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An evolutionary ecology of sexual traits
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Opinion

Towards an evolutionary ecology of sexual traits

Charlie K. Cornwallis and Tobias Uller

Edward Grey Institute, Department of Zoology, University of Oxford, South Parks Road, Oxford, UK, OX1 3PS

Empirical studies of sexual traits continue to generate conflicting results, leading to a growing awareness that the current understanding of this topic is limited. Here we argue that this is because studies of sexual traits fail to encompass three important features of evolution. First, sexual traits evolve via natural selection of which sexual selection is just one part. Second, selection on sexual traits fluctuates in strength, direction and form due to spatial and temporal environmental heterogeneity. Third, phenotypic plasticity is ubiquitous and generates selection and responses to selection within and across generations. A move from purely gene-focused theories of sexual selection towards research that explicitly integrates development, ecology and evolution is necessary to break the stasis in research on sexual traits.

The evolution of sexual phenotypes is not just about sexual selection

To understand phenotypic evolution the causes and consequences of variation in reproductive success and survival need to be identified. However, it is currently very difficult to gain a clear understanding of phenotypic evolution in the wild because only a small proportion of variation in reproductive success is ever explained [1,2]. This is particularly apparent in studies examining the association between sexual traits and reproductive success, which is often weak and not explained by current theory: almost any relationship between sexual traits and reproductive success can be found in well-studied species (e.g. [3,4]). Here, we argue that low predictive power is expected because current approaches ignore that the evolution of sexual traits is determined by a dynamic interplay between environmental heterogeneity and phenotypic plasticity operating at different temporal and spatial scales that cause selection on traits to fluctuate in strength, form and direction.

There are several important issues that are currently poorly understood or even ignored by current research on sexual traits. First, the evolution of sexual traits is affected by viability, sexual and kin selection, which together make up natural selection (see Glossary). However, these selection pressures are often treated in isolation with only basic life-history trade-offs between reproduction (sexual selection) and survival (viability selection) being seriously considered. Therefore only part of the selection acting on sexual traits is ever examined [5–7]. Second, environmental heterogeneity within and among generations is typically not addressed and studies often extrapolate under the assumption that selection and the distribution of phenotypes are constant over spatial and temporal scales [8]. Such unrealistic assumptions have resulted in debates about how variation is maintained in fitness-related traits [9], despite evidence for its depletion being scarce. Third, sexual traits are typically studied in isolation, but in reality reproductive success is determined by an integrated set of traits ('sexual phenotype') whose relationships need to be quantified and

Glossary

Direct benefits (sexual selection theory): the benefits individuals gain from sexual partners that enable greater investment in the production of offspring. This is confusing because of the overlap in terminology used in inclusive fitness theory. Perhaps a clearer term is 'resource benefits' as this is a component of direct fitness as defined by inclusive fitness theory.

Direct fitness (inclusive fitness theory): the component of fitness gained by producing your own offspring.

Fluctuating selection: changes in the form (directional, stabilising or disruptive), direction and/or strength of selection over time and space.

Inclusive fitness: the summed total of direct and indirect fitness.

Indirect benefits or genetic benefits (sexual selection theory): the component of direct fitness (inclusive fitness theory) gained by choosing sexual partners that provide genes resulting in higher offspring fitness. The term 'indirect benefits' also has confusing overlap with terminology used in inclusive fitness theory, so we suggest sticking to the term 'genetic benefits'. As with any genetic effect, they are likely to be context dependent.

Indirect fitness (inclusive fitness theory): the component of inclusive fitness gained by affecting the reproductive success or survival of relatives (individuals that are genetically more similar than the average for the reference population).

Kin selection: any variation in indirect fitness among different phenotypes caused by their ability to affect the reproductive success and survival of genetically similar individuals.

Lek paradox: is used to describe situations where directional selection on sexual traits via female choice deplete genetic variation and therefore relax or eliminate selection on female choice.

Lifetime reproductive success: same as direct fitness (inclusive fitness theory).

Natural selection: any variation in inclusive fitness caused by variation among phenotypes. This is sometimes used inter-changeably by some authors with viability selection (see 'viability selection'), but here we use natural selection to specifically refer to the summed total of viability selection, sexual selection and kin selection.

Phenotypic plasticity: the change in the phenotypic expression of a genotype across different environmental conditions in time and space. The terms 'adaptive' and 'non-adaptive' have often been used in conjunction with phenotypic plasticity. We interpret these as cases where they 'do' and 'do not' increase inclusive fitness and, therefore, can be seen as an evolved outcome of natural selection or an inability to cope with environmental conditions.

Sexual phenotypes: all sexual traits that contribute to gaining access to mates and producing viable offspring.

Sexual selection: any variation in direct fitness among different phenotypes caused by their ability to gain sexual partners, produce fertile eggs and generate offspring.

Viability selection: any variation in direct fitness among different phenotypes caused by their ability to survive. Some researchers use 'natural selection' instead of 'viability selection' to describe differences in survival and consider the sum of natural and sexual selection as total selection. However, here we use natural selection to describe the summed total of sexual, viability and kin selection.

Corresponding author: Cornwallis, C.K. (charlie.cornwallis@zoo.ox.ac.uk).

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Box 1. Fluctuating selection on sexual phenotypes

Several recent examples have illustrated that temporal and spatial environmental heterogeneity can cause large fluctuations in both the strength and direction of selection. Using 12 populations of blue-tailed damselflies, *Ischnura elegans* (Figure I), Gosden and Svensson demonstrated that sexual selection on male body size varied dramatically across a coastal to inland gradient over a five-year study period (Figure 1) [16]. They suggest that this is driven by changes in the density and frequency of females of different body sizes and colour morphs, revealing that selection can be strongly contingent upon local biotic conditions that are subject to rapid fluctuations over time [16].


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Figure I. A mating pair of *I. elegans* (photo courtesy of Erik Svensson).

Environmental heterogeneity can also cause fluctuations in selection by changing the interactions between different selection pressures. This was shown by Robinson *et al.* in Soay sheep, *Ovis aries* (Figure II), where sexual selection and viability selection on male horn-size act in opposing directions, but their relative strengths are dependent upon environmental conditions that are linked to abiotic factors that vary continuously [5]. During favourable conditions, sexual selection overrides viability selection leading to individuals with larger horns having increased lifetime reproductive success; however, when conditions deteriorate, the reverse occurs (Figure 2) [5]. Together, these studies illustrate that fluctuations in selection and their interaction frequently arise due to changes in biotic and abiotic environmental conditions than can constantly drive shifts in phenotypic optima.


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Figure II. Two male Soay sheep on the St. Kilda Archipelago (photo courtesy of Arpat Ozgul).

interpreted within a life-history context [10–13]. This is widely accepted for phenotypic evolution more generally [14], but empirical studies that quantify the relationships between multiple sexual traits, particularly across temporal and spatial environmental gradients, are still rare [15–17]. Fourth, consideration of phenotypic plasticity centres almost exclusively on condition dependence in the expression of sexual phenotypes. As a result, it is largely unknown how phenotypic plasticity in sexual traits influences fitness, selection and responses to selection [18]. Finally, populations are usually studied in a non-random range of habitats, typically where abundance is highest and data collection is most efficient. This can give a biased perception of variation in sexual phenotypes, and selection on these phenotypes, while also ignoring the importance of interpopulation processes such as meta-population dynamics [17–19]. These omissions should not be taken to mean that there is little value in past and current research on sexual traits; however, taking these issues seriously could provide a way to resolve or dissolve some longstanding issues (e.g. the importance of genetic benefits for understanding fitness variation in the wild, or the role of sexual trait evolution in speciation [9,20]) and help to integrate sexual selection research into the study of phenotypic evolution more widely.

Here, we use recent examples to emphasise how environmental heterogeneity and phenotypic plasticity influence selection on sexual traits and, consequently, how predictions of current theory can be affected. We argue that these studies show the importance of bringing the interaction between organisms and the environment into focus, thereby moving away from treating sexual selection as a sufficient explanatory framework on its own and towards an evolutionary ecology of sexual traits.

Selection is not constant in time and space

Evolution in a constant environment can be different from evolution in variable environments [21–23]. This is as relevant for sexual traits as it is for non-sexual traits, but surprisingly fluctuations in the strength, direction and form of selection on sexual traits have been largely ignored. As a result, its documentation is novel (Box 1 and Figures 1 and 2). In fact, a recent review examining gene-by-environment interactions on sexual traits only found 20 (out of 10605 on sexual selection, i.e. 0.2%) empirical studies addressing how selection varies across environments, all of which found selection to vary widely [8].

The strength, direction and form of sexual, viability and kin selection potentially all vary across and within

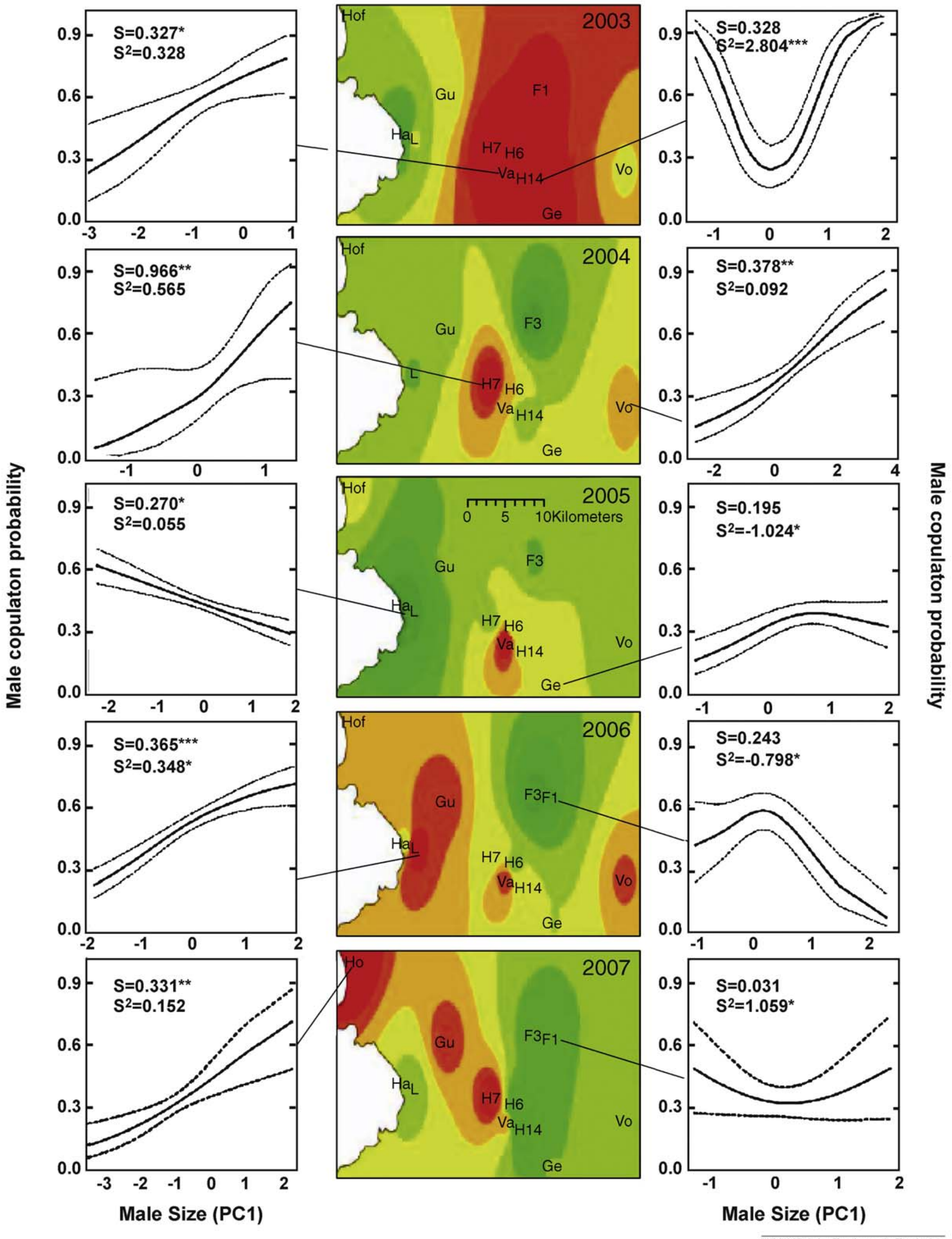

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Figure 1. Temporal and spatial variation in sexual selection on male body size in blue-tailed damselflies, *I. elegans*. This figure demonstrates how fluctuating selection generates selection mosaics in the wild. Central panels map variation in selection differentials on male copulation probability across the 12 study populations during 2003–2007 (top to bottom: red = positive directional selection, green = negative directional selection). Panels each side of the central panels give examples of changes in selection (cubic splines ± bootstrap SE) for six populations, two per year (reproduced with permission from [16]).

populations and thereby modify the overall (natural) selection on phenotypes. In common lizards, *Lacerta vivipara*, experimental manipulation of population sex ratios modified interactions between males and females and generated changes in both sexual and viability selection, which influenced population dynamics [24]. Furthermore, in several species, variance in relatedness within and among populations, and the costs and benefits of interacting with individuals, vary substantially, for instance as a result of environmental-dependent reproductive skew and

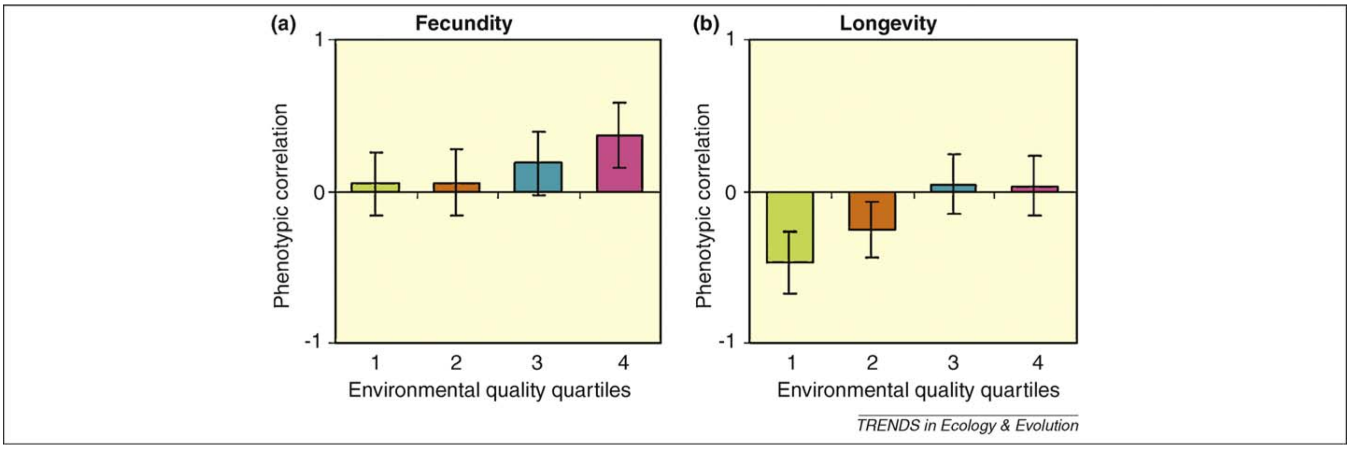

Figure 2. Changes in sexual **(a)** and viability **(b)** selection on male horn-size across varying environmental conditions in Soay sheep, *O. aries*, as indicated by changes in the phenotypic correlation between horn size and fecundity and horn size and longevity respectively. The environmental quality that an individual experienced during its birth year was defined as the proportion of lambs that survived their first winter. This was split into four quartiles with '1' representing poor environments and '4' good environments (reproduced with permission from [5]). This figure demonstrates the importance of environmental heterogeneity in determining the interactions between different selection pressures.

dispersal [25–27]. For example, in white-winged choughs, *Corcorax melanorhamphos,* severe drought can cause the breakdown of stable groups of cooperatively breeding relatives [28,29]. This generates new reproductive opportunities for unrelated individuals and increases variance in relatedness [28] leading to changes in the opportunity for sexual selection and kin selection. Consequently, fluctuations in kin selection and how it interacts with sexual selection and viability selection can influence the way sexual phenotypes evolve by changing the relationships between sexual traits and the direct and indirect components of inclusive fitness (Glossary) [6,7,25–27]. Such spatial and temporal variation could contribute to maintaining variation in sexually selected traits and suggests that studies limited to a single site, point in time or type of selection will produce different conclusions about how sexual traits evolve (Boxes 2 and 3) [8,30].

These and other recent examples illustrate that assumptions of consistent directional, stabilising or disruptive selection on a particular sexual trait are biologically unrealistic. We predict that with increasing data on reproductive success in natural populations, spatial and temporal selection mosaics will turn out to be the rule rather than the exception. Many authors have taken the resulting genotype-by-environment interactions to be an explanation for the maintenance of sexual traits signalling genes for viability ('good genes': Box 2), thereby resolving the lek paradox [8,20]. Instead, we argue that gene–environment interactions represent a statistical signature of a biological reality in which good genes selection *sensu strictu* occurs only under restricted circumstances unlikely to be frequently met in natural populations of most organisms (Boxes 2 and 3).

Box 2. Environmental heterogeneity and plasticity: implications for classic sexual selection models

The implications of environmental heterogeneity and plasticity for phenotypic evolution may be far ranging [14] but here we focus on the direct consequences for some traditional theories of the evolution of sexual traits via intersexual selection.

Genetic benefit indicator models [12,32] can be united under a single umbrella because they all make the central prediction that sexual traits signal the genetic benefits that individuals transfer to offspring. It is expected that the expression of sexual traits is genotype specific, that offspring with this genotype will have higher survival or reproductive success, and that choosing to breed with individuals with a certain phenotype on average results in higher fitness [12,32]. The lek paradox arises because directional sexual selection should deplete genetic variation (recent studies on the lek paradox have highlighted the potential importance of direct benefits in maintaining variation in sexual traits but here we focus on models of sexual selection that deal with genetic benefits).

Sexual antagonistic coevolution poses that, because males have a higher potential rate of reproduction than females, an evolutionary arms race ensues whereby males are selected to manipulate females, and females are selected to avoid being manipulated [51]. This generates the prediction that an increase in the fitness of one sex causes a reduction in the fitness of the other sex, which is revealed through sex-by-genotype effects on fitness.

Genetic compatibility occurs when offspring fitness is influenced by the epistatic interactions between genomes inherited from both parents. This is predicted to generate non-directional sexual selection for genetically compatible mates, such as individuals with different disease resistance genes.

Environmental heterogeneity and plasticity can influence the main predictions listed above by:

(i) Causing unpredictable links between genotypes and phenotypes. For instance, during poor conditions, individuals with high chances of survival might reduce the expression of their sexual traits to reserve resources for times when reproductive success might be higher, whereas individuals with low chances of survival might do the opposite [20,34,60,61].
(ii) Causing differences in the environment that parents and offspring experience. This creates fluctuating selection within and across generations, alters the severity of sexual conflict, and can modify the benefits that parental genes transfer to offspring [5,8,16,42].
(iii) Reducing or exaggerating selection. For example, individuals might increase their investment in reproductive attempts with chosen or manipulative sexual partners, further exaggerating selection on targets of mate choice [50,62]. Alternatively, individuals might do the opposite to compensate for reproductive attempts with less favoured partners [63].

Box 3. The importance of scale

The spatial and temporal scales at which individuals interact have profound implications for how evolution proceeds, particularly with traits affected by social interactions. This has been clearly illustrated by research on the evolution of altruism [64]. Social interactions are also fundamental to the evolution of sexual traits and, although the details of how the scale at which individuals interact influences sexual traits are different from altruism, the principles are the same [65,66]. When individuals interact globally, different genotypes will on average experience the complete variation in environments and the traditional predictions made by models of sexual selection should hold (Box 2). By contrast, if individuals only interact locally, such as when gene flow is restricted, there will be high variation in how sexual traits evolve across populations as the interplay between environmental conditions, selection and plastic responses progresses. Predictions made by traditional models of sexual selection (see Box 2) that assume constant selection will therefore only apply to fine scales. If competition is somewhere in between global and local or there is high temporal variation, the predictions of classic sexual selection models will not be met because the environments that parents and offspring experience will continually be different. The signature of spatial heterogeneity on sexual trait evolution will therefore depend on temporal variation. Consequently, to understand the evolution of sexual phenotypes the scale that individuals interact and how this affects the dynamics between heterogeneity, selection and plasticity needs to be ascertained. For example, in the golden orb-web spider, *Nephila plumipes*, density and sex ratios change both seasonally and across spatial scales, resulting in inconsistent selection on male body size and weight across and within populations [42] (Figure I). Consequently, model predictions of body size evolution via intra- or inter-sexual selection will only be fulfilled at local scales and depending on, for example, rates of dispersal and demographic fluctuations.

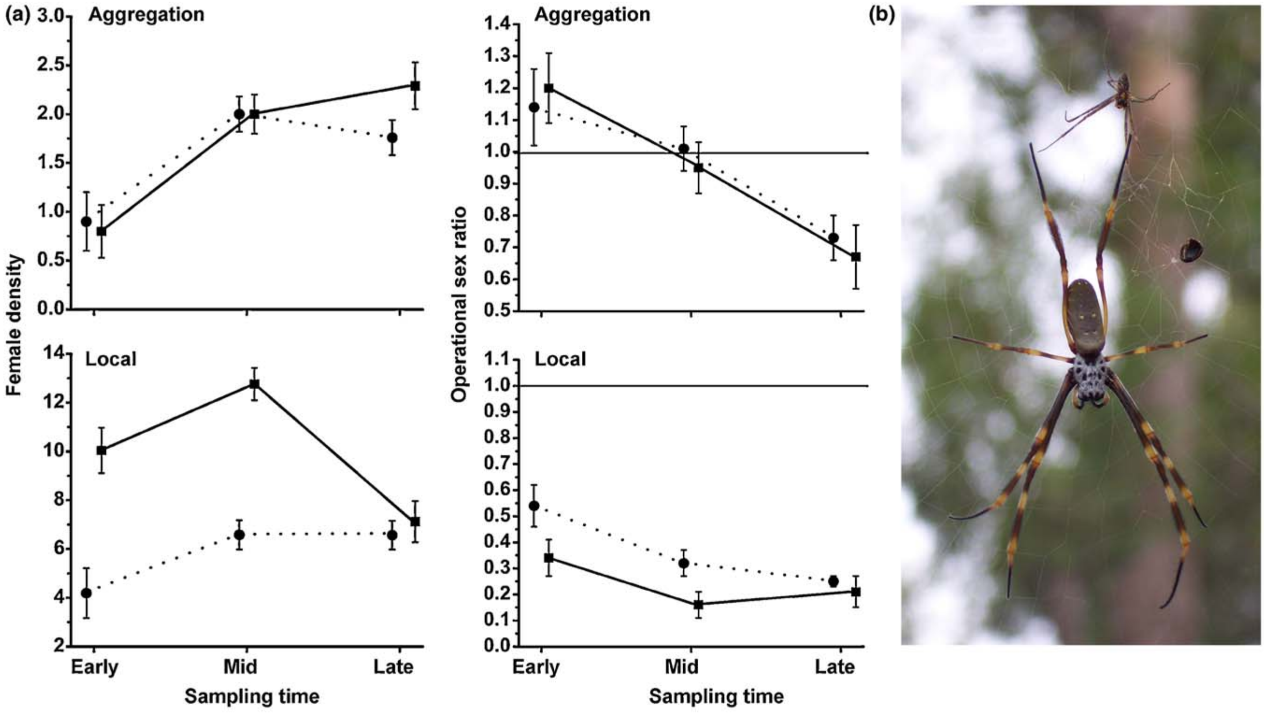

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Figure I. **(a)** Variation in female density and operational sex ratio (OSR) across the breeding season in the golden orb-web spider, *N. plumipes*, at three spatial scales: (i) Aggregations, which are groups of webs that share support strands (top panels); (ii) local scale defined as a radius of 5 m around focal aggregations (bottom panels); and (iii) the population level (squares and solid lines = high density population; circles and dashed lines = low density population) (reproduced with permission from [42]). Female density and OSR determine sexual selection on male copulation success and paternity. Together these results illustrate how theories of sexual selection need to take into account the temporal and spatial scales at which interactions between individuals take place. **(b)** A male (top) and female (bottom) *N. plumipes* (photo courtesy of Michael Kasumovic).

Sexual phenotypes are plastic

Changes in environmental and physiological states tend to cause variation in trait expression, i.e. phenotypic plasticity [14,21]. Phenotypic plasticity in non-sexual traits has been so well documented [14,22] that non-plastic phenotypes are almost considered an anomaly that is in more need of explanation than plasticity itself [31]. However, models of sexual selection commonly assume a direct relationship between genes and phenotypes, and phenotypic plasticity is normally only considered in the context of condition dependence (Box 2) [12,32]. Condition dependence implies that expression of a sexual trait is contingent upon the physiological state (condition) of the individual, which represents a measure of individual quality passed on in terms of offspring quantity or quality [32]. This assumes that condition dependence is an evolved outcome in response to directional selection, which ignores that the relationship between condition and the phenotype might be different across individuals, environments and sexual traits [11,20,33,34]. Thus, considering plasticity only from the perspective of condition dependence fails to capture: (i) the multi-dimensional aspect of plasticity; (ii) the functional integration of sexual phenotypes across spatial and temporal contexts [13]; (iii) its role in creation of novel variation and as an initiator of phenotypic evolution; and (iv) plasticity as a cause of selection [14,35–37]. In fact, even at the most basic level, plasticity in sexual phenotypes beyond condition dependence can change the predictions of sexual selection models (Boxes 2 and 3). At a broader level, understanding plasticity can be the key to understanding evolutionary patterns, such as rapid evolutionary divergence in sexual phenotypes that underlie speciation [14,18,38], a key aim of current sexual selection research [39,40]. Consequently, plastic responses cannot be ignored when attempting to understand the micro- and macro-evolution of sexual phenotypes.

The lack of research on the role of phenotypic plasticity in the evolution of sexual traits does not reflect that plasticity is rare. On the contrary, plasticity in sexual morphology and behaviour should be common because interactions with partners or competitors typically vary as a result of changes in environmental and demographic factors [16,25,41,42]. Indeed, several recent studies have shown that both the expression of sexual traits, and preferences for such traits, can vary at different timescales within and between populations [16,17,43,44]. This has led several authors to question the basis for some sexual selection theories, such as the presence of genetic benefits of mate choice, for natural populations [45–47]. Furthermore, plasticity in the form of differential allocation or sex ratio bias could reduce or enhance, for instance, intralocus sexual conflict [33,48–51], thereby creating different evolutionary dynamics than when allocation is constrained. At the very least, such plasticity needs to be considered when making inferences about sexual conflict (Box 2). More likely, plasticity represents a common evolutionary response to natural selection that makes most current research overestimate the importance of genetic conflict as an explanation for the evolution of sexual phenotypes in natural populations (Box 2).

Environmental heterogeneity, plasticity and selection are intertwined

Environmental variation, plasticity and selection must be considered in concert because they are intimately intertwined [14,36,52]. Environmental heterogeneity generates fluctuating selection that causes phenotypic plasticity. Plasticity changes the temporal and spatial distribution of phenotypes (social environment), which in turn determines selection. The importance of this feedback loop between heterogeneity, selection and plasticity for the evolution of sexual traits depends on the scale at which individuals interact, a necessary component of any theory of the evolution of traits involving social interactions (Box 3). For example, in the house finch, *Carpodacus mexicanus,* the expression of a male secondary sexual trait as well as genetic relatedness between mates varies temporally as a result of sex-biased dispersal over the breeding season, which generate changes in the targets of mate choice [17]. Furthermore, the strength and direction of this selection acting on secondary sexual traits can be amplified or reduced when differential allocation in relation to mate phenotype affects the development of primary or secondary sexual traits in offspring (Box 2) [33,53]. As changes in sexual traits affect both trait distributions and selection on those traits [54] interactions between competitors, partners and environmental conditions continuously modify selection. Studies that take snapshots in time and/or space are therefore expected to show inconsistent results with respect to the covariance between genes, sexual phenotypes and proxies of fitness.

Heterogeneity and plasticity can be studied

Complex interactions between individuals and environments make it difficult to generate and test clear-cut predictions about how sexual phenotypes evolve. This is perhaps why sexual selection research has tended to be relatively detached from ecology. However, spectacular scenarios of the importance of sexual selection are only good science as long as they are firmly based on the biology of our study organisms. Therefore what we advocate is largely a change in research focus rather than an overwhelming change in methodology. We believe a greater understanding of the evolution of sexual traits will come by developing several areas.

First, to generate testable predictions we need more explicit theory on how sexual traits evolve when selection on both phenotypes and preferences for those phenotypes, vary at different spatial and temporal scales due to environmental heterogeneity. Furthermore, greater theoretical insight is needed into how phenotypic plasticity affects the evolution of sexual traits, for example, by altering selection through changing the social environment.

Second, we need a better understanding of the developmental basis of, and plasticity in, sexual phenotypes in natural populations that enables the genetic and phenotypic integration of sexual and non-sexual traits across different contexts to be explored [13,55]. For example, several recent laboratory studies have documented long-term effects of early developmental conditions on sexual traits, but their importance in the wild is poorly understood [33,48]. Similarly, behavioural plasticity across repeated intra- and intersexual interactions can have important implications for the evolution of sexual traits by changing the costs and benefits of sexual strategies [46,56]. However, detailed data that can be used to construct mechanistic models are scarce.

Third, measuring heterogeneity and plasticity will help identify the scale at which interactions between individuals occur. This is important to determine the appropriate scale for models of the evolution of sexual traits under specific contexts, and hopefully will enable more general patterns to be deduced as data on sexual traits across wider temporal and spatial scales becomes available for more species. This is likely to be facilitated by novel methodology that enables remote monitoring of individual interactions in the wild (e.g. [57]).

Fourth, the extent to which selection (sexual, viability and kin) on sexual traits varies temporally and spatially can only be addressed by empirical studies across ecologically relevant settings [5,16,19,24,42]. For example, experimental manipulation of population demography or resource distribution has substantially improved the understanding of the shape of fitness surfaces for various morphological traits [24,55,58] and we argue that this approach is also needed for sexual traits [55]. This data can then be used to integrate measurements of sexual, viability and kin selection on the expression of, and relationships between, sexual traits across different spatial and temporal scales under natural conditions.

Ideally, all four points can be integrated, facilitating a joint progression of theoretical research and empirical studies that manipulate phenotypes, plasticity in phenotypic traits, and environmental contexts. This will generate a much better understanding of the mechanistic and evolutionary causes behind the inconsistencies in empirical results that seem so difficult for sexual selection research to reconcile.

Summary

Although the concept of sexual selection was inspired by phenotypic diversity [59], sexual selection studies have been based on a narrow gene-centric view, leaving little room for responsive, plastic phenotypes inhabiting and creating heterogeneous environments [11]. We have argued here that there is much to gain from explicitly addressing how environmental heterogeneity, phenotypic plasticity, and the different selection pressures they create, affect the evolutionary ecology of sexual phenotypes. Existing models of sexual selection have their place in this framework. The challenge is now to provide an accurate description of their shifting dynamics as organisms and environments change and how they fit into the wider framework of phenotypic evolution.

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