03 g; female: 0.27 ± 0.05 g per item) to the nest (Radford & du Pleissis, 2003). Similarly, in the Magellanic Woodpecker, males delivered most of the large prey, including wood-boring larvae and vertebrates, while females brought most of smaller prey such as arachnids (Ojeda & Chazarreta, 2006). Raptors often have striking sexual size dimorphism, and while both sexes hunt during the non-breeding season, this is replaced with a strict division of labour during the breeding season (Krüger, 2005). The tension (from the female perspective) where the male can be a useful carer but also consumes resources himself exists outside birds too (for a beetle example, see Keppner et al., 2020).

We did not consider challenges of biparental care explicitly; here, should sexual conflict be a minor issue (high parentage certainty of both parents), there may be a route to dimorphism that differs somewhat from pure 'gentlemanliness' (where males simply agree to leave the most profitable resources to females). In systems where male and female food deliveries combine to determine offspring production, division of labour in terms of foraging techniques might promote sexual dimorphism in manners not explicitly considered by us. We leave this exploration for further work.

Such work could also usefully examine whether factors such as overlapping territories, home range or foraging areas, seasonal resource use, or limited temporal duration of pair bonds could cause deviation from the patterns we derived. All these factors can make the spatial scale of resource competition differ from the scale of mating competition—our model, for simplicity, assumed these to be identical. It appears plausible that the longer, out of a year, an individual's resource use occurs in competition with more than just the mate (a long non-breeding season spent e.g. in flocks), the slimmer the chances for significant sexual dimorphism. In this sense, our model could be considered as an investigation of some of the best-case scenarios for sexual dimorphism to evolve under resource competition, but future work is needed to investigate details such as the likely effect of genetic correlation between sexually selected traits and resource-use traits, sex-specific dispersal, evolving territories with fluid boundaries, or life-history aspects such as the influence of floater individuals or flexible forms of parental care. Obviously, there is also the task of integrating natural with sexual selection in the evolution of sexual dimorphism, as these can interact to produce the final outcome (Krüger et al., 2014).

To conclude, both sexual selection and natural selection can contribute to the evolution of sexual dimorphism, but the relative importance and the exact mechanisms of the two forces and their interactions are often hard to disentangle (De Lisle, 2019; Punzalan & Hosken, 2010; Slatkin, 1984). Our results explain why the condition for resource competition (as an important form of natural selection) alone to drive the evolution of sexual dimorphism can be limited, even in the absence of genetic constraints and competing species. Very interestingly, sexual conflict, where male resource-use

phenotypes do not evolve based on what is in the females' interests but to maximize paternity gain under male–male competition, can be a significant factor preventing sexual dimorphism in niche-use traits. We thus encourage future empirical work to test our predictions in tentative cases of sexual niche dimorphism driven by resource competition, and to look for cases of ecological character displacement between sexes in systems that satisfy the conditions we predicted.

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AUTHORS' CONTRIBUTIONS

Both authors conceived the ideas, designed the models, produced results, wrote the manuscript and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Simulation code for our individual-based model is available from the Zenodo digital repository <https://doi.org/10.5281/zenodo.4614490> (Li & Kokko, 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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