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Ecological sexual dimorphism is modulated by the spatial scale of intersexual resource competition

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Abstract

In Focus: Li, X-Y., & H. Kokko. (2021). Sexual dimorphism driven by intersexual resource competition: Why is it rare, and where to look for it? *Journal of Animal Ecology*, 00, 1–13. Ecological sexual dimorphism, that is differences between the sexes in traits that are naturally selected as opposed to sexually selected, is gaining increasing attention after having often been dismissed as the 'less-parsimonious' explanation for differences between sexes. One potential driver of ecological sexual dimorphism is intersexual resource competition, in a process analogous to ecological character displacement between species; yet, clear empirical examples are scarce. Li and Kokko present mathematical models that introduce novel pieces to the puzzle: the role of the scale of mating competition and the spatial variation in resource availability. They show that ecological sexual dimorphism evolves when local mating groups are small (e.g. monogamous pairs) and when different resources are homogeneously available across habitats. Counterintuitively, larger mating groups (e.g. polygyny), and consequently higher intralocus sexual conflict, lead to sexual monomorphism. Habitat heterogeneity also leads to overlapping niches, although it can sometimes drive polymorphism within sexes. This study highlights why the conditions for intrasexual resource competition to drive evolution of sexual dimorphism are stringent, even in the absence of genetic constraints or competing species. Crucially, it highlights the importance of considering the mating system and the spatial scale of resource competition for understanding the occurrence of ecological sexual dimorphism, showing a large potential for future work considering different aspects of species' life histories and spatial dynamics.

KEYWORDS

ecological character displacement, intrasexual resource competition, mating system, niche partitioning, polymorphism, sexual conflict, sexual dimorphism, spatial heterogeneity

Differences between sexes (i.e. sexual dimorphism) are widespread in nature and have sparked substantial interest in their causes and consequences at least since Darwin realised that both natural and sexual selection may act differently on males and females (Darwin, 1871). While three major hypotheses have been proposed for the evolution of sexual dimorphism, invoking sexual selection, intersexual resource competition (i.e. ecological sexual dimorphism) and reproductive role division (Hedrick & Temeles, 1989), by far the most popular, and rich of fascinating examples, explanation has been sexual selection (Andersson, 1994; Fairbairn et al., 2007; Székely et al., 2000). On the other hand, the role of natural selection has been underappreciated and often dismissed on the basis that it is the less-parsimonious explanation, compared to sexual selection, and it is much harder to test empirically (Shine, 1989). However, the role of natural selection and of the ecological context in shaping sexual dimorphism is beginning to gain momentum and the boundaries of its action together, or in place of, sexual selection, are only starting to be delineated (Connallon et al., 2018; de Lisle, 2019; de Lisle & Rowe, 2015; Fryxell et al., 2019).

Initial theoretical models have highlighted the analogy between interspecific and intersexual competition for shared resources and, accounting for the possible genetic correlations between males and females, these models show that competition may in fact drive evolution of sexual dimorphism in ecological traits, in a process analogous to ecological character displacement (Bolnick & Doebeli, 2003; Cooper et al., 2011; Slatkin, 1984). Yet, empirical evidence remains sparse (de Lisle, 2019; Shine, 1989). Li and Kokko (2021) turn the problem on its head and ask why ecological sexual dimorphism driven by intersexual resource competition seems to be rare, and where should we look in searching for evidence? They address this question by bringing the spatial component to the puzzle. Specifically, they present a mathematical model that considers (a) the spatial scale of mating competition, a fundamental aspect of a species' mating system and (b) the spatial variation in resource availability. By introducing previously neglected ecological factors and characteristics of the mating system, Li and Kokko's (2021) model shines new light on the conditions under which we should expect to observe (or not) ecological sexual dimorphism (with a couple of intriguing twists), and highlights, once again, how there is a large unexplored potential of gaining new understanding by considering the interactions between ecology, life history and evolution (Connallon et al., 2018; Svensson, 2019).

Li and Kokko's (2021) model is rich in complexity and results, but perhaps the most striking results are emerging from the first implementation of the model, assuming a unimodal distribution of resource sizes and varying the size of the local mating group, from monogamous pairs to polygyny (Figure 1). After recovering Slatkin's (1984) result that a broad individual niche (e.g. bills are able to

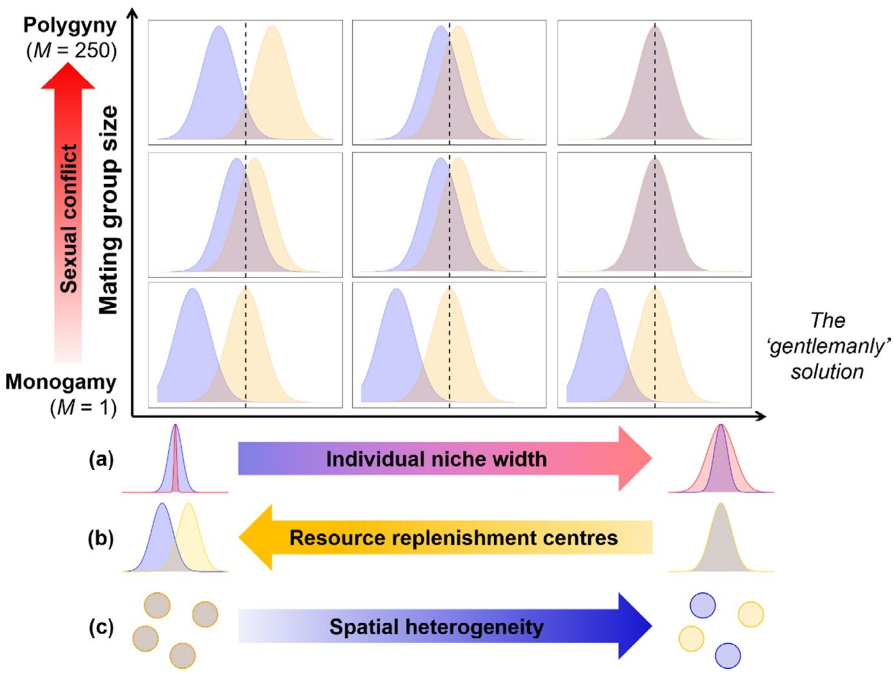

FIGURE 1 Summary of Li and Kokko's (2021) main model findings about the evolution of the two sexes (male blue and female orange) resource utilisation niches under different scales of mating competition and resource availability. In each panel, the x-axis shows the continuous variation of a resource characteristic x (e.g. seed size) as well as the trait value z, with the dashed black line indicating the resource replenishment centre. When $z = x$, the sex is perfectly adapted to the local resource. Rows show results for increasing size of the local mating group (from monogamy to polygyny), also corresponding to increasing intralocus sexual conflict. Increasing mating group size generally decreases the opportunity for sexual dimorphism to evolve. Under monogamy, the 'gentlemanly' solution evolves, where males consistently move away from the resource replenishment centre. (a) Narrow individual niche widths favour evolution of sexual dimorphism. Results are arranged along the axis of increasing individual niche width (columns from left to right): on the left, individual niche (in red) is narrower than the resource replenishment distribution (in blue; e.g. each bill size is specialised for a particular sized seed) while on the right it is wider. Only one type of resource is present. (b) Multimodal resource distribution favours sexual dimorphism. Results are shown for cases where two different resource types are available (blue and yellow) and individual resource utilisation niches are slightly narrower than the resource distribution. On the left, the two resources differ in their replenishment centre while on the right they completely overlap. (c) Spatial heterogeneity in resource distribution hampers evolution of sexual dimorphism. Results are shown along the axis of increasing spatial heterogeneity, for a case where individual niches are slightly narrower than the resource distribution and the two resources differ in their replenishment centres (most left case in b). On the left, the two resources are homogeneously available across all habitat patches; on the right, each habitat patch has only one type of resource (i.e. the two resources are completely separated in space)

utilise seeds of different size rather than being specialised for one particular seed size) will hamper evolution of sexual dimorphism (Figure 1a, right column), the first twist emerges: the 'gentlemanly' solution. Under monogamy, a special form of sexual dimorphism evolves where males deviate from the resource replenishment centre while female do not and thereby are able to utilise the most profitable resource (Figure 1, bottom row). This is explained by the fact that in monogamous pairs males are not involved in local mating competition, and a male's reproductive success solely depends on his female's reproductive success. As the size of the local mating group increases, moving from monogamy to polygyny, male–male competition for access to females increases, males 'disregard' the best solution for the female and the 'gentlemanly' solution quickly vanishes. Whether ecological sexual dimorphism evolves under polygyny depends on the width of the individual niche: narrow niches lead to sexual dimorphism with both sexes equally diverging from the resource replenishment centre (Figure 1, left column), while wide niches lead to sexual monomorphism (Figure 1, right column).

The second novel and counterintuitive twist appears when we consider the fact that increasing the scale of mating competition introduces intralocus sexual conflict, that is when a shared trait has different fitness optima for males and females (Bonduriansky, 2011; Bonduriansky & Chenoweth, 2009; Cox & Calsbeek, 2009). What is surprising is that while intralocus sexual conflict is usually assumed to be a driver of evolution of sexual dimorphism, Li and Kokko (2021) show that, on the contrary, sexual conflict could lead to sexual monomorphism, with the sexes' competition for the most valuable resource leading to overlapping resource utilisation niches. This result nicely highlights the importance, and the persistent knowledge gap, of considering ecology and characteristics of the species' mating system and life history for understanding the role of sexual conflict in promoting or constraining evolution of sex differences (Connallon et al., 2018; de Lisle, 2019).

Li and Kokko (2021) then go further and investigate what happens when there are multiple resources in the environment and there is variation in their spatial distribution. In a spatially homogeneous environment, where both resources are present in all habitat patches, a multimodal resource distribution favours sexual dimorphism (Cooper et al., 2011), and more so the larger the difference between the distributions of different resource types (Figure 1b, left column). In spatially heterogeneous environments, where the proportion of patches that contain both resource types is gradually reduced (hence, increasing spatial heterogeneity), polygyny hampers evolution of sexual dimorphism (Figure 1c, right column). Under monogamy, the 'gentlemanly' solution appears once again. This time, however, females can maximise their resource utilisation only in a proportion of patches; nonetheless, conservative bet-hedging (Starrfelt & Kokko, 2012) prevails over specialisation on one of the two types of resources.

Finally, varying the strength of selection acting on females and/or males (in the form of varying the way a better adapted individual enjoys disproportionally higher productivity for females and mating success for males) impacts on evolution of ecological sexual dimorphism. In a one resource scenario, larger size dimorphism evolves when selection on females is stronger; on the contrary, stronger selection on males hampers evolution of sexual dimorphism. This is an interesting result as situations with strong male–male competition are typically situations of strong sexual selection where dimorphism in secondary sexual characters is expected (Andersson, 1994; Székely et al., 2000). In the two resource types scenario, when resources differ in their distributions and are spatially heterogeneous, and local mating groups are large (thus a situation that disfavours evolution of sexual dimorphism), strong intrasexual selection leads to the evolution of intrasexual polymorphisms, where the sexes hedge their bets by diversifying in resource use.

Although Li and Kokko (2021) conclude their results imply that the conditions for intersexual resource competition alone to drive the evolution of sexual dimorphism are limited (i.e. narrow individual niche width, relative small scale of mating competition, low degrees of intralocus sexual conflict and reliable co-presence of different resource types), even in the absence of genetic constraints and competing species, their results also focus the light on situations that might be usefully tested empirically. Importantly, they also highlight how the role of natural selection in promoting or not sexual dimorphism can be critically modulated by different aspects of the species' ecology and life history that are only starting to be considered (Connallon, 2015; Connallon et al., 2018, 2019; Ronco et al., 2019). Finally, they highlight how the interplay between natural and sexual selection in shaping sexual conflicts and evolution of sex differences is still far from being fully understood, the importance of different mechanisms has yet to be disentangled, and how their interactions can lead to previously unconsidered insights (de Lisle, 2019; Krüger et al., 2014; Littleford-Colquhoun et al., 2019; Punzalan & Hosken, 2010; Svensson, 2019).

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