Despite the increasing knowledge that ecology and evolution are often contemporary processes, our understanding of how sexual selection affects (and is affected by) eco-evolutionary feedbacks is limited. We discuss examples of such eco-evolutionary processes in the context of sexual selection in an attempt to understand: 1) The challenges related to identifying and characterizing causal relationships within these processes, as well as their consequences. 2) When and how eco-evolutionary feedbacks of sexual selection may help us appreciate the effects of sexual selection in shaping evolutionary processes.

**Synthesis**

**Introduction**

Traditionally, the field of evolutionary ecology has considered that ecology and evolution operate at different time-scales (Slobodkin 1961, Pianka 2011, Schoener 2011). However, in the last decades it has been acknowledged that evolutionary changes are contemporary with ecological changes, leading to eco-evolutionary
feedbacks. These can be broadly defined as the contemporary reciprocal effect of 1) an ecological factor (be it biotic or abiotic) upon the evolutionary trajectory of a population and 2) the effect of this evolutionary change on an ecological factor (Carroll et al. 2007, Fussmann et al. 2007, Schoener 2011, Kinnison et al. 2015, Hendry 2016). Therefore, in accordance with the current literature, eco-evolutionary feedbacks can be divided into eco-to-evo and evo-to-eco processes, whenever one refers to 1) or 2) respectively (Hendry 2016). When the feedback is open, the same eco-evolutionary feedback can affect different traits, individuals or species; in contrast, a closed eco-evolutionary feedback, also called an ‘eco-evolutionary loop’, is defined as a tight closed interaction such that the initial driver of the feedback will also be the subsequent object. Thus, eco-evolutionary feedbacks not only encompass tight evolutionary interactions traditionally defined as coevolution, but also indirect ecological interactions, whenever such interactions drive an evolutionary response.

Sexual selection is a fertile ground for the occurrence of feedbacks between ecology and evolution (Carroll et al. 2007, Svensson and Gosden 2007, Giery and Layman 2019, Svensson 2019). First, sexual selection concerns the interaction between two sexes in which one is part of the ecology of the other, and in which rapid evolutionary dynamics have been amply demonstrated (Gosden and Svensson 2009, Rodrigues et al. 2016). For instance, in the presence of predation risk, female guppies become less receptive to male sexual displays, which in turn drives a switch in male behaviour towards female coercion (Godin and Briggs 1996, Gong and Gibson 1996). In this context, females are part of the males’ ecology and their behaviour drives male evolution. Note that this can be conceptually different from coevolution, where both the changes happening in one sex and the response of the other sex are necessarily genetic. Second, sexual selection strongly shapes and is shaped by the ecological setting of populations (Maynard-Smith 1991, Anderson 1994). Indeed, it is increasingly evident that the evolution of traits under sexual selection can take place rapidly, potentially modifying the ecological context and the selection pressures to which individuals are exposed. The ecological conditions that organisms are exposed to, in turn, can modify the strength and direction of sexual selection. Therefore, traits under sexual selection may be important players in eco-evolutionary feedbacks (Seehausen et al. 2008, Grieshop et al. 2016). In this manuscript, we discuss the importance of eco-evolutionary feedbacks in sexual selection. We first set a clear distinction between processes in which ecology drives evolution and those in which the contemporary evolution of populations may change their ecology. We then discuss how and to which extent we can distinguish such processes. Finally, we evaluate how the study of eco-evolutionary feedbacks can help us understand the impact of sexual selection on key evolutionary processes. Our goal is to establish a systematic (and as unambiguous as possible) approach to the study of eco-evolutionary feedbacks in the context of sexual selection.

Figure 1. Different traits – abiotic (a), biotic heterospecific (b) or biotic conspecific (c) – can function as ecological factors driving sexual selection. Distinct colour tones represent different genotypes; distinct colours represent different species; dashed lines encircle ecological drivers; full lines encircle objects of selection; dashed arrows point from ecological drivers to objects of selection; grey arrows represent evolutionary change; bars in graphs indicate the change over time of the mean value of the trait under selection.
Evidences of eco-evolutionary feedbacks of sexual selection

Ecological change as a driver of sexual selection

In the context of sexual selection, we can group ecological factors imposing a selection pressure on individuals in a population into three broad categories (Fig. 1): 1) abiotic factors, such as light (Gamble et al. 2003, Cole and Endler 2015), temperature (Punzalan et al. 2008), or habitat heterogeneity (Lukasik et al. 2006); 2) biotic heterospecific factors, such as predation (Endler 1980), parasitism (Kennedy et al. 1987, Milinski and Bakker 1990), prey availability (Engqvist 2007, Albo et al. 2014), or heterospecific competition (Gröning and Hochkirch 2008, Rodrigues et al. 2016); and 3) biotic conspecific factors, including intra-specific competitors for food, mates and territory (Rodrigues et al. 2016), population density (Kokko and Rankin 2006), sex ratio (Kokko et al. 2012), or population structure (Macke et al. 2014). Notice that abiotic factors may have a biotic origin. For instance, Seehausen et al. (1997) provided evidence that eutrophication increased water turbidity, which interfered with mate choice, relaxing sexual selection and resulting in a reduction of colour diversity in cichlids. Another example stems from Drosophila melanogaster females adapting to ethanol. When mated with control males, such females produced a higher proportion of offspring sired by their first mate as compared to females adapted to the other environment (cadmium). In this case, a change in diet (ecological change) led to different patterns of female sperm use (evolutionary change). This thus provides evidence for an ecological process driving evolutionary change, i.e. an eco-to-evo process (Arbuthnott et al. 2014).

Sexual selection as driver of ecological change

Evo-to-eco processes (i.e. evolutionary change driving an ecological response) have been much less explored than eco-to-evo processes so far. Indeed, to determine how contemporary evolutionary changes can influence ecology, at the population, community and ecosystem levels has been one of the main goals of the eco-evolutionary dynamics field (Palkovacs and Hendry 2010). To reveal an evo-to-eco process, the evolution of a trait needs to be studied and complemented by an analysis of its ecological consequences. To accomplish this, it is necessary to detect or manipulate a contemporary evolutionary response. It is important to acknowledge that this evolutionary change is itself a product of a particular ecological pressure. Thus, the existence of an evo-to-eco process is inevitably part of an eco-evolutionary feedback, be it open or closed.

A few manipulative experimental studies have focused on the role of sexual selection on ecological adaptation, revealing an eco-to-eco process. Using an experimental evolution approach (Plesnar-Bielak et al. 2012), tested resistance to a thermal environmental challenge in populations of bulb mites Rhizoglyphus robini evolving under enforced monogamy (few reproductive interactions, i.e. weak sexual selection) or polyandry (multiple reproductive interactions, i.e. strong sexual selection). They found that all populations persisted after 17 generations, except those evolving under weak sexual selection and subjected to high-temperature conditions. Another study investigated how sexual selection influenced the ability of populations to withstand inbreeding in the flour beetle Tribolium castaneum, also using experimental evolution (Lumley et al. 2015). They manipulated sexual selection by creating the following regimes: male-biased (strong sexual selection), female-biased (weak sexual selection) and polygamous (strong sexual selection) or monogamous (weak sexual selection) populations. After 45 generations, populations were subjected to inbreeding (sib×sib mating) for up to 20 generations. While lineages under weak sexual selection showed a rapid decline in fitness, lineages under strong selection were significantly more resilient to the mutational load. Importantly, the authors confirmed that during the first 45 generations, effective population size and heterozygosity were maintained as identical between treatments. These two studies strongly suggest that sexual selection (evolutionary change) allowed these populations to avoid extinction (ecological change) and can be seen as examples of evolutionary rescue.

Phenotypic differences driven by sexual selection can also result in significant ecological consequences upon secondary contact between diverging populations. For instance, two lineages of the European wall lizards Podarcis muralis, one Italian and one western European, experience different intensities of sexual selection, resulting in Italian males being more aggressive in their mating attempts. As a result, when in secondary contact, a large proportion of males from the Italian lineage mated with females from the western European lineage (MacGregor et al. 2017). Thus, differences in the evolutionary history of sexual selection (evolutionary change) led to substantial changes in the mating pool of both populations when in sympathy (ecological change). For a comprehensive review of evidence of evo-to-eco processes in vertebrate populations in the field, see Giery and Layman (2019).

Challenges in identifying the players involved in eco-evolutionary feedbacks of sexual selection

Demonstrating an eco-evolutionary feedback is not trivial. Researchers are often biased in terms of framing experiments within a single context (e.g. how ecological factors affect the strength or mode of sexual selection), rather than trying to reverse the direction of causality (e.g. how sexual selection can change the ecological context) or looking for feedbacks. Even though there are several examples where eco-evolutionary feedbacks of sexual selection have been unravelled (Box 1), we feel that the field is far from exploiting its full potential. To do so, there are some challenges ahead.
Box 1. Empirical examples of eco-evolutionary feedbacks of sexual selection

Abiotic factors
In fish from the genus *Pundamilia*, female preference for male colour is necessary and sufficient for assortative mating between *P. pundamilia* and *P. nyererei*, two closely related species that co-occur in narrow water depth ranges (Selz et al. 2014). Indeed, *P. nyererei* is found in greater mean water depths than *P. pundamilia* and deeper water selects for better detection of red light, presumably via more efficient foraging (while shallow water selects for better blue light detection; Seehausen et al. 2008). This change in female sensory perception selects for altered male nuptial colouration (redder in deep water, bluer in shallow water), in order to increase conspicuousness during courtship (Seehausen et al. 2008). In sympathy, female preference for males of a given colour reinforces speciation, and molecular data confirm that this behavioural change has a genetic basis. In this case, we have an example of a comparative study of an eco-evolutionary feedback mediated by an abiotic factor. Different light environments (ecological change) promote changes in female’s mating colour preferences (evolutionary change), which in turn promotes habitat specialization along a depth gradient (ecological change).

Biotic factors

**Heterospecifics**
Magurran and Seghers (1994) studied the reproductive behaviour of the guppy *Poecilia reticulata* in the wild. Using a comparative approach, they compared several traits across multiple populations, such as the number of mating attempts in males and the frequency of mating avoidance in females. In locations with high predation risk, females suffered more harassment from males and evaded more mating attempts (Seghers 1974). Furthermore, females that evaded males tended to forage less (Dussault and Kramer 1981). This shows that sexual conflict evolved in the presence of predators, probably because of predation risk, resulted in a change from a female-biased to an evenly balanced sex-ratio, thus increasing the strength of sexual selection (Seghers 1974). Taken together, these studies unravel an eco-evolutionary feedback mediated by heterospecific interactions: Predation risk (ecological change) increased male harassment and female mating evasion (evolutionary change), thus reducing the foraging time of females and consequently their diet (ecological change).

**Conspecifics**
Seminal work by Bill Rice disentangled the coevolution between males and females of *Drosophila melanogaster* and exposed an eco-evolutionary feedback (Rice 1996). In this work, using an experimental evolution approach, coevolution of the two sexes was prevented using genetic manipulation, allowing males to evolve but preventing females from doing so. Females were thereby transformed into an ecological resource for males, but their role as an evolutionary player was abolished. In the face of non-evolving females, males evolved an increased re-mating rate and increased seminal fluid toxicity, which reduces female survival. Thus, blocking the females’ response exposed the evolution of male harassment. Furthermore, because under male and female coevolution these negative effects of males upon females are not detected, these results suggest that females respond to the evolution of male harassment by becoming resistant. In this case, an eco-evolutionary feedback between conspecifics emerged: In the presence of non-evolving females (ecological change) male became more aggressive (evolutionary change). In turn, male aggressiveness selects for female resistance behaviour (evolutionary change).

Identifying the components of the feedback

Enough must be known about the system to identify potential components of a feedback, in order to design appropriate experimental manipulations and decide which phenotypes to track. Once a response to an ecological change has been measured, additional manipulations will often be necessary to determine the chain of causality. This might be difficult to address in a single study. For instance, Lesna and Sabelis (1999) found that hybrids of two field populations of the soil predatory mite *Hypoaspis aculeifer* performed well on one diet, but badly in another. Accordingly, females from each population mated disassortatively or assortatively, this way always producing fit offspring. This study thus shows that different food conditions (ecological change) — led to changes in mating behaviour. While this change in mating behaviour may cause a change in the frequency of each morph in the population (in which case it would constitute an evolutionary change), this change was not formally demonstrated. Hence, the whole eco–evo process was not fully documented. Still, this type of study can be a necessary first step to fully identify such processes.

Limitations in defining ecological and evolutionary change

In the previous sections, we used various examples to illustrate the distinction between ecological and evolutionary change as components of eco-evolutionary feedbacks. We define ecological change as variation in the quantity of a variable, that is, changes occurring in number, frequency or proportion (Smallegange and Coulson 2013). For instance, modifications in predator number, or frequency of mating partners or competitors are all ecological changes. Evolutionary changes are alterations in gene frequencies, and are expressed as shifts in the shape of the distribution of allele frequencies involved
in the expression of a character/phenotype (Smallegange and Coulson 2013). These may include changes in the heritable component of traits, such as the size or colour of a sexual trait, or the expression of a behaviour. Although this distinction is evident in examples where ecological and evolutionary change occur at different time scales, at similar time scales – and especially when studying feedbacks involving conspecific interactions – it is often very hard to disentangle ecological and evolutionary change from each other. Furthermore, if we consider sexual interactions within a population, it would not be meaningful to argue that a change in male harassment levels should be considered an ecological effect, and the response of females to harassment (e.g. by becoming more resistant) an evolutionary effect, given that 1) both changes probably happen simultaneously or at least on approximately the same timescale, and 2) both may or may not involve changes in allelic frequencies in the population. Moreover, ecological and evolutionary change may sometimes be too intertwined to be teased apart (Fig. 2). We therefore argue that there is a need to be very careful in using a conceptual distinction between ecological and evolutionary change when studying eco-evolutionary feedbacks, as these can be context-dependent or ambiguous. The risk is otherwise the creation of a false dichotomy between eco-to-evo and evo-to-eco processes, providing an incomplete description of the eco-evolutionary interaction.s

Inferring causality in an eco-evolutionary feedback

One possible alternative, at least in some cases, is to focus on the distinction between drivers and objects of change. The driver of change will produce a response in the object of change, regardless of whether the driver is an ecological or evolutionary effect, and whether the response is considered an ecological or evolutionary change. This approach focuses on the agents of change, accepting that ecological and evolutionary change can be happening at the same time and therefore difficult (or not useful) to disentangle. However, it is important to note that the continuous nature of the eco-evolutionary dynamics means that the choice of any particular starting point for a feedback is essentially arbitrary, and that classifying one agent as driver or object of change is dependent on that starting point but not on the agent itself. For example, in Box 1, we present an example where predation pressure leads to increased male mating harassment in guppies, causing a change in female diet as a result of avoiding males (Dussault and Kramer 1981, Magurran and Seghers 1994). One could easily start by saying that predation risk is a driver of change that acts on males, the object of change. However, one could also start with male harassment and focus on its effect on female avoidance behaviour (Magurran and Seghers 1994). From this new starting point, male behaviour, which was previously classified as an object of change, becomes a driver of change in females (the new object of change).

When determining drivers and objects of change, one should pay particular attention to the difference between sequentially-evolved and coevolving traits (Fig. 2). Two different trait interactions, with distinct eco-evolutionary processes, can result in the same evolutionary outcome, potentially leading researchers to wrongly identify a causal relationship. As a hypothetical example, consider a given experimental evolution design with two regimes: in one of them, females are allowed to mate with several males (multiple mating, high sexual selection) while in the other, females mate with a single male (monogamy, low sexual selection). After some generations, males from the multiple mating regime show increased mating rate. Females from the single mating treatment also have higher mortality than females from the multiple mating treatment when they are

Figure 2. The same evolutionary outcome can result from different eco-evolutionary processes. In this example, there are two alternative evolutionary processes: 1) a common selective pressure (here abiotic), or 2) a first trait that is selected, and another that responds to the change in this selected trait. If 1), an eco-evolutionary process occurs and affects males and females simultaneously. However, there is no eco-evolutionary feedback. In 2), an environmental factor drives a change in a certain trait in females. This change in trait value, in turn, acts as an environmental factor for male evolution. This is a good example of an eco-evolutionary feedback. Distinct colour tones represent different genotypes. Dashed lines encircle ecological drivers; full lines encircle objects of selection; dashed arrows point from ecological drivers to objects of selection; grey arrows represent evolutionary change; white arrows indicate alternative processes; bars graphs indicate the change over time of the mean value of the trait under selection.
crossed with males from the multiple mating treatment. Laying out all the events, we have:

1) Two ecological regimes that impose different selective pressures.
2) The evolutionary response of males, which show increased mating rate in the multiple mating regime.
3) The evolutionary response of females, with females from the multiple mating regime showing higher resistance to male harm than females from the single regime.

From an initial change in an ecological factor 1), several causality cascades are possible with this simple example (Fig. 2). First, both 2 and 3 may evolve as a response to the selection pressure described in 1. In this case, we cannot consider this as an eco-evolutionary feedback, but as evidence of two traits jointly evolving in response to a common selection pressure (i.e. the ecological factor of larger group size is the driver of change, and both mating rate in males and resistance in females are the objects of change). The other possibility is that 1 is a selection pressure for just one of those traits, either 2 or 3, and the other responds to this selected trait. For example, trait 2 (male mating rate) is the object of the initial selection pressure, but then in turn it becomes the ecological driver of change in trait 3 (female resistance; note that the reverse chain of causality is also possible). This is a good example of an eco-evolutionary feedback. The way to disentangle these two options is not straightforward. Indeed, one would need to show that the responding trait 3) would not evolve in populations exposed to the same ecological conditions 1), but in which the selected trait 2) did not evolve. That is, one would not expect females to evolve resistance to male harassment in an environment where females mate multiply, but in which males do not evolve increased harassment of females.

Choosing suitable methodologies

The complexity associated with eco-evolutionary processes advises against any ambitions of having a single universal approach fit for all studies. Instead, each question and biological system will determine the best strategy used. Here, we provide some examples that have already been used successfully.

Experimental evolution provides a degree of environmental and population control that is particularly suited to investigate eco-evolutionary feedbacks. Indeed, most experimental evolution studies start by imposing different selective pressures on replicate populations originating from a common stock population. After some generations, individual and population traits are measured in one or several environments. Often, different selective pressures lead to significant differences in trait values. Hence, at their onset, experimental evolution studies are examples of eco-to-evo processes. Commonly enough though, they lead to new ecological dynamics that can provide empirical evidence for evo-to-eco processes (Box 1). However, experimental evolution is not without its limitations. For example, if density-dependence plays a role in the dynamics of populations or trait changes, this will be masked by set-ups that rely on fixed population sizes and non-overlapping generations (Smallegange et al. 2018).

Another means to identify an eco-evolutionary process is to thoroughly compare populations of the same species that are exposed (or not, as a control) to a specific ecological factor which causes evolutionary changes in one or more traits, and then study the consequences of these evolutionary changes. Apart from requiring a deep knowledge of the populations involved, this approach will often have limitations in determining a contemporary relationship between the traits involved but may be useful in species where experimental evolution is not an option. In addition, causality may in some cases be determined via further experimental manipulations (Duckworth and Aguillon 2015).

Finally, independently of the approach used, to confirm that the changes that have been observed are truly evolutionary in nature, the existence of a genetic response must be documented. Tracking changes in the frequencies of alternative reproductive tactics are good examples of the latter methodology, as changes in allele frequencies can be inferred from morph frequencies. A good example of negative frequency-dependent selection in alternative reproductive tactics is found in the blue-tailed damselfly Ischnura elegans, in which male mating harassment mediates the frequency of the three female morphs, one of which (Androchrome) is a male mimic and the other two are more cryptic (Infuscans and Infuscans obsoleta), collectively known as Gynochromes (Cordero et al. 1998, Svensson et al. 2005). In this system, the female morphs are genetically determined by three alleles at a single autosomal locus, being simple enough for allele frequencies to be tracked over generations and making it possible to establish that frequency changes in the field are consistent with negative frequency-dependence (Svensson et al. 2005, Le Rouzic et al. 2015). Indeed, males seek the most common morphotype, and these females are subjected to higher frequencies of harassment. Recognition of male-mimic Androchromes as females is additionally influenced by their frequency relative to the male frequency, thus population density and sex ratio influence feedbacks of sexual selection in this system. Altogether, male harassment decreases the frequency of the most common female morphotype in the population (evolutionary change), while male preference depends on the frequency of female morphs (ecological change).

Implications for the study of evolutionary ecology

Sexual selection appears to play a dual role in the adaptation of populations to novel environments (Chenoweth et al. 2015, Grieshop et al. 2016). On the one hand, it can enhance adaptation via more efficient purging of deleterious mutations (Agrawal 2001, Whitlock and Agrawal 2009, Grieshop et al. 2016), via a reduction of genetic drift in
small populations (Whitlock 2000), or via good genes mechanisms of sexual selection (Lorch et al. 2003, Parrett and Knell 2018) – not only because sexually selected traits are good indicators of genetic quality (Parrett and Knell 2018, Martinossi-Allibert et al. 2019) but also because sexual selection favours the maintenance of this association between display and genetic quality (Lorch et al. 2003). However, such benefits of sexual selection have been predicted by theory to decrease in small populations experiencing environmental change (Martinossi-Allibert et al. 2019). Moreover, sexual and natural selection may operate in opposite directions (Houle and Kondrashov 2002, Chenoweth et al. 2015), and the reproductive interests of the sexes are frequently antagonistic, which suggests that sexual selection can also hamper adaptation. Which of these outcomes is most likely should depend on the ecological context a population finds itself in.

Consider for instance the Allee effect, where a decrease in population density or size is correlated with a decrease in the mean reproductive success of individuals (Allee 1927, Allee and Bowen 1932). Such an effect can stem from an increasing reproductive skew due to sexually selected female choice. In this case, a strong female preference can decrease the probability of finding a suitable male mating partner, thus decreasing the reproductive output of the population and effectively leading to the Allee effect (Møller and Legendre 2001, Kokko and Rankin 2006). Alternatively, if we consider a population adapting to a novel environment, sexually selected female choice can drive an increase in the reproductive success of fitter individuals if female preference is correlated with male good genes or condition. In this case, the initial decrease in population size can be surpassed by an increase in the rate of adaptation of the population. In this case, the Allee effect is transient and disappears as the population adapts. Hence, the evolutionary consequences of the Allee effect are a function of the ecological context, suggesting this phenomenon can be better understood in an eco-evolutionary framework.

An analogous scenario can be described for populations experiencing fluctuating population dynamics. For instance, under the Chitty hypothesis, population dynamics are self-regulated by competitive interactions among individuals within the population. In the context of sexual selection, in a high-density population, male–male competition selects for an increase in the harassment of females, which can have a cost in female fecundity and survival (Pitnick and García–González 2002, Martin and Hosken 2004). Such a cost can result in a decrease in population size and, as density decreases, a decrease in male harassment. This, in turn, causes an increase in population size, which again leads to increased male mating harassment. This kind of dynamics has been suggested by Chitty (1952), as means by which interactions between individuals limit population growth and density and account for the maintenance of intrapopulation diversity. While the higher levels of sexual selection and male competition can promote faster fixation of good genes and the purging of deleterious ones, the negative frequency-dependence can promote the maintenance of intrapopulation diversity. Together, both processes can be beneficial to the adaptation of a population to a novel environment. However, in small populations, the very same demographic instability has also been predicted to increase the risk of extinction (Martínez-Ruiz and Knell 2017). Again, a detailed knowledge of the species’ ecological context is essential to determine the outcome of the costs and benefits of sexual selection.

Overall, it is clear that the dynamics of sexual selection are strongly intertwined with those of ecological processes. Still, identifying how and in what contexts a given selective pressure or ecological change will drive a particular evolutionary outcome remains elusive. Predicting evolution is certainly not an easy task and – if anything – the study of the eco-evolutionary dynamics of sexual selection shows that the balance between the costs and benefits of sexually selected traits are strongly dependent on the ecological context, in particular on how they feed back into the dynamics of the population (Martínez-Ruiz and Knell 2017, Yun et al. 2018).

To conclude, there is potential in expanding the study of eco-evolutionary dynamics of sexual selection. A correct and unambiguous identification of eco-evolutionary processes involving sexual selection is an essential step towards developing successful methodologies that allow to systematically consider how this force can contribute to shape evolutionary processes. Ultimately, an objective characterization of eco-evolutionary feedbacks of sexual selection will allow researchers to better understand the causal relations within such feedbacks and to acquire a more acute knowledge of the dynamics involved in these processes.

Acknowledgements – Funding – This project was funded by an ERC grant (COMPCON GA725419) to S. Magalhães and by an ERC grant (ERC-StG-2015-678148 (ComplexSex)), to J. Abbott. J. Alpedrinha had a Post-Doc grant (SFRH/BPD/109533/2015) funded by FCT (Fundação para a Ciência e Tecnologia). J. Abbott was also funded by the Swedish Research Council (VR-2015-04680).

Author contributions – J. Alpedrinha and L. R. Rodrigues contributed equally to this paper.

References

Agrawal, A. F. 2001. Sexual selection and the maintenance of sexual reproduction. – Nature 411: 692–695.

Albo, M. J. M. J. et al. 2014. Evolution of worthless gifts is favoured by male condition and prey access in spiders. – Anim. Behav. 92: 25–31.

Allee, W. C. 1927. Animal aggregations. – Q. Rev. Biol. 2: 367–398.

Allee, W. C. and Bowen, E. S. 1932. Studies in animal aggregations: mass protection against colloidal silver among goldfishes. – J. Exp. Zool. 61: 185–207.

Anderson, M. 1994. Sexual selection. – Princeton Univ. Press.

Arbuthnott, D. et al. 2014. Remating and sperm competition in replicate populations of Drosophila melanogaster adapted to alternative environments. – PLoS One 9: e90207.
Carroll, S. P. et al. 2007. Evolution on ecological time-scales. – Funct. Ecol. 21: 387–393.

Chenoweth, S. F. et al. 2015. Genomic evidence that sexual selection impedes adaptation to a novel environment. –Curr. Biol. 25: 1860–1866.

Chitty, D. 1952. Mortality among voles (Microtus agrestis) at Lake Vyrnwy, Montgomeryshire in 1936–1939. – Phil. Trans. R. Soc. B 236: 505–552.

Cole, G. L. and Endler, J. A. 2015. Variable environmental effects on a multicompartment sexually selected trait. – Am. Nat. 185: 452–468.

Cordero, A. et al. 1998. Mating opportunities and mating costs are reduced in androchrome female damselflies, Ischnura elegans (Odonata). – Anim. Behav. 55: 185–197.

Duckworth, R. A. and Aguillon, S. M. 2015. Eco-evolutionary dynamics: investigating multiple causal pathways linking changes in behavior, population density and natural selection. – J. Ornithol. 156: 115–124.

Dussault, G. V. and Kramer, D. L. 1981. Food and feeding behavior of the guppy, Poecilia reticulata (Pisces: Poeciliidae). – Can. J. Zool. 59: 684–701.

Endler, J. A. 1980. Natural selection on color patterns in Poecilia reticulata. – Evolution 34: 76–91.

Engqvist, L. 2007. Sex, food and conflicts: nutrition dependent nuptial feeding and pre-mating struggles in scorpionflies. – Behav. Ecol. Sociobiol. 61: 703–710.

Fussmann, G. F. et al. 2007. Eco-evolutionary dynamics of communities and ecosystems. – Funct. Ecol. 21: 465–477.

Gamble, S. et al. 2003. Environmental variation and the maintenance of polymorphism: the effect of ambient light spectrum on mating behaviour and sexual selection in guppies. – Ecol. Lett. 6: 463–472.

Giery, S. T. and Layman, C. A. 2019. Ecological consequences of sexually selected traits: an eco-evolutionary perspective. – Q. Rev. Biol. 94: 29–74.

Godin, J.-G. J. and Briggs, S. E. 1996. Female mate choice under predation risk in the guppy. – Anim. Behav. 51: 117–130.

Gong, A. and Gibson, R. M. 1996. Reversal of a female preference after visual exposure to a predator in the guppy, Poecilia reticulata. – Anim. Behav. 52: 1007–1015.

Gosden, T. P. P. and Svensson, E. I. I. 2009. Density-dependent effects in mating systems. – Phil. Trans. R. Soc. B 361: 319–334.

Gong, A. and Gibson, R. M. 1996. Reversal of a female preference after visual exposure to a predator in the guppy, Poecilia reticulata. – Anim. Behav. 51: 117–130.

Godin, J.-G. J. and Briggs, S. E. 1996. Female mate choice under predation risk in the guppy. – Anim. Behav. 51: 117–130.

Gong, A. and Gibson, R. M. 1996. Reversal of a female preference after visual exposure to a predator in the guppy, Poecilia reticulata. – Anim. Behav. 52: 1007–1015.

Gosden, T. P. P. and Svensson, E. I. I. 2009. Density-dependent effects in mating systems. – Phil. Trans. R. Soc. B 361: 319–334.

Gong, A. and Gibson, R. M. 1996. Reversal of a female preference after visual exposure to a predator in the guppy, Poecilia reticulata. – Anim. Behav. 51: 117–130.

Gong, A. and Gibson, R. M. 1996. Reversal of a female preference after visual exposure to a predator in the guppy, Poecilia reticulata. – Anim. Behav. 51: 117–130.

Gosden, T. P. P. and Svensson, E. I. I. 2009. Density-dependent effects in mating systems. – Phil. Trans. R. Soc. B 361: 319–334.

Gong, A. and Gibson, R. M. 1996. Reversal of a female preference after visual exposure to a predator in the guppy, Poecilia reticulata. – Anim. Behav. 51: 117–130.

Gosden, T. P. P. and Svensson, E. I. I. 2009. Density-dependent effects in mating systems. – Phil. Trans. R. Soc. B 361: 319–334.

Gong, A. and Gibson, R. M. 1996. Reversal of a female preference after visual exposure to a predator in the guppy, Poecilia reticulata. – Anim. Behav. 51: 117–130.

Gosden, T. P. P. and Svensson, E. I. I. 2009. Density-dependent effects in mating systems. – Phil. Trans. R. Soc. B 361: 319–334.
Schoener, T. W. 2011. The newest synthesis: understanding the interplay of evolutionary and ecological dynamics. – Science 331: 426–429.

Seehausen, O. et al. 1997. Cichlid fish diversity threatened by eutrophication that curbs sexual selection. – Science 277: 1808–1811.

Seehausen, O. et al. 2008. Speciation through sensory drive in cichlid fish. – Nature 455: 620–626.

Seghers, B. H. 1974. Geographic variation in the responses of guppies (Poecilia reticulata) to aerial predators. – Oecologia 14: 93–98.

Selz, O. M. et al. 2014. Female preference for male color is necessary and sufficient for assortative mating in 2 cichlid sister species. – Behav. Ecol. 25: 612–626.

Slobodkin, L. B. 1961. Growth and regulation of animal populations. – Holt, Rinehart and Winston.

Smallegange, I. M. and Coulson, T. 2013. Towards a general, population-level understanding of eco-evolutionary change. – Trends Ecol. Evol. 28: 143–148.

Smallegange, I. M. et al. 2018. Population consequences of individual heterogeneity in life histories: overcompensation in response to harvesting of alternative reproductive tactics. – Oikos 127: 738–749.

Svensson, E. I. 2019. Eco-evolutionary dynamics of sexual selection and sexual conflict. – Funct. Ecol. 33: 60–72.

Svensson, E. I. and Gosden, T. P. 2007. Contemporary evolution of secondary sexual traits in the wild. – Funct. Ecol. 21: 422–433.

Svensson, E. I. et al. 2005. Female polymorphism, frequency dependence and rapid evolutionary dynamics in natural populations. – Am. Nat. 165: 567–576.

Whitlock, M. C. 2000. Fixation of new alleles and the extinction of small populations: drift load, beneficial alleles and sexual selection. – Evolution 54: 1855–1861.

Whitlock, M. C. and Agrawal, A. F. 2009. Purging the genome with sexual selection: reducing mutation load through selection on males. – Proc. R. Soc. B 63: 569–582.

Yun, L. et al. 2018. Competition for mates and the improvement of nonsexual fitness. – Proc. Natl Acad. Sci. USA 115: 6762–6767.