

Songs *versus* colours *versus* horns: what explains the diversity of sexually selected traits?

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ABSTRACT

Papers on sexual selection often highlight the incredible diversity of sexually selected traits across animals. Yet, few studies have tried to explain why this diversity evolved. Animals use many different types of traits to attract mates and outcompete rivals, including colours, songs, and horns, but it remains unclear why, for example, some taxa have songs, others have colours, and others horns. Here, we first conduct a systematic survey of the basic diversity and distribution of different types of sexually selected signals and weapons across the animal Tree of Life. Based on this survey, we describe seven major patterns in trait diversity and distributions. We then discuss 10 unanswered questions raised by these patterns, and how they might be addressed. One major pattern is that most types of sexually selected signals and weapons are apparently absent from most animal phyla (88%), in contrast to the conventional wisdom that a diversity of sexually selected traits is present across animals. Furthermore, most trait diversity is clustered in Arthropoda and Chordata, but only within certain clades. Within these clades, many different types of traits have evolved, and many types appear to have evolved repeatedly. By contrast, other major arthropod and chordate clades appear to lack all or most trait types, and similar patterns are repeated at smaller phylogenetic scales (e.g. within insects). Although most research on sexual selection focuses on female choice, we find similar numbers of traits (among sampled species) are involved in male contests (44%) and female choice (55%). Overall, these patterns are largely unexplained and unexplored, as are many other fundamental questions about the evolution of these traits. We suggest that understanding the diversity of sexually selected traits may require a shift towards macroevolutionary studies at relatively deep timescales (e.g. tens to hundreds of millions of years ago).

Key words: contest competition, macroevolution, mate choice, ornaments, phylogeny, sexual selection, weapons

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I. INTRODUCTION

Dozens, if not hundreds, of papers on sexual selection begin in much the same way. They start off by highlighting the incredible diversity of sexually selected traits across animals, often referencing Andersson’s (1994) classic book. This diversity includes bright colours, long tails, complex songs, elaborate dances, and massive horns (Fig. 1). Yet, despite being mentioned so frequently, this diversity itself has actually gone largely unexplained. Here, we will outline this general problem and several other fundamental but unresolved questions about the evolution of sexually selected traits.

Sexually selected traits can differ in many ways. First, sexually selected traits can have different *functions*, such as attracting females or repelling rival males. Second, they can involve different *sensory modalities*, including visual (e.g. colour), acoustic (e.g. songs), olfactory (e.g. pheromones), and tactile traits (e.g. horns) used as weapons during fights over access to mates. Third, sexually selected traits can include many different *types*. That is, even for a single function (e.g. attracting females) and a single sensory modality (e.g. visual), there can be many different kinds of traits (e.g. colours, elongated tails, head ornaments, dances). Fourth, a trait can have many different *forms* within and



Fig. 1. Examples of the diversity of sexually selected traits in animals (left to right): top: songs and colouration in warblers, colouration in jumping spiders, exaggerated eyespans in stalk-eyed flies, elongated tails in swordtail fishes; middle: enlarged claws in fiddler crabs, calls in frogs, cheek flanges in primates, colouration in damselflies; bottom: wattles in fowl, antlers and calls in elk, colours and pheromones in butterflies, neck frills in agamid lizards. All photos from Wikimedia Commons. Photo credits: Wolfgang Wander, Thomas Shahan, Jojo Cruzado, Loury Cédric, Wilfredo R. Rodriguez H., Vikram Gupchup, Eric Kilby, Alan Schmierer, Muhammad Mahdi Karim, Luc Viatour, Dinesh Valke, Miklos Schiberna.

among species, such as the remarkable diversity in colouration among African cichlids (Maan & Sefc, 2013), call structure among crickets (Otte, 1992), and horn location among dung beetles (Emlen *et al.*, 2005). Herein, we focus specifically on functions, sensory modalities, and types of traits, because these levels of variation are relatively understudied and challenging to understand.

Many papers mention the diversity of sexually selected traits, but few try to explain it. At some level, this is perfectly understandable: elucidating the mechanisms of sexual selection within species is an exciting challenge, and clearly difficult enough. Remarkable progress has been made, and we now have a detailed understanding of many classic model systems, including guppies (Houde, 1997), red deer (Clutton-Brock, Guinness & Albon, 1982), túngara frogs (Ryan, 1985), house finches (Hill, 2002), and crickets (Zuk & Simmons, 1997). However, broad-scale patterns in the evolution and distribution of sexually selected traits across the animal Tree of Life remain largely unexplored. At finer scales, even for well-studied taxa (e.g. birds), the factors that explain the evolution of different trait types among species are poorly understood.

Our review is not simply a summary or call for phylogenetic studies of sexual selection. In fact, researchers have been using phylogenies to study these traits for the last 30 years (e.g. Basolo, 1990b), but typically among closely related species. Instead, we emphasize the patterns and unanswered questions that arise from considering deeper phylogenetic scales.

II. DOCUMENTING THE DIVERSITY AND DISTRIBUTION OF SEXUALLY SELECTED TRAITS

A first step towards understanding the diversity of sexually selected traits is to document that diversity. For example, what types of traits are found in which clades? To our knowledge, this diversity has not been systematically reviewed across animals. Andersson's (1994) book reviewed all traits known at the time, but was not necessarily systematic (e.g. no search methods given). A more recent book reviewed sexual dimorphism across animals (Fairbairn, 2013), but not different types of signals and weapons. Rico-Guevara & Hurme (2019) recently surveyed intrasexually selected weapons across animals, but not traits used in mate choice.

We systematically surveyed the literature for sexually selected signals and weapons across animal phyla (methods, full results, and references are provided as online Supporting information in Appendices S1–S3). Following Andersson (1994), the main criteria for including traits were: (i) a significant relationship between that trait and mating success; and (ii) an identified mechanism of sexual selection (i.e. mate choice, contest competition). Our goal was not to include every case of sexual selection in every species, nor to provide an unbiased sampling of species within clades. Instead we

highlight the diverse types of traits and their distribution among major clades. Moreover, bias towards more well-studied species within clades should not be problematic. Specifically, because we focus on clades above the level of families, it should not matter that some species in a family are more likely to be studied than others (again, we are not estimating the frequency of traits among species within clades). Conversely, our results would likely misrepresent the distribution of traits among clades if we only included randomly sampled species, because relatively few species have been studied for sexual selection. However, see Appendix S1 for caveats about some patterns.

We define a sexually selected trait as a character associated with differential mating success of reproductively mature conspecifics (e.g. Andersson, 1994). Therefore, we did not include traits used exclusively for species or sex recognition.

We also excluded two important classes of traits, given our emphasis on signals and weapons. First, we excluded overall body size and sexual size dimorphism. Body size is a frequent target of sexual selection in animals (Andersson, 1994; Hunt *et al.*, 2009), but does not necessarily evolve primarily as a signal or a weapon (unlike most other traits that we focus on here). Furthermore, our goal is to describe the *diversity* of types of traits. Thus, excluding one type of trait should not overturn our conclusions. Second, we excluded postcopulatory traits (e.g. enlarged testes, complex genitalia), which may confer a fitness advantage in the context of sperm competition or cryptic female choice (Eberhard, 1996; Birkhead & Møller, 1998; Simmons, 2001). These traits are not necessarily signals or weapons. In summary, we focus on a somewhat restricted set of traits (i.e. precopulatory signals and weapons, excluding body size).

III. GENERAL PATTERNS IN TRAIT DIVERSITY AND DISTRIBUTION

Our survey (Table 1; Appendix S2) suggests several intriguing patterns. First, these traits are absent from most animal phyla (Fig. 2). Among the 34 currently recognized animal phyla, these traits appear to be present in only four: Arthropoda, Chordata, Mollusca, and Rotifera. Thus, even though it is common to talk about sexually selected traits as present 'across animals' most signals and weapons are actually documented in only a handful of phyla. Furthermore, many phyla that seem to lack these traits are relatively diverse, mobile, conspicuous, and well studied (e.g. Annelida, Cnidaria, Echinodermata, Nematoda, Onychophora, Platyhelminthes). Even if further studies (or other criteria) yield additional traits in some of the other 30 phyla, there is still a striking disparity in trait distribution among phyla. Importantly, if we include documented sexually selected traits related to body size and postcopulatory selection (Appendix S1), the distribution of these traits among phyla remains basically unchanged (i.e. these excluded trait types have been documented mostly in arthropods and chordates).

Second, even within phyla having these traits, their distribution is highly restricted (Appendix S2). For example, in Rotifera, we found a single trait (pheromone) in one species. In Mollusca, these traits are documented in only one class (Cephalopoda) among seven commonly recognized classes. Sexually selected signals and weapons are widespread in Chordata and Arthropoda, but many classes still appear to lack these traits (6 of 13 in Chordata, 9 of 12 in Arthropoda). Thus, these traits appear to be surprisingly rare among major animal clades.

Third, the *diversity* of these traits is clumped phylogenetically, with multiple types of traits evolving within a few major clades (Appendix S2). For example, most types of traits (e.g. colours, calls, pheromones, enlarged structures, and displays) have evolved in ray-finned fishes, frogs, salamanders, squamate reptiles (lizards and snakes), mammals, birds, insects, malacostracan crustaceans, and arachnids (Table 1).

Fourth, there were multiple origins of the same trait type within these phyla (Appendix S2). Many traits seem to represent independent origins because the taxa having them are phylogenetically isolated among taxa lacking them. For example, in Chordata, acoustic signals in ray-finned fishes, frogs, mammals, turtles, and birds most likely represent separate origins (Chen & Wiens, 2020). Similarly, conspicuous colouration apparently evolved separately in dragonflies, wasps, beetles, flies, and butterflies. Many traits also appear to have independent origins because the specific traits differ. For example, in arthropods, the enlarged structures used in contest competition differ across clades, including cerci (earwigs), mandibles (ants, wasps, thrips), hindlimbs (leaf-footed bugs), horns (beetles), antlers and stalked eyes (flies), and claws (decapod crustaceans).

Fifth, despite the concentration of trait diversity in a limited number of clades, most species have relatively few traits (Appendix S2). We found that only 12.7% of the species with sexually selected traits in this survey have more than one type ($N = 28$ of 220; Appendix S2). There are clearly exceptions. For example, male dung beetles (*Onthophagus taurus*) have horns, behavioural displays, and pheromones (Appendix S2). But even these exceptions appear to have only a subset of the traits present in the major clades to which they belong (Table 1). To our knowledge, no single species has been documented to have sexually selected colours, calls, pheromones, enlarged structures, and behavioural displays. In our survey, the species that come closest include some birds (e.g. *Phasianus colchicus* with elongated tail and head feathers, colours, and behavioural displays) and fish (e.g. *Gasterosteus aculeatus* with colours, pheromones, and behavioural displays). Of course, further research may reveal additional traits in many species (e.g. pheromones). Nevertheless, the dominant pattern is apparently for most species to have few traits, and for different traits instead to be present in different species.

Sixth, contest competition and mate choice are both widespread (Appendix S2). We found that a similar percentage of traits are used in male contests (44%) *versus* female choice

Table 1. Summary of the different types of sexually selected traits present in major animal clades

Phylum	Class	Trait
Arthropoda	Insecta	Colouration, calls, pheromones, enlarged appendages, horns, leg ornaments, enlarged eyespans, nuptial food gifts, behavioural displays
Arthropoda	Arachnida	Colouration, vibrational calls, pheromones, enlarged appendages, leg ornaments, behavioural displays
Arthropoda	Malacostraca (crabs, etc.)	Colouration, pheromones, enlarged appendages, behavioural displays
Mollusca	Cephalopoda	Colouration, behavioural displays
Chordata	Actinopterygii (ray-finned fish)	Colouration, calls, electric calls, pheromones, enlarged or elongated fins, tubercles, enlarged snouts, behavioural displays
Chordata	Amphibia	Colouration, calls, pheromones, enlarged limbs, dorsal crests
Chordata	Squamata (lizards, snakes)	Colouration, pheromones, head ornaments (crests, dewlaps), behavioural displays
Chordata	Aves	Colouration, calls, pheromones, elongated feathers, spurs, fleshy ornaments (shields, wattles, combs), behavioural displays
Chordata	Mammalia	Colouration, calls, pheromones, enlarged limbs, tusks, antlers, horns, head ornaments (manes, crests, cheek flanges), behavioural displays
Rotifera	Monogononta	Pheromone

(55%; $N = 272$ traits, among 213 species; Appendix S4). The 272 include 26 cases in which the same trait is used for both functions in the same species, and 28 species with multiple trait types (methods in Appendix S1). Including nine traits among seven species in which the trait was used for male mate choice and/or female contest competition yields similar values (44% *versus* 56%, $N = 281$). Recent reviews have highlighted the idea that most research on sexual selection has focused on female choice over contest competition (McCullough, Miller & Emlen, 2016; Tinghitella *et al.*, 2018). Here, we provide evidence suggesting that male–male competition may be nearly as important as female choice for the origins of sexually selected traits across major animal clades.

Seventh, many traits are used both to attract females and repel rivals. We found at least 65 examples of a single trait used in both mate choice and contest competition, either in the same species or among close relatives (Appendix S5; see also Berglund, Bisazza & Pilastro, 1996).

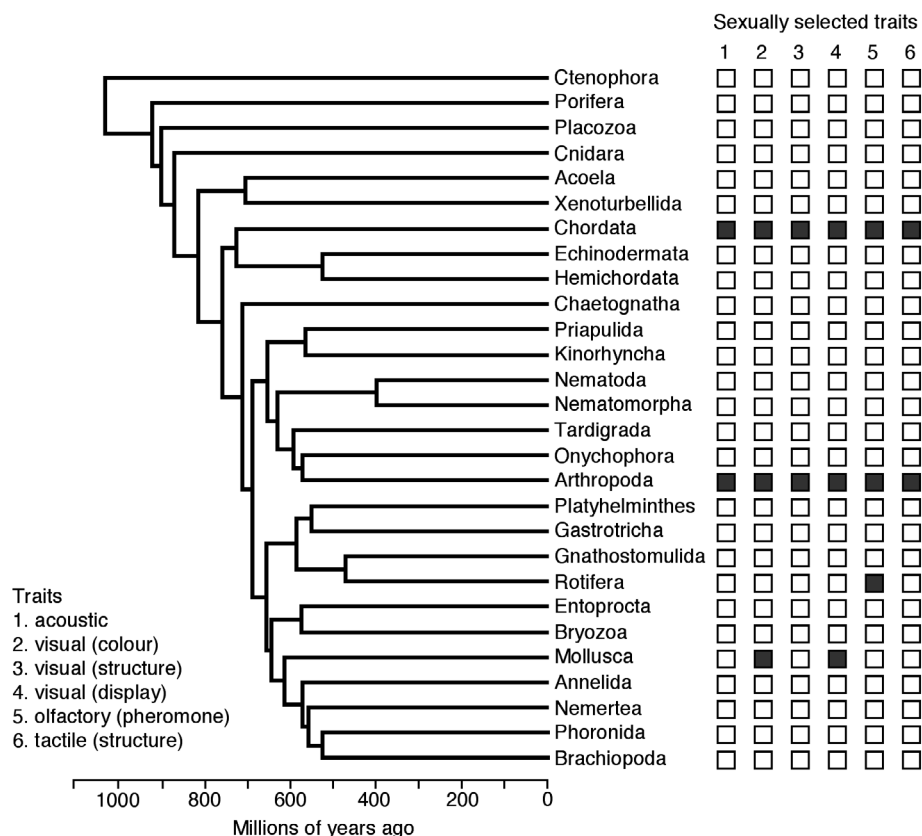


Fig. 2. The distribution of six major types of sexually selected traits among 28 animal phyla. Filled boxes indicate that a trait type is present in at least one species in that phylum (irrespective of prevalence), whereas open boxes indicate that the trait is absent from that phylum (as far as is currently known). There are many ways to subdivide most of these trait types (e.g. there are many different types of enlarged structures, and they can be used as visual signals or weapons). Details on the specific traits and their distributions within phyla are given in Appendix S2. The time-calibrated phylogeny (Wiens, 2015) includes 28 of the 34 commonly recognized phyla. These traits are also apparently absent in the six phyla not shown here (Appendix S2).

IV. UNANSWERED QUESTIONS ABOUT THE EVOLUTION OF SEXUALLY SELECTED TRAITS

The patterns observed in our survey raise many questions for future research. Most of these questions have not been addressed or even posed in previous studies (although a few have been). We do not resolve any of these questions here, but we do outline some potential hypotheses and some ways in which they might be tested.

(1) Why do so many clades lack sexually selected signals and weapons?

A striking pattern from our survey is that most animal phyla appear to lack sexually selected signals and weapons (Fig. 2). A trivial explanation would be that most animal phyla lack sexual reproduction. However, sexual reproduction is largely ubiquitous among these clades, even if some species are capable of asexual reproduction (review in Jezkova & Wiens, 2017).

Instead, a more general explanation is that conditions that favour sexually selected signals and weapons are rare among major animal clades. These traits are expected to evolve

when there is intense competition for access to reproduction, driven by skewed operational sex ratios (Emlen & Oring, 1977; Kvarnemo & Ahnesjö, 1996). They may also evolve when there are steep Bateman gradients (e.g. Arnold, 1994; Jones, 2009; Janicke *et al.*, 2016). Many phyla lacking sexually selected traits (Fig. 2) are marine or parasitic (Jezkova & Wiens, 2017). Thus, the primary challenge for individuals in these clades may be simply to locate a mate, and so such traits may do little to improve a male's mating success (Kokko & Rankin, 2006). Interestingly, many phyla lacking these traits may solve the problem of mate scarcity by being simultaneous hermaphrodites (Fairbairn, 2013; see fig. 1 of Jezkova & Wiens, 2017). Many phyla lacking these traits are also marine clades with broadcast spawning and thus limited opportunities for male–male competition and precopulatory female choice. Yet, simply being marine seems insufficient to explain this pattern, given the many traits in marine ray-finned fishes (calls, colouration, enlarged structures, pheromones, behavioural displays; Appendix S2). These hypotheses can be tested using phylogenetic comparative methods, including Pagel's (1994) test for dependent evolution of discrete traits.

(2) Why do some phyla have so many different kinds of sexually selected traits?

Our results suggest that most types of signals and weapons evolved convergently in arthropods and chordates (Fig. 2). The presence of different sensory systems may be one of the most important factors that drives this pattern. Many phyla lacking these traits lack vision and hearing. By contrast, many arthropods and chordates share vision, hearing, and olfaction. These are the two phyla in which diverse signals and weapons evolved (Fig. 2). Thus, different types of traits may be clumped across the animal Tree of Life because different sensory systems are. Eyes (lens-bearing or compound) are present in only four phyla (Annelida, Arthropoda, Chordata, Mollusca), although photoreceptors in general are more widespread (16 of 28 phyla; Jezkova & Wiens, 2017). Olfaction is also widespread, but it is unclear if it has been surveyed widely across phyla. Minimally, olfaction occurs in arthropods, chordates, molluscs, and nematodes (Eisthen, 2002). Hearing may be more restricted, and is apparently confined to arthropods (where it evolved ~19 times; Yager, 1999) and vertebrates (where it evolved once; Popper & Fay, 1997). Surprisingly, hearing seems to have evolved only in phyla with vision and olfaction. Overall, the clustered distribution of different types of traits may arise because of a clustered distribution of sensory systems. Explaining if and why different sensory systems are correlated in their distribution should be an interesting area for future research.

Future studies can also use phylogenetic approaches to test how closely the origin of different types of traits is related to their corresponding sensory systems. For example, vision (photoreceptors and/or eyes) is present in many phyla apparently lacking visual signals (e.g. Acoela, Annelida, Bryozoa, Chaetognatha, Cnidaria, Echinodermata, Kinorhyncha, Nematoda, Nematomorpha, Onychophora, Platyhelminthes, Rotifera, Tardigrada; Jezkova & Wiens, 2017). Thus, visual signals are dependent on vision, but vision and visual signals might still be only weakly correlated across taxa. By contrast, hearing and acoustic signals may be more closely tied. Ancestral-state reconstructions on time-calibrated phylogenies could be used to quantify the ‘waiting time’ between when a sensory system originates in a given clade and the earliest origin of the corresponding signal, and compare these waiting times across sensory systems and clades.

The idea that sensory systems are important in shaping the evolution of sexually selected traits is well established (e.g. Endler, 1992; Endler & Basolo, 1998; Boughman, 2002; Price, 2017). However, this idea is generally applied to different trait forms among closely related species (e.g. blue *versus* red nuptial colouration in cichlids; Seehausen *et al.*, 2008). Here, we suggest that the type of sensory systems present in different phyla may help shape which types of traits are present in which clades, and the overall clumping of traits among phyla. Nevertheless, this is just one hypothesis that may potentially explain this pattern.

(3) Why do some clades within phyla have so many traits?

Just as sexually selected traits seem to be clumped in certain phyla (Fig. 2), they also appear to be clumped in certain clades within phyla (Table 1). Thus, a few clades have many different types, whereas most others have few or none (Appendix S2). For example, among insect orders, Coleoptera (beetles) and Diptera (flies) each have 10 types of traits (e.g. in Coleoptera: horns, enlarged mandibles, enlarged hindlegs, enlarged forelegs, enlarged antennae, elongated rostra, colouration, pheromones, drumming displays, and flashing displays). By contrast, five orders have only one type, and 16 appear to have none (Appendix S6). Similarly, among bird orders, Passeriformes (perching birds), Galliformes (landfowl), and Charadriiformes (shorebirds) each have at least eight different types of traits documented (e.g. in Galliformes: elongated tail and head feathers, plumage colouration, flesh colouration, tarsal spurs, fleshy head ornaments, calls, and tidbitting displays). Yet, 11 orders appear to have none explicitly documented (Appendix S6).

The least interesting explanation for these patterns is that clades with more species have more types of traits. Thus, if clade A has a million species and clade B has 10, we would expect all types to evolve in A and none in B, by chance alone. But there seems to be more to this pattern than a simple relationship between species richness and trait diversity. For example, despite their high trait diversity, Galliformes (~300 species) are not exceptionally species rich relative to other bird orders (Gill & Donsker, 2018) or other animal clades.

We speculate that certain clades have accelerated rates of trait origins relative to their age and species richness. These high rates might be associated with individual traits (e.g. multiple origins of conspicuous colours in birds) and may be correlated across traits (e.g. accelerated rates in the same clades for different traits). These hypotheses can be tested using maximum likelihood to estimate transition rates for each trait in each clade (e.g. orders of birds), given a time-calibrated phylogeny and trait data within each clade. Phylogenetic ANOVA and regression can then be used to test whether rates are significantly higher in some clades, and whether rates are correlated between pairs of traits among clades.

This research could then open the door to testing which ecological and evolutionary factors are correlated with these accelerated rates. Thus, certain mating systems may promote trait origins (Emlen & Oring, 1977; Kvarnemo & Ahnesjö, 1996; Kokko, Klug & Jennions, 2012). Other relevant factors may include habitat or genetic systems (e.g. Reeve & Pfennig, 2003; Mank *et al.*, 2006), and trade-offs between pre- and postcopulatory sexual selection (Pollux *et al.*, 2014; Simmons, Lüpold & Fitzpatrick, 2017).

(4) Why do different species have different types of traits?

The observation that different species often have different types of traits may be fundamental to explaining trait

diversity among taxa. Given this, the signalling environments in which taxa occur may be one key to understanding their different traits. An obvious example is diel (day–night) activity patterns. Nocturnal activity may favour acoustic or chemical signals over visual signals, because acoustic and chemical signals can function in darkness (Kronfeld-Schor & Dayan, 2003). Many taxa with acoustic traits are nocturnal, including most bats, frogs, crickets, and moths (Appendix S2). Furthermore, acoustic signals in some diurnal species may have originated in nocturnal ancestors (e.g. calls in the largely diurnal dendrobatid frogs, whereas frogs are ancestrally nocturnal; songs in birds; Anderson & Wiens, 2017). A recent analysis supports the hypothesis that nocturnal activity favours the origins of acoustic communication in terrestrial vertebrates, including frogs, geckoes, crocodilians, mammals, and birds (Chen & Wiens, 2020). The idea that signalling environments influence signal evolution and sensory systems is widespread (e.g. Endler, 1992; Endler & Basolo, 1998; Boughman, 2002; Price, 2017). But again this idea is generally applied to trait form among close relatives. The relationship between trait origins and signalling environments (e.g. diel activity) can be tested using phylogenetic approaches (e.g. Pagel, 1994), especially within major clades (e.g. among families of birds, mammals, squamates, ray-finned fish, spiders, insects, and crustaceans; Table 1).

Most animals must also locomote and avoid predators in a given environment, and this might also influence which traits they evolve. For example, in birds, few (if any) have bony horns used in male combat (Appendix S2). But such horns occur in many non-flying vertebrates (e.g. chamaeleonid lizards, artiodactyl mammals), and other traits used in male contests are widespread in birds (Appendix S2). One potential explanation is that constraints related to flight (e.g. thinner bones) influence which weapons evolve (e.g. no heavy, bony horns used in fights).

Similarly, constraints related to predation may help determine which traits evolve in which lineages. For example, in lizards, dorsal crests and cranial horns tend to be absent in species that escape predators by hiding in crevices and burrows (Ord & Stuart-Fox, 2006). Instead, these species often have bright male colouration (e.g. *Platysaurus*). By contrast, enlarged male crests and horns have evolved repeatedly in arboreal lizards, which do not generally flee into crevices to escape predators (e.g. in agamids, chamaeleonids, corytophanids, iguanids; Pough *et al.*, 2016). Both colours and horns can be sexually selected in lizards (Appendix S2). Thus, different anti-predator strategies may influence which traits evolve in which lineages, potentially contributing to trait diversity. More broadly, trade-offs between sexually selected traits and other types of traits may help explain which traits evolve in which taxa.

(5) Does mate choice or mate competition explain most trait origins?

Another potential explanation for why different traits evolve in different taxa is that different traits are associated with

different functions (e.g. mate choice *versus* competition). For example, horns and antlers are often used to fight rivals, whereas elongated tails and conspicuous colouration are often used to attract mates (Appendix S2). At the same time, this dichotomy is not so simple. Instead, we found many examples (Appendix S5) in which the same trait (either in the same species or close relatives) is used both to deter rivals and attract mates (see also Berglund *et al.*, 1996). Thus, different trait functions may explain only some trait diversity among animals.

These patterns also suggest a related question: in what context did most sexually selected traits initially evolve? Some authors have proposed that traits are likely to evolve first in the context of male–male competition, as signals of a male's fighting ability or social dominance, and then subsequently become co-opted for use in mate choice (Berglund *et al.*, 1996). This 'armament–ornament' hypothesis assumes that signals used in aggressive interactions are more honest because unreliable signals of fighting ability will generate immediate fitness costs in combat (Berglund *et al.*, 1996). Few studies have tested this hypothesis, but there is evidence of aggressive signals being co-opted for courtship (e.g. 'skrraa' calls in bowerbirds; Borgia & Coleman, 2000), and courtship signals co-opted for aggression (e.g. 'vertical bar' pigment patterns in swordtail fish; Morris, Tudor & Dubois, 2007). More research is needed to determine if there are general patterns in which function tends to evolve first, and if differences in function help drive trait diversity (i.e. if certain traits tend to have one function only).

Overall, one of the most basic questions about sexually selected traits remains unanswered: what function is typically associated with their origins? This question may be unresolved because it requires data on trait function for many species, combined with phylogenetic information. Although most sexual selection research has focused on mate choice (McCullough *et al.*, 2016; Tinghitella *et al.*, 2018), our survey suggests that both functions might have similar importance in explaining why these traits arise (Appendix S4).

(6) Why do traits evolve through mate choice *versus* mate competition, and as signals *versus* weapons?

The observation that traits often have different functions raises the question: what ecological and evolutionary factors might explain why a trait evolves in association with one function instead of another (i.e. mate choice *versus* mate competition; signal *versus* weapon for mate competition)? For example, do some environments or ecologies favour one mechanism over the other (Andersson *et al.*, 2002), such as weapons evolving more frequently in terrestrial and herbivorous taxa (Rico-Guevara & Hurme, 2019)? Are weapons the default, with ornaments evolving *via* female choice primarily when females are able to avoid male coercion (Pradhan & van Schaik, 2009)? These questions can be addressed using ancestral reconstructions to estimate initial trait functions, and using phylogenetic tests to relate trait functions to other ecological and evolutionary factors.

(7) Trading off or piling on: are traits positively or negatively related among species?

Another unresolved question is whether sexually selected signals and weapons tend to be negatively associated (i.e. trade-offs) or positively associated among species, and whether this depends on phylogenetic scale. Our survey suggests that different trait types are positively related among phyla (Fig. 2) and within phyla (Table 1). However, studies of more closely related species have found conflicting patterns. For example, there appears to be a trade-off between chemical signalling (pheromones) and visual signalling (colourful skin pigmentation) in Old World monkeys and apes (Liman & Innan, 2003). Further, song elaboration is negatively correlated with colourful plumage in some birds (e.g. Badyaev, Hill & Weckworth, 2002), but not others (Ornelas, González & Espinosa de los Monteros, 2009; Mason, Shultz & Burns, 2014). Future studies should test explicitly for positive *versus* negative relationships between traits at different scales using phylogenetic tests, and address why certain traits are favoured over others in different taxa (for negative relationships) and why some types occur together (for positive relationships). Some hypotheses described above may be relevant to explaining both negative relationships (e.g. different signalling environments) and positive relationships (e.g. clustering of sensory systems in certain phyla). Positive relationships among traits among species might also be related to the origins of multiple traits within species (see Section IV.(8)).

(8) How is the presence of multiple traits within species related to trait diversity within clades?

Our survey indicates that some species have multiple trait types (e.g. birds with colours, long feathers, and songs), whereas others have just one (e.g. wrasses with only colours). Understanding why a single species has multiple signals may help explain the overall diversity of traits and their uneven distribution among species.

At least four hypotheses have been proposed to explain the evolution of multiple sexual signals [multiple message, redundant signal, unreliable signal (Møller & Pomiankowski, 1993); multiple receiver (Andersson *et al.*, 2002)]. These hypotheses are not mutually exclusive, and there is support for more than one hypothesis in several systems (e.g. Møller & Pomiankowski, 1993; Taff *et al.*, 2012; Guindre-Parker *et al.*, 2013).

Importantly, these hypotheses suggest that once a single trait evolves, other traits may follow, so extant species might differ in trait diversity because they represent different time-points in this overall process. However, the process might also work in the opposite direction. Thus, multiple traits might evolve within a single ancestral species, but then traits might be lost in various lineages, generating variation in the number of traits in each species across the clade. These scenarios could potentially be distinguished with ancestral-state reconstructions (i.e. to determine whether the earliest ancestral species with each trait in a clade most likely had multiple traits or single traits). These scenarios also raise the question

of whether gains or losses are more prevalent in the evolution of sexually selected traits.

(9) Are sexually selected traits more frequently gained or lost?

Our survey implies that the same types of traits have evolved repeatedly, both within and among clades (Table 1), suggesting a strong pattern of repeated gains. Yet, an older review noted that sexually selected traits are frequently lost (Wiens, 2001). However, the examples in that review were from shallow phylogenetic scales (within families or genera), whereas our examples of repeated gains involve deeper scales (among families, orders, and phyla). This contrast raises the possibility that there are biased patterns in trait gain and loss that depend on phylogenetic scale. On the other hand, these patterns might simply reflect random trait gain and loss. Future studies could test for significant biases in gain and loss using phylogenetic maximum-likelihood models (e.g. comparing the fit of a model with unbiased rates of gain and loss to one allowing different rates, and models with only gains or only losses). These tests could be applied to different types of traits, and at different phylogenetic scales.

(10) How long do sexually selected traits last?

Once they evolve, for how long do these traits persist? Can a trait that originated hundreds of millions of years ago be maintained to the present day? Or do traits tend to last just a few million years, or less? Do some types last longer than others (e.g. acoustic *versus* visual)? As one example of how different trait types might have different lifespans, we predict that morphological traits that are effectively permanent may incur high fitness costs (due to conspicuousness to predators, decreased locomotion, etc.) and may be more likely to be lost macroevolutionarily. Thus, the branches on which they are inferred to have originated should be relatively young. By contrast, traits expressed for only limited time periods (e.g. seasonally), especially behaviours that can be halted when disadvantageous (e.g. calls, dances), may incur fewer costs and might be maintained over longer timescales. For example, acoustic signals are widespread across frogs and birds, and these traits may have been maintained in these clades over long timescales (frogs: ~200 million years; birds: ~100 million years; Chen & Wiens, 2020). On the other hand, we do not know of permanent morphological traits that have been maintained over similar timescales. Among the oldest morphological traits that we know of, coloured belly patches in sceloporine phrynosomatid lizards (*Sceloporus*, *Urosaurus*) have been present for ~41 million years (Wiens, 1999; Zheng & Wiens, 2016), and coloured dewlaps have been present in dactyloid lizards (*Anolis*) for ~49 million years (Nicholson, Harmon & Losos, 2007; Zheng & Wiens, 2016). In both families, these colour traits are largely concealed unless used in behavioural displays, which may promote their long-term macroevolutionary maintenance. By contrast, conspicuous male colouration on the dorsum (i.e. constantly

exposed) has evolved in some species in both families (e.g. Wiens, Reeder & Nieto Montes de Oca, 1999; Muñoz *et al.*, 2013), but is not present in any older clades. These examples are not intended as a formal test, and we acknowledge that we may be inappropriately comparing general trait types (i.e. acoustic signals) to specific traits (i.e. belly patches). However, these examples do illustrate the type of information that could be used to test these ideas more rigorously.

V. CONCLUSIONS

- (1) One of the most frequent observations about sexually selected traits is that they are diverse across animals. Here, we summarize the diversity and distribution of these traits across the animal Tree of Life. We describe seven main patterns and discuss 10 unanswered questions arising from these patterns.
- (2) Surprisingly, we find that most types of sexually selected signals and weapons are not widespread among animal clades. Instead, most trait types are apparently absent from 88% of animal phyla, including many phyla that are relatively common, diverse, and well studied.
- (3) These traits are also highly restricted in their distribution within phyla. Most occur only in Arthropoda and Chordata, and are absent in many (or most) major clades within these two phyla. Similar patterns appear within younger groups, such as insects.
- (4) Within those clades in which these traits are present, there is often a high diversity of different trait types. Furthermore, most trait types appear to have evolved multiple times within these clades. Nevertheless, most individual species appear to have relatively few traits.
- (5) Despite widespread focus on mate choice in sexual selection research, our survey implies that traits evolve in association with mate competition almost as often as they evolve through mate choice, and many traits are used both to attract mates and to repel rivals.
- (6) Our survey highlights several unanswered questions about evolutionary patterns in sexually selected traits. We propose some hypotheses to explain these patterns and outline methods that could be used to test these hypotheses. An obvious question is why most traits are so uncommon among phyla. We suggest that many phyla may lack these traits because they lack separate sexes. Many phyla also seem to lack one or more of the sensory systems that are associated with many sexually selected signals and weapons (vision, hearing). Interestingly, different sensory systems (e.g. visual, acoustic, olfactory) appear to be clumped in those phyla with a diversity of sexually selected traits (e.g. arthropods, chordates).
- (7) Our results raise numerous other questions for future research. Do certain clades have accelerated rates of trait origins for individual traits, or for multiple traits?

If so, why? Why do different types of traits evolve in different taxa? Do most sexually selected traits originate in association with mate choice or mate competition? Is the evolution of these traits dominated by repeated trait origins, multiple losses, or is it simply stochastic? For how long do traits last?

- (8) Overall, considering these patterns in the diversity of sexually selected signals and weapons raises many new questions for the field, and many new areas for future research. Answering these basic questions and explaining these patterns may require a shift in the study of sexual selection towards macroevolutionary analyses at relatively deep timescales (tens or hundreds of millions of years ago).

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VII. REFERENCES

References identified with asterisks are used in the supporting information.

- *ADAMO, S. A. & HANLON, R. T. (1996). Do cuttlefish (Cephalopoda) signal their intentions to conspecifics during agonistic encounters? *Animal Behaviour* **52**, 73–81.
- *ADAMS, E. S. & CALDWELL, R. L. (1990). Deceptive communication in asymmetric fights of the stomatopod crustacean *Gonodactylus bredini*. *Animal Behaviour* **39**, 706–716.
- *ADDESSO, K. M., SHORT, K. A., MOORE, A. J. & MILLER, C. W. (2014). Context-dependent female mate preferences in leaf-footed cactus bugs. *Behaviour* **151**, 479–492.
- *AHUJA, A. & SINGH, R. S. (2008). Variation and evolution of male sex combs in *Drosophila*: nature of selection response and theories of genetic variation for sexual traits. *Genetics* **179**, 503–509.
- *ALBO, M. J. & COSTA, F. G. (2010). Nuptial gift-giving behaviour and male mating effort in the Neotropical spider *Paratrechalea ornata* (Trechaleidae). *Animal Behaviour* **79**, 1031–1036.
- *ALISAUSKAS, R. T. (1987). Morphometric correlates of age and breeding status in American Coots. *The Auk* **104**, 640–646.
- *ALONSO, J. C., MAGAÑA, M., MARTÍN, C. A. & PALACÍN, C. (2010a). Sexual traits as quality indicators in lekking male great bustards. *Ethology* **116**, 1084–1098.
- *ALONSO, J. C., MAGAÑA, M., PALACÍN, C. & MARTÍN, C. A. (2010b). Correlates of male mating success in great bustard leks. *Behavioral Ecology and Sociobiology* **64**, 1589–1600.
- *AMCOFF, M. & KOLM, N. (2013). Does female feeding motivation affect the response to a food-mimicking male ornament in the swordtail characin *Corynopoma rüsei*? *Journal of Fish Biology* **83**, 343–354.
- *AMCOFF, M. & KOLM, N. (2015). Multiple male sexual signals and female responsiveness in the swordtail characin, *Corynopoma rüsei*. *Environmental Biology of Fishes* **98**(7), 1731–1740.
- *AMORIM, M. C. P. & NEVES, A. S. M. (2008). Male painted gobies (*Pomatoschistus pictus*) vocalise to defend territories. *Behaviour* **145**, 1065–1083.
- *AMORIM, M. C. P., PEDROSO, S. S., BOLGAN, M., JORDO, J. M., CAIANO, M. & FONSECA, P. J. (2013). Painted gobies sing their quality out loud: acoustic rather than visual signals advertise male quality and contribute to mating success. *Functional Ecology* **27**, 289–298.
- *AMORIM, M. C. P., SIMÕES, J. M., MENDONÇA, N., BANDARRA, N. M., ALMADA, V. C. & FONSECA, P. J. (2010). Lusitanian toadfish song reflects male quality. *Journal of Experimental Biology* **213**, 2997–3004.
- *AMUNDSEN, T. & FORSGREN, E. (2001). Male mate choice selects for female coloration in a fish. *Proceedings of the National Academy of Sciences of the United States of America* **98**, 13155–13160.

- *AMUNDSEN, T., FORSGREN, E. & HANSEN, L. T. (1997). On the function of female ornaments: male bluethroats prefer colourful females. *Proceedings of the Royal Society of London B: Biological Sciences* **264**, 1579–1586.
- ANDERSON, S. R. & WIENS, J. J. (2017). Out of the dark: 350 million years of conservatism and evolution in diel activity patterns in vertebrates. *Evolution* **71**, 1944–1959.
- *ANDERSSON, M. (1982). Female choice selects for extreme tail length in a widowbird. *Nature* **299**, 818–820.
- *ANDERSSON, M. (1994). *Sexual Selection*. Princeton University Press, Princeton.
- *ANDERSSON, S. (1989). Sexual selection and cues for female choice in leks of Jackson's widowbird *Euplectes jacksoni*. *Behavioral Ecology and Sociobiology* **25**, 403–410.
- *ANDERSSON, S. (1991). Bowers on the savanna: display courts and mate choice in a lekking widowbird. *Behavioral Ecology* **2**, 210–218.
- ANDERSSON, S., PRYKE, S. R., ÖRNBERG, J., LAWES, M. J. & ANDERSSON, M. (2002). Multiple receivers, multiple ornaments, and a trade-off between agonistic and epigamic signaling in a widowbird. *American Naturalist* **160**, 683–691.
- *ARAK, A. (1983). Sexual selection by male–male competition in natterjack toad choruses. *Nature* **306**, 261–262.
- *ARNOLD, K. E., OWENS, I. P. F. & MARSHALL, N. J. (2002). Fluorescent signaling in parrots. *Science* **295**, 92.
- *ARNOLD, S. J. (1994). Bateman's principles and the measurement of sexual selection in plants and animals. *American Naturalist* **144**, S126–S149.
- *ATWOOD, J. L., FITZ, V. L. & BAMESBERGER, J. E. (1991). Temporal patterns of singing activity at leks of the white-bellied emerald. *The Wilson Bulletin* **103**, 373–386.
- *AYASSE, M., ENGELS, W., LÜBKE, G., TAGHIZADEH, T. & FRANCKE, W. (1999). Mating expenditures reduced via female sex pheromone modulation in the primitively eusocial halictine bee, *Lasius glossus* (*Eurygaster*) (*Hymenoptera: Halictidae*). *Behavioral Ecology and Sociobiology* **45**, 95–106.
- *BABBITT, G. A. & FREDERICK, P. C. (2007). Selection for sexual bill dimorphism in ibises: an evaluation of hypotheses. *Waterbirds* **30**, 199–206.
- *BACKWELL, P. R. Y. & PASSMORE, N. I. (1996). Time constraints and multiple choice criteria in the sampling behaviour and mate choice of the fiddler crab, *Uca annulipes*. *Behavioral Ecology and Sociobiology* **38**, 407–416.
- BADAYEV, A. V., HILL, G. E. & WECKWORTH, B. V. (2002). Species divergence in sexually selected traits: increase in song elaboration is related to decrease in plumage ornamentation in finches. *Evolution* **56**, 412–419.
- *BAHR, A., SOMMER, S., MATTLE, B. & WILSON, A. B. (2012). Mutual mate choice in the potbellied seahorse (*Hippocampus abdominalis*). *Behavioral Ecology* **23**, 869–878.
- *BAJER, K., MOLNÁR, O., TÖRÖK, J. & HERCZEG, G. (2010). Female European green lizards (*Lacerta viridis*) prefer males with high ultraviolet throat reflectance. *Behavioral Ecology and Sociobiology* **64**, 2007–2014.
- *BAJER, K., MOLNÁR, O., TÖRÖK, J. & HERCZEG, G. (2011). Ultraviolet nuptial colour determines fight success in male European green lizards (*Lacerta viridis*). *Biology Letters* **7**, 866–868.
- *BALDWIN, J. & JOHNSEN, S. (2012). The male blue crab, *Callinectes sapidus*, uses both chromatic and achromatic cues during mate choice. *Journal of Experimental Biology* **215**, 1184–1191.
- *BALTZ, A. P. & CLARK, A. B. (2010). Cere colour as a basis for extra-pair preferences of paired male budgerigars (*Melopsittacus undulatus*: Psittacidae: Aves). *Ethology* **102**, 109–116.
- *BARATA, E. N., HUBBARD, P. C., ALMEIDA, O. G., MIRANDA, A. & CANÁRIO, A. V. (2007). Male urine signals social rank in the Mozambique tilapia (*Oreochromis mossambicus*). *BMC Biology* **5**, 54.
- *BARATA, E. N., SERRANO, R. M., MIRANDA, A., NOGUEIRA, R., HUBBARD, P. C. & CANÁRIO, A. V. M. (2008). Putative pheromones from the anal glands of male blennies attract females and enhance male reproductive success. *Animal Behaviour* **75**, 379–389.
- *BARON, M., DAVIES, S., ALEXANDER, L., SNELGROVE, D. & SLOMAN, K. A. (2008). The effect of dietary pigments on the coloration and behaviour of flame-red dwarf gourami, *Colisa lalia*. *Animal Behaviour* **75**, 1041–1051.
- *BARRETTE, C. & VANDAL, D. (1986). Social rank, dominance, antler size, and access to food in snow-bound wild woodland caribou. *Behaviour* **97**, 118–145.
- *BASOLO, A. L. (1990a). Female preference for male sword length in the green swordtail, *Xiphophorus helleri* (Pisces: Poeciliidae). *Animal Behaviour* **40**, 332–338.
- BASOLO, A. (1990b). Female preference predates the evolution of the sword in swordtail fish. *Science* **58**, 808–810.
- *BAUBE, C. L. (1997). Manipulations of signalling environment affect male competitive success in three-spined sticklebacks. *Animal Behaviour* **53**, 819–833.
- *BEAN, D. & COOK, J. M. (2001). Male mating tactics and lethal combat in the nonpollinating fig wasp *Sycosapter australis*. *Animal Behaviour* **62**, 535–542.
- *BEANI, L. & DESSI-FULGHERI, F. (1995). Mate choice in the grey partridge, *Pedix pedix*: role of physical and behavioural male traits. *Animal Behaviour* **49**, 347–356.
- *BEHR, O., KNÖRNSCHILD, M. & VON HELVERSEN, O. (2009). Territorial counter-singing in male sac-winged bats (*Saccolaryx bilineata*): low-frequency songs trigger a stronger response. *Behavioral Ecology and Sociobiology* **63**, 433–442.
- *BENNET-CLARK, H. C. & EWING, A. W. (1969). Pulse interval as a critical parameter in the courtship song of *Drosophila melanogaster*. *Animal Behaviour* **17**, 755–759.
- *BENSON, K. E. & BASOLO, A. L. (2006). Male–male competition and the sword in male swordtails, *Xiphophorus helleri*. *Animal Behaviour* **71**, 129–134.
- *BENTON, T. G. (1992). Determinants of male mating success in a scorpion. *Animal Behaviour* **43**, 125–135.
- *BERGLUND, A. & ROSENQVIST, G. (2001). Male pipefish prefer ornamented females. *Animal Behaviour* **61**, 345–350.
- *BERGLUND, A. & ROSENQVIST, G. (2009). An intimidating ornament in a female pipefish. *Behavioral Ecology* **20**, 54–59.
- *BERGLUND, A., ROSENQVIST, G. & SVENSSON, I. (1986). Mate choice, fecundity and sexual dimorphism in two pipefish species (Syngnathidae). *Behavioral Ecology and Sociobiology* **19**, 301–307.
- BERGLUND, A., BISAZZA, A. & PILASTRO, A. (1996). Armaments and ornaments: an evolutionary explanation of traits of dual utility. *Biological Journal of the Linnean Society* **58**, 385–399.
- *BERTUCCI, F., BEAUCHAUD, M., ATTIA, J. & MATHEVON, N. (2010). Sounds modulate males' aggressiveness in a cichlid fish. *Ethology* **116**, 1179–1188.
- *BETANCUR-R., R., WILEY, E. O., ARRATIA, G., ACERO, A., BAILLY, N., MIYA, M., LECOINTRE, G. & ORTÍ, G. O. (2017). Phylogenetic classification of bony fishes. *BMC Evolutionary Biology* **17**, 162.
- *BININDA-EMONDS, O. R. P., CARDILLO, M., JONES, K. E., MACPHEE, R. D. E., BECK, R. M. D., GRENYER, R., PRICE, S. A., VOS, R. A., GITTLEMAN, J. A. & PURVIS, A. (2007). The delayed rise of present-day mammals. *Nature* **446**, 507–512.
- BIRKHEAD, T. R. & MÖLLER, A. P. (eds) (1998). *Sperm Competition and Sexual Selection*. Academic Press, London.
- *BISCHOFF, R. J., GOULD, J. L. & RUBENSTEIN, D. I. (1985). Tail size and female choice in the guppy (*Poecilia reticulata*). *Behavioral Ecology and Sociobiology* **17**, 253–255.
- *BOLAND, C. R. J., DOUBLE, M. C. & BAKER, G. B. (2004). Assortative mating by tail streamer length in Red-tailed Tropicbirds *Phaethon rubricauda* breeding in the Coral Sea. *Ibis* **146**, 687–690.
- *BORGIA, G. (1985). Bower quality, number of decorations and mating success of male satin bowerbirds (*Ptilonorhynchus violaceus*): an experimental analysis. *Animal Behaviour* **33**, 266–271.
- BORGIA, G. & COLEMAN, S. W. (2000). Co-option of male courtship signals from aggressive display in bowerbirds. *Proceedings of the Royal Society B* **267**, 1735–1740.
- *BORLOTTI, G. R., GONZÁLEZ, L. M., MARGALIDA, A., SÁNCHEZ, R. & ORIA, J. (2008). Positive assortative pairing by plumage colour in Spanish imperial eagles. *Behavioural Processes* **78**, 100–107.
- BOUGHMAN, J. W. (2002). How sensory drive can promote speciation. *Trends in Ecology & Evolution* **17**, 571–577.
- *BRANHAM, M. A. & GREENFIELD, M. D. (1996). Flashing males win mate success. *Nature* **381**, 745–746.
- *BRAUN, C., MICHELS, N., SIEBECK, U. & SPRENGER, D. (2014). Signalling function of long wavelength colours during agonistic male-male interactions in the wrasse *Coris julis*. *Marine Ecology Progress Series* **504**, 277–286.
- *BREED, M. D., SMITH, S. K. & GALL, B. G. (1980). Systems of mate selection in a cockroach species with male dominance hierarchies. *Animal Behaviour* **28**, 130–134.
- *BREITHAUP, T. & EGER, P. (2002). Urine makes the difference. *Journal of Experimental Biology* **205**, 1221–1231.
- *BREUER, T., ROBBINS, A. M., BOESCH, C. & ROBBINS, M. M. (2012). Phenotypic correlates of male reproductive success in western gorillas. *Journal of Human Evolution* **62**, 466–472.
- *BRIGHT, A. & WAAS, J. R. (2002). Effects of bill pigmentation and UV reflectance during territory establishment in blackbirds. *Animal Behaviour* **64**, 207–213.
- *BUCHHOLZ, R. (1995). Female choice, parasite load and male ornamentation in wild turkeys. *Animal Behaviour* **50**, 929–943.
- *BURKHARDT, D. & DE LA MOTTE, I. (1988). Big 'antlers' are favoured: female choice in stalk-eyed flies (Diptera, Insecta), field collected harems and laboratory experiments. *Journal of Comparative Physiology A* **162**, 649–652.
- *BURLEY, N. (1977). Parental investment, mate choice, and mate quality. *Proceedings of the National Academy of Sciences of the United States of America* **74**, 3476–3479.
- *BURLEY, N. (1981). Mate choice by multiple criteria in a monogamous species. *American Naturalist* **117**, 515–528.
- *BURLEY, N. & COOPERSMITH, C. B. (1987). Bill color preferences of zebra finches. *Ethology* **76**, 133–151.
- *BUZZATTO, B. A. & MACHADO, G. (2014). Male dimorphism and alternative reproductive tactics in harvestmen (Arachnida: Opiliones). *Behavioural Processes* **109**, 2–13.
- *BUZZATTO, B. A., ROBERTS, J. D. & SIMMONS, L. W. (2015). Sperm competition and the evolution of precopulatory weapons: increasing male density promotes sperm competition and reduces selection on arm strength in a chorusing frog. *Evolution* **69**, 2613–2624.
- *CALDWELL, R. L. (1987). Assessment strategies in stomatopods. *Bulletin of Marine Science* **41**, 135–150.
- *CALKINS, J. D. & BURLEY, N. T. (2003). Mate choice for multiple ornaments in the California quail, *Callipepla californica*. *Animal Behaviour* **65**, 69–81.
- *CAMFIELD, A. F. (2003). Quality of food source affects female visitation and display rates of male broad-tailed hummingbirds. *The Condor* **105**, 603–606.

- *CANDOLIN, U. (2004). Opposing selection on a sexually dimorphic trait through female choice and male competition in a water boatman. *Evolution* **58**, 1861–1864.
- *CARAZO, P., SANCHEZ, E., FONT, E. & DESFILIS, E. (2004). Chemosensory cues allow male *Tenebrio molitor* beetles to assess the reproductive status of potential mates. *Animal Behaviour* **68**, 123–129.
- *CHARLTON, B. D., REBY, D. & MCCOMB, K. (2007). Female red deer prefer the roars of larger males. *Biology Letters* **3**, 382–385.
- *CHARLTON, B. D., ELLIS, W. A. H., BRUMM, J., NILSSON, K. & FITCH, W. T. (2012). Female koalas prefer bellows in which lower formants indicate larger males. *Animal Behaviour* **84**, 1565–1571.
- *CHARLTON, B. D., WHISSON, D. A. & REBY, D. (2013). Free-ranging male koalas use size-related variation in formant frequencies to assess rival males. *PLoS ONE* **8**, e70279.
- *CHARRIER, I., AHONEN, H. & HARCOURT, R. G. (2011). What makes an Australian sea lion (*Neophoca cinerea*) male's bark threatening? *Journal of Comparative Psychology* **125**, 385–392.
- *CHELLIAH, K. & SUKUMAR, R. (2013). The role of tusks, musth and body size in male–male competition among Asian elephants, *Elephas maximus*. *Animal Behaviour* **86**, 1207–1214.
- CHEN, Z. & WIENS, J. J. (2020). The origins of acoustic communication in vertebrates. *Nature Communications* **11**, 369.
- *CHILDRESS, R. B. & BENNUN, L. A. (2002). Sexual character intensity and its relationship to breeding timing, fecundity and mate choice in the great cormorant *Phalacrocorax carbo lucidus*. *Journal of Avian Biology* **33**, 23–30.
- *CHIOU, T.-H., MARSHALL, N. J., CALDWELL, R. L. & CRONIN, T. W. (2011). Changes in light-reflecting properties of signalling appendages alter mate choice behaviour in a stomatopod crustacean *Haptosquilla trispinosa*. *Marine and Freshwater Behaviour and Physiology* **44**, 1–11.
- *CHRISTY, J. H. (1987). Female choice and the breeding behavior of the fiddler crab *Uca beebei*. *Journal of Crustacean Biology* **7**, 624–635.
- *CLARK, D. C. & MOORE, A. J. (1995). Genetic aspects of communication during male–male competition in the Madagascar hissing cockroach: honest signalling of size. *Heredity* **75**, 198–205.
- *CLAYTON, D. H. (1990). Mate choice in experimentally parasitized rock doves: lousy males lose. *American Zoologist* **30**, 251–262.
- *CLOTFELTER, E. D., ARDIA, D. R. & MCGRAW, K. J. (2007). Red fish, blue fish: trade-offs between pigmentation and immunity in *Betta splendens*. *Behavioral Ecology* **18**, 1139–1145.
- *CLUTTON-BROCK, T. H. (1982). The functions of antlers. *Behaviour* **79**, 108–124.
- *CLUTTON-BROCK, T. H. & ALBON, S. D. (1979). The roaring of red deer and the evolution of honest advertisement. *Behaviour* **69**, 145–170.
- CLUTTON-BROCK, T. H., GUINNESS, F. E. & ALBON, S. D. (1982). *Red Deer: Behavior and Ecology of Two Sexes*. University of Chicago Press, Chicago.
- *COLTMAN, D. W., FESTA-BIANCHET, M., JORGENSEN, J. T. & STROBECK, C. (2002). Age-dependent sexual selection in bighorn rams. *Proceedings of the Royal Society of London B: Biological Sciences* **269**, 165–172.
- *CONNER, W. E., EISNER, T., VAN DER MEER, R. K., GUERRERO, A. & MEINWALD, J. (1981). Precopulatory sexual interaction in an arctiid moth (*Utetheisa ornatrix*): role of a pheromone derived from dietary alkaloids. *Behavioral Ecology and Sociobiology* **9**, 227–235.
- *COTHREN, R. D., KUZMIG, A., WELLBORN, G. A. & RELYEA, R. A. (2010). Phenotypic manipulation provides insights into the function of a sexually selected trait in a freshwater crustacean species complex. *Animal Behaviour* **80**, 543–549.
- *CRAIG, J. K. & FOOTE, C. J. (2001). Countergradient variation and secondary sexual color: phenotypic convergence promotes genetic divergence in carotenoid use between sympatric anadromous and nonanadromous morphs of sockeye salmon (*Oncorhynchus nerka*). *Evolution* **55**, 380–391.
- *CRATSLY, C. K. & LEWIS, S. M. (2003). Female preference for male courtship flashes in *Photinus ignitus* fireflies. *Behavioral Ecology* **14**, 135–140.
- *CRAUL, M., ZIMMERMANN, E. & RADESPIEL, U. (2004). First experimental evidence for female mate choice in a nocturnal primate. *Primates* **45**, 271–274.
- *CRESPI, B. J. (1986). Territoriality and fighting in a colonial thrips, *Hoplothrips pedicularius*, and sexual dimorphism in Thysanoptera. *Ecological Entomology* **11**, 119–130.
- *CREWS, D. (1975). Effects of different components of male courtship behaviour on environmentally induced ovarian recrudescence and mating preferences in the lizard, *Anolis carolinensis*. *Animal Behaviour* **23**, 349–356.
- *CROTHERS, L. R. & CUMMINGS, M. E. (2015). A multifunctional warning signal behaves as an agonistic status signal in a poison frog. *Behavioral Ecology* **26**, 560–568.
- *CROTHERS, L., GERING, E. & CUMMINGS, M. (2011). Aposematic signal variation predicts male–male interactions in a polymorphic poison frog. *Evolution* **65**, 599–605.
- *CROWLEY, C. E. & MAGRATH, R. D. (2004). Shields of offence: signalling competitive ability in the dusky moorhen, *Gallinula tenebrosa*. *Australian Journal of Zoology* **52**, 463–474.
- *CURTIS, C. C. & STODDARD, P. K. (2003). Mate preference in female electric fish, *Brachyhyopomus pinnicaudatus*. *Animal Behaviour* **66**, 329–336.
- *DAKIN, R. & MONTGOMERIE, R. (2013). Eye for an eyespot: how iridescent plumage ocelli influence peacock mating success. *Behavioral Ecology* **24**, 1048–1057.
- *DANFORTH, B. N. (1991). The morphology and behavior of dimorphic males in *Perdita portalis* (Hymenoptera: Andrenidae). *Behavioral Ecology and Sociobiology* **29**, 235–247.
- *DAUNT, F., MONAGHAN, P., WANLESS, S. & HARRIS, M. P. (2003). Sexual ornament size and breeding performance in female and male European Shags *Phalacrocorax aristotelis*. *Ibis* **145**, 54–60.
- *DAVIDSON, S. M. & WILKINSON, G. S. (2004). Function of male song in the greater white-lined bat, *Saccopteryx bilineata*. *Animal Behaviour* **67**, 883–891.
- *DAVIES, N. B. & HALLIDAY, T. R. (1978). Deep croaks and fighting assessment in toads *Bufo bufo*. *Nature* **274**, 683–685.
- *DEARBORN, D. C., ANDERS, A. D. & WILLIAMS, J. B. (2005). Courtship display by great frigatebirds, *Fregata minor*. *Behavioral Ecology and Sociobiology* **58**, 397–406.
- *DEMARTSEV, V., ZIV, E. B., SHANI, U., GOLL, Y., KOREN, L. & GEFFEN, E. (2016). Harsh vocal elements affect counter-singing dynamics in male rock hyrax. *Behavioral Ecology* **27**, 1397–1404.
- *DETTO, T. & BACKWELL, P. R. Y. (2009). The fiddler crab *Uca mjoebergi* uses ultraviolet cues in mate choice but not aggressive interactions. *Animal Behaviour* **78**, 407–411.
- *DIAZ, E. & THIEL, M. (2004). Chemical and visual communication during mate searching in rock shrimp. *The Biological Bulletin* **206**, 134–143.
- *DIJKSTRA, P. D., SEEHAUSEN, O. & GROOTHUIS, T. G. G. (2005). Direct male–male competition can facilitate invasion of new colour types in Lake Victoria cichlids. *Behavioral Ecology and Sociobiology* **58**, 136–143.
- *DIMARCO, F. P. & HANLON, R. T. (2010). Agonistic behavior in the squid *Loligo plei* (Loliginidae, Teuthoidea): fighting tactics and the effects of size and resource value. *Ethology* **103**, 89–108.
- *DIXON, B. J. & VASEY, P. L. (2012). Beards augment perceptions of men's age, social status, and aggressiveness, but not attractiveness. *Behavioral Ecology* **23**, 481–490.
- *DODSON, G. N. (1997). Resource defense mating system in antlered flies, *Phytalmia* spp. (Diptera: Tephritidae). *Annals of the Entomological Society of America* **90**, 496–504.
- *DOUGLAS, H. D. (2008). Prenuptial perfume: allooinating in the social rituals of the crested auklet (*Aethia cristatella*) and the transfer of arthropod deterrents. *Naturwissenschaften* **95**, 45–53.
- *DRICKAMER, L. C. (1992). Oestrous female house mice discriminate dominant from subordinate males and sons of dominant from sons of subordinate males by odour cues. *Animal Behaviour* **43**, 868–870.
- *DUBUC, C., ALLEN, W. L., MAESTRIPIERI, D. & HIGHAM, J. P. (2014). Is male rhesus macaque red color ornamentation attractive to females? *Behavioral Ecology and Sociobiology* **68**, 1215–1224.
- *DUNN, C. W., GRIBET, G., EDGEcombe, G. & HEJNOL, A. (2014). Animal phylogeny and its evolutionary implications. *Annual Review of Ecology, Evolution, and Systematics* **45**, 371–395.
- EBERHARD, W. G. (1996). *Female Control: Sexual Selection by Cryptic Female Choice*. Princeton University Press, Princeton.
- *EENS, M., PINKTEN, P. & VERHEYEN, R. F. (1991). Male song as a cue for mate choice in the European Starling. *Behaviour* **116**, 210–238.
- EISTHEN, H. L. (2002). Why are olfactory systems of different animals so similar? *Brain, Behavior and Evolution* **59**, 273–293.
- *ELLAS, D. O., HEBETS, E. A., HOY, R. R. & MASON, A. C. (2005). Seismic signals are crucial for male mating success in a visual specialist jumping spider (Araneae: Salticidae). *Animal Behaviour* **69**, 931–938.
- *ELLIS, W., BERCOVITCH, F., FITZGIBBON, S., ROE, P., WIMMER, J., MELZER, A. & WILSON, R. (2011). Koala bellows and their association with the spatial dynamics of free-ranging koalas. *Behavioral Ecology* **22**, 372–377.
- *EMLEN, D. J. (1997). Alternative reproductive tactics and male-dimorphism in the horned beetle *Onthophagus acuminatus* (Coleoptera: Scarabaeidae). *Behavioral Ecology and Sociobiology* **41**, 335–341.
- EMLEN, S. T. & ORING, L. W. (1977). Ecology, sexual selection, and the evolution of mating systems. *Science* **197**, 215–223.
- *EMLEN, S. T. & WREGE, P. H. (2004). Size dimorphism, intrasexual competition, and sexual selection in wattled jacana (*Jacana jacana*), a sex-role-reversed shorebird in Panama. *The Auk* **121**, 391–403.
- EMLEN, D. J., MARANGELO, J., BALL, B. & CUNNINGHAM, C. W. (2005). Diversity in the weapons of sexual selection: Horn evolution in the beetle genus *Onthophagus* (Coleoptera: Scarabaeidae). *Evolution* **59**, 1060–1084.
- *ENDLER, J. A. (1983). Natural and sexual selection on color patterns in poeciliid fishes. *Environmental Biology of Fishes* **9**, 173–190.
- ENDLER, J. A. (1992). Signals, signal conditions, and the direction of evolution. *American Naturalist* **139**, S125–S153.
- ENDLER, J. A. & BASOLO, A. L. (1998). Sensory ecology, receiver biases and sexual selection. *Trends in Ecology & Evolution* **13**, 415–420.
- *ENGEL, F. & FOLSTAD, I. (1999). Cod courtship song: a song at the expense of dance? *Canadian Journal of Zoology* **77**, 542–550.
- *EVANS, C. S. (1985). Display vigour and subsequent fight performance in the siamese fighting fish, *Betta splendens*. *Behavioural Processes* **11**, 113–121.

- *EVANS, M. R. & NORRIS, K. (1996). The importance of carotenoids in signaling during aggressive interactions between male firemouth cichlids (*Cichlasoma meeki*). *Behavioral Ecology* **7**, 1–6.
- FAIRBAIRN, D. J. (2013). *Odd Couples: Extraordinary Differences between the Sexes in the Animal Kingdom*. Princeton University Press, Princeton.
- *FEA, M. & HOLWELL, G. (2018). Combat in a cave-dwelling wētā (Orthoptera: Rhaphidophoridae) with exaggerated weaponry. *Animal Behaviour* **138**, 85–92.
- *FISHER, H. S. & ROSENTHAL, G. G. (2006). Female swordtail fish use chemical cues to select well-fed mates. *Animal Behaviour* **72**, 721–725.
- *FISHER, H. S., SWAISGOOD, R. & FITCH-SNYDER, H. (2003). Countermarking by male pygmy lorises (*Nycticebus pygmaeus*): do females use odor cues to select mates with high competitive ability? *Behavioral Ecology and Sociobiology* **53**, 123–130.
- *FLEMING, I. A. & GROSS, M. R. (1994). Breeding competition in a Pacific salmon (Coho: *Oncorhynchus kisutch*): measures of natural and sexual selection. *Evolution* **48**, 637–657.
- *FOOTE, C. J., BROWN, G. S. & HAWRYSHYN, C. W. (2004). Female colour and male choice in sockeye salmon: implications for the phenotypic convergence of anadromous and nonanadromous morphs. *Animal Behaviour* **67**, 69–83.
- *FORSBERG, L. A., DANNEWITZ, J., PETERSSON, E. & GRAHN, M. (2007). Influence of genetic dissimilarity in the reproductive success and mate choice of brown trout – Females fishing for optimal MHC dissimilarity. *Journal of Evolutionary Biology* **20**, 1859–1869.
- *FORSGRÉN, E. (1997). Female sand gobies prefer good fathers over dominant males. *Proceedings of the Royal Society of London B: Biological Sciences* **264**, 1283–1286.
- *FOWLER-FINN, K. D. & HEBETS, E. A. (2006). An examination of agonistic interactions in the whip spider *Phrynos marginemaculatus* (Arachnida, Amblypygi). *Journal of Arachnology* **34**, 62–76.
- *FRANKLIN, A. M., MARSHALL, N. J. & LEWIS, S. M. (2016). Multimodal signals: ultraviolet reflectance and chemical cues in stomatopod agonistic encounters. *Royal Society Open Science* **3**, 160329.
- *FRANKLIN, A. M., APPEGATE, M. B., LEWIS, S. M. & OMENETTO, F. G. (2017). Stomatopods detect and assess achromatic cues in contests. *Behavioral Ecology* **28**, 1329–1336.
- *FREEMAN, H. D., VALUSKA, A. J., TAYLOR, R. R., FERRIE, G. M., GRAND, A. P. & LEIGHTY, K. A. (2016). Plumage variation and social partner choice in the greater flamingo (*Phoenicopterus roseus*). *Zoo Biology* **35**, 409–414.
- *FUNK, D. H. & TALLAM, D. W. (2000). Courtship role reversal and deceptive signals in the long-tailed dance fly, *Rhamphomyia longicauda*. *Animal Behaviour* **59**, 411–421.
- *GALEOTTI, P., SACCHI, R., ROSA, D. P. & FASOLA, M. (2005). Female preference for fast-rate, high-pitched calls in Hermann's tortoises *Testudo hermanni*. *Behavioral Ecology* **16**, 301–308.
- *GEBERZAHN, N., GOYMAN, W. & CATE, C. (2010). Threat signaling in female song - evidence from playbacks in a sex-role reversed bird species. *Behavioral Ecology* **21**, 1147–1155.
- *GERALD, M. S. (2001). Primate colour predicts social status and aggressive outcome. *Animal Behaviour* **61**, 559–566.
- *GERHARDT, H. C. (1991). Female mate choice in treefrogs: static and dynamic acoustic criteria. *Animal Behaviour* **42**, 615–635.
- *GERLACH, G. & LYSIAK, N. (2006). Kin recognition and inbreeding avoidance in zebrafish, *Danio rerio*, is based on phenotype matching. *Animal Behaviour* **71**, 1371–1377.
- *GERLACH, T., SPRENGER, D. & MICHELS, N. K. (2014). Fairy wrasses perceive and respond to their deep red fluorescent coloration. *Proceedings of the Royal Society of London B: Biological Sciences* **281**, 20140787.
- *GIBSON, R. M. & BRADBURY, J. W. (1985). Sexual selection in lekking sage grouse: phenotypic correlates of male mating success. *Behavioral Ecology and Sociobiology* **18**, 117–123.
- GILL, F. & DONSKER, D. (2018). IOC world bird list (v8.1). Electronic file available at <https://www.worldbirdnames.org/>. Accessed 01.06.2019.
- *GONÇALVES, D. M., BARATA, E. N., OLIVEIRA, R. F. & CANÁRIO, A. V. M. (2002). The role of male visual and chemical cues on the activation of female courtship behaviour in the sex-role reversed peacock blenny. *Journal of Fish Biology* **61**, 96–105.
- *GÖRANSSON, G., VON SCHANTZ, T., FRÖBERG, I., HELGEE, A. & WITTELL, H. (1990). Male characteristics, viability and harem size in the pheasant, *Phasianus colchicus*. *Animal Behaviour* **40**, 89–104.
- *GOSLING, L. M. & MCKAY, H. V. (1990). Competitor assessment by scent matching: an experimental test. *Behavioral Ecology and Sociobiology* **26**, 415–420.
- *GOYENS, J., DIRCKX, J. & AERTS, P. (2015). Built to fight: variable loading conditions and stress distribution in stag beetle jaws. *Bioinspiration & Biomimetics* **10**, 046006.
- *GREEN, A. J. (1991). Large male crests, an honest indicator of condition, are preferred by female smooth newts, *Triturus vulgaris* (Salamandridae) at the spermatophore transfer stage. *Animal Behaviour* **41**, 367–369.
- *GRETH, G. F. (1996). Intrasexual competition alone favors a sexually dimorphic ornament in the rubyspot damselfly *Hetaerina americana*. *Evolution* **50**, 1949–1957.
- *GRILLET, M., DARTEVELLE, L. & FERVEUR, J.-F. (2006). A *Drosophila* male pheromone affects female sexual receptivity. *Proceedings of the Royal Society of London B: Biological Sciences* **273**, 315–323.
- *GRONSTOL, G. B. (1996). Aerobic components in the song-flight display of male lapwings *Vanellus vanellus* as cues in female choice. *Ardea* **84**, 45–55.
- GUINDRE-PARKER, S., GILCHRIST, H. G., BALDO, S., DOUCET, S. M. & LOVE, O. P. (2013). Multiple achromatic plumage ornaments signal to multiple receivers. *Behavioral Ecology* **24**, 672–682.
- *GULLION, G. W. (1951). The frontal shield of the American coot. *The Wilson Bulletin* **63**, 157–166.
- *GVOZDIK, L. & VAN DAMME, R. (2003). Evolutionary maintenance of sexual dimorphism in head size in the lizard *Zootoca vivipara*: a test of two hypotheses. *Journal of Zoology* **259**(1), 7–13.
- *GWYNNE, D. T. (1982). Mate selection by female katydids (Orthoptera: Tettigoniidae, *Conocephalus nigropleurum*). *Animal Behaviour* **30**, 734–738.
- *GWYNNE, D. T. (1984). Courtship feeding increases female reproductive success in bushcrickets. *Nature* **307**, 361–363.
- *HAGEDORN, M. & ZELICK, R. (1989). Relative dominance among males is expressed in the electric organ discharge characteristics of a weakly electric fish. *Animal Behaviour* **38**, 520–525.
- *HAGELIN, J. C. (2002). The kinds of traits involved in male-male competition: a comparison of plumage, behavior, and body size in quail. *Behavioral Ecology* **13**, 32–41.
- *HAGELIN, J. C. (2007). The citrus-like scent of crested auklets. *Journal of Ornithology* **148**, 195–201.
- *HAGELIN, J. C. & LIGON, J. D. (2001). Female quail prefer testosterone-mediated traits, rather than the ornate plumage of males. *Animal Behaviour* **61**, 465–476.
- *HAMILTON, P. S. & SULLIVAN, B. K. (2005). Female mate attraction in ornate tree lizards, *Urosaurus ornatus*: a multivariate analysis. *Animal Behaviour* **69**, 219–224.
- *HAMILTON, D. G., WHITING, M. J. & PRYKE, S. R. (2013). Fiery frills: carotenoid-based coloration predicts contest success in frillneck lizards. *Behavioral Ecology* **24**, 1138–1149.
- *HAMMERSCHMIDT, K., RADYUSHKIN, K., EHRENREICH, H. & FISCHER, J. (2009). Female mice respond to male ultrasonic 'songs' with approach behaviour. *Biology Letters* **5**, 589–592.
- *HANIK, S. & KRAMER, B. (2005). Intra-male variability of its communication signal in the weakly electric fish, (South African form), and possible functions. *Behaviour* **142**, 145–166.
- *HANKS, L. M., MILLAR, J. G. & PAINE, T. D. (1996). Mating behavior of the eucalyptus longhorned borer (Coleoptera: Cerambycidae) and the adaptive significance of long "horns". *Journal of Insect Behavior* **9**, 383–393.
- *HARDOUN, L. A., REBY, D., BAVOUX, C., BURNELEAU, G. & BRETAGNOLLE, V. (2007). Communication of male quality in owl hoots. *American Naturalist* **169**, 552–562.
- *HEBETS, E. A. & UETZ, G. W. (2000). Leg ornamentation and the efficacy of courtship display in four species of wolf spider (Araneae: Lycosidae). *Behavioral Ecology and Sociobiology* **47**, 280–286.
- *HEDRICK, A. (1986). Female preferences for male calling bout duration in a field cricket. *Behavioral Ecology and Sociobiology* **19**, 73–77.
- *HELFEINSTEIN, F., WAGNER, R. H., DANCHIN, E. & ROSSI, J.-M. (2003). Functions of courtship feeding in black-legged kittiwakes: natural and sexual selection. *Animal Behaviour* **65**, 1027–1033.
- *HENRY, C. S. & WELLS, M. L. M. (2009). Sexually dimorphic intrasexual duetting in an otherwise monomorphic green lacewing (Neuroptera, Chrysopidae, *Chrysoperla plorabunda*): sexual selection or sex recognition? *Journal of Insect Behavior* **22**, 289–312.
- *HERREL, A., MOORE, J. A., BREDEWEG, E. M. & NELSON, N. J. (2010). Sexual dimorphism, body size, bite force and male mating success in tuatara. *Biological Journal of the Linnean Society* **100**, 287–292.
- *HICKS, R. E., LARNED, A. & BORGIA, G. (2013). Bower paint removal leads to reduced female visits, suggesting bower paint functions as a chemical signal. *Animal Behaviour* **85**, 1209–1215.
- *HIEBERT, S. M., STODDARD, P. K. & ARCESE, P. (1989). Repertoire size, territory acquisition and reproductive success in the song sparrow. *Animal Behaviour* **37**, 266–273.
- *HILL, G. E. (1990). Female house finches prefer colourful males: sexual selection for a condition-dependent trait. *Animal Behaviour* **40**, 563–572.
- HILL, G. E. (2002). *A Red Bird in a Brown Bag*. Oxford University Press, New York.
- *HILL, G. E. (2006). Female mate choice for ornamental coloration. In *Bird Coloration* (Volume 2, eds G. E. Hill and K. J. McGraw). Harvard University Press, Cambridge.
- *HÖGLUND, J. & LUNDBERG, A. (1987). Sexual selection in a monomorphic lek-breeding bird: correlates of male mating success in the great snipe *Gallinago media*. *Behavioral Ecology and Sociobiology* **21**, 211–216.
- *HÖGLUND, J. & ROBERTSON, J. G. M. (1990). Female preferences, male decision rules and the evolution of leks in the great snipe *Gallinago media*. *Animal Behaviour* **40**, 15–22.
- *HÖGLUND, J., ERIKSSON, M. & LINDELL, L. E. (1990). Females of the lek-breeding great snipe, *Gallinago media*, prefer males with white tails. *Animal Behaviour* **40**, 23–32.
- *HOLMBERG, K., EDMSAN, L. & KLINT, T. (1989). Female mate preferences and male attributes in mallard ducks *Anas platyrhynchos*. *Animal Behaviour* **38**, 1–7.

- *HONGO, Y. (2007). Evolution of male dimorphic allometry in a population of the Japanese horned beetle *Trypoxylus dichotomus septentrionalis*. *Behavioral Ecology and Sociobiology* **62**, 245–253.
- HOUE, A. (1997). *Sex, Color, and Mate Choice in Guppies*. Princeton University Press, Princeton.
- *HOWARD, R. D. (1978). The evolution of mating strategies in bullfrogs, *Rana catesbeiana*. *Evolution* **32**, 850–871.
- HUNT, J., BREUKER, C. J., SADOWSKI, J. A. & MOORE, A. J. (2009). Male–male competition, female mate choice and their interaction: determining total sexual selection. *Journal of Evolutionary Biology* **22**, 13–26.
- *HURST, J. L. (1993). The priming effects of urine substrate marks on interactions between male house mice, *Mus musculus domesticus* Schwarz & Schwarz. *Animal Behaviour* **45**, 55–81.
- *IBÁÑEZ, A., LÓPEZ, P. & MARTÍN, J. (2012). Discrimination of conspecifics' chemicals may allow Spanish terrapins to find better partners and avoid competitors. *Animal Behaviour* **83**, 1107–1113.
- *IBÁÑEZ, A., MARZAL, A., LÓPEZ, P. & MARTÍN, J. (2014). Chemosensory assessment of rival body size is based on chemosignal concentration in male Spanish terrapins. *Behavioral Ecology and Sociobiology* **68**, 2005–2012.
- *IYENGAR, V. K., ROSSINI, C. & EISNER, T. (2001). Precopulatory assessment of male quality in an arctiid moth (*Uletheisa ornatrix*): hydroxydanaidal is the only criterion of choice. *Behavioral Ecology and Sociobiology* **49**, 283–288.
- *IZZO, A. S. & TIBBETTS, E. A. (2012). Spotting the top male: sexually selected signals in male *Polistes dominulus* wasps. *Animal Behaviour* **83**, 839–845.
- *JACOB, A., EVANNO, G., RENAI, E., SERMIER, R. & WEDEKIND, C. (2009). Male body size and breeding tubercles are both linked to intrasexual dominance and reproductive success in the minnow. *Animal Behaviour* **77**, 823–829.
- *JAEGER, R. G., GOY, J. M., TARVER, M. & MÁRQUEZ, C. E. (1986). Salamander territoriality: pheromonal markers as advertisement by males. *Animal Behaviour* **34**, 860–864.
- *JANG, Y. & GREENFIELD, M. D. (1996). Ultrasonic communication and sexual selection in wax moths: female choice based on energy and asynchrony of male signals. *Animal Behaviour* **51**, 1095–1106.
- JANICKE, T., HÄDERER, I. K., LAJEUNESSE, M. J. & ANTHES, N. (2016). Darwinian sex roles confirmed across the animal kingdom. *Science Advances* **2**, e1500983.
- *JARVI, T. (1990). The effects of male dominance, secondary sexual characteristics and female mate choice on the mating success of male Atlantic Salmon *Salmo salar*. *Ethology* **84**, 123–132.
- *JARVIS, E. D., MIRABAB, S., ABERER, A. J., LI, B., HOUE, P., LI, C., HO, S. Y. W., FAIRCLOTH, B. C., NABHOLZ, B., HOWARD, J. T., SUH, A., WEBER, C. C., DA FONSECA, R. R., LI, J., ZHANG, F., et al. (2014). Whole genome analyses resolve early branches in the tree of life of modern birds. *Science* **346**, 1320–1331.
- JEZKOVA, T. & WIENS, J. J. (2017). What explains patterns of diversification and richness among animal phyla? *American Naturalist* **189**, 201–212.
- *JIGUET, F. & BRETAGNOLLE, V. (2001). Courtship behaviour in a lekking species: individual variations and settlement tactics in male little bustard. *Behavioural Processes* **55**, 107–118.
- *JIGUET, F. & BRETAGNOLLE, V. (2014). Sexy males and choosy females on exploded leks. *Behavioural Processes* **103**, 246–255.
- *JOHNSON, L. K. (1982). Sexual selection in a brentid weevil. *Evolution* **36**, 251–262.
- *JOHNSON, K. (1988). Sexual selection in pinyon jays I: female choice and male–male competition. *Animal Behaviour* **36**, 1038–1047.
- *JOHNSON, K., ROSETTA, D. & BURLEY, D. N. (1993). Preferences of female American goldfinches (*Carduelis tristis*) for natural and artificial male traits. *Behavioral Ecology* **4**, 138–143.
- *JONES, A. G. (2009). On the opportunity for sexual selection, the Bateman gradient and the maximum intensity of sexual selection. *Evolution* **63**, 1673–1684.
- *JONES, I. L. (1990). Plumage variability functions for status signalling in least auklets. *Animal Behaviour* **39**, 967–975.
- *JONES, I. L. & HUNTER, F. M. (1993). Mutual sexual selection in a monogamous seabird. *Nature* **362**, 238–239.
- *JONES, I. L. & HUNTER, F. M. (1999). Experimental evidence for mutual inter- and intrasexual selection favouring a crested auklet ornament. *Animal Behaviour* **57**, 521–528.
- *JONES, I. L. & MONTGOMERIE, R. (1992). Least auklet ornaments: do they function as quality indicators? *Behavioral Ecology and Sociobiology* **30**, 43–52.
- *JONES, T. M. & HAMILTON, J. G. C. (1998). A role for pheromones in mate choice in a lekking sandfly. *Animal Behaviour* **56**, 891–898.
- *JOUVENTIN, P., NOLAN, P. M., DOBSON, F. S. & NICOLAUS, M. (2008). Coloured patches influence pairing rate in King Penguins. *Ibis* **150**, 193–196.
- *KARINO, K. (1997). Female mate preference for males having long and symmetric fins in the bower-holding cichlid *Cyathopharynx furcifer*. *Ethology* **103**, 883–892.
- *KARSTEN, K. B., ANDRIAMANDIMBARISOA, L. N., FOX, S. F. & RAXWORTHY, C. J. (2009). Sexual selection on body size and secondary sexual characters in two closely related, sympatric chameleons in Madagascar. *Behavioral Ecology* **20**, 1079–1088.
- *KATAYAMA, N., ABBOTT, J. K., KJERANDSEN, J., TAKAHASHI, Y. & SVENSSON, E. I. (2014). Sexual selection on wing interference patterns in *Drosophila melanogaster*. *Proceedings of the National Academy of Sciences of the United States of America* **111**, 15144–15148.
- *KATSUKI, M., YOKOI, T., FUNAKOSHI, K. & OOTA, N. (2014). Enlarged hind legs and sexual behavior with male–male interaction in *Sagra femorata* (Coleoptera: Chrysomelidae). *Entomological News* **124**, 211–220.
- *KAVALIERS, M. & COLWELL, D. D. (1995). Discrimination by female mice between the odours of parasitized and non-parasitized males. *Proceedings of the Royal Society of London B: Biological Sciences* **261**, 31–35.
- *KEDDAR, I., ALTMAYER, S., COUCHOUX, C., JOUVENTIN, P., DOBSON, F. S. & FOSTER, S. (2015). Mate choice and colored beak spots of king penguins. *Ethology* **121**, 1048–1058.
- *KEKÄLÄINEN, J., VALKAMA, H., HUUSKONEN, H. & TASKINEN, J. (2010). Multiple sexual ornamentation signals male quality and predicts female preference in minnows. *Ethology* **116**, 895–903.
- *KEKÄLÄINEN, J., LEPPÄNEN, H.-R., HUUSKONEN, H., LAI, Y.-T., VALKAMA, H. & TASKINEN, J. (2011). The information content of odour, colour and tactile cues in the mate choice of minnows. *Behaviour* **148**, 909–925.
- *KELLY, C. D. (2005). Allometry and sexual selection of male weaponry in Wellington tree weta, *Hemideina crassidens*. *Behavioral Ecology* **16**, 145–152.
- *KELLY, C. D. (2006). Fighting for harems: assessment strategies during male–male contests in the sexually dimorphic Wellington tree weta. *Animal Behaviour* **72**, 727–736.
- *KEMPENAEERS, B., LANCTOT, R. B., GILL, V. A., HATCH, S. A. & VALCU, M. (2007). Do females trade copulations for food? An experimental study on kittiwakes (*Rissa tridactyla*). *Behavioral Ecology* **18**, 345–353.
- *KITCHEN, D. M., SEYFARTH, R. M., FISCHER, J. & CHENEY, D. L. (2003). Loud calls as indicators of dominance in male baboons (*Papio cynocephalus ursinus*). *Behavioral Ecology and Sociobiology* **53**, 374–384.
- *KITCHEN, D. M., CHENEY, D. L., ENGH, A. L., FISCHER, J., MOSCOVICE, L. R. & SEYFARTH, R. M. (2013). Male baboon responses to experimental manipulations of loud “wahoo calls”: testing an honest signal of fighting ability. *Behavioral Ecology and Sociobiology* **67**, 1825–1835.
- *KNOTT, C. D., THOMPSON, M. E., STUMPF, R. M. & MCINTYRE, M. H. (2010). Female reproductive strategies in orangutans, evidence for female choice and counterstrategies to infanticide in a species with frequent sexual coercion. *Proceedings of the Royal Society of London B: Biological Sciences* **277**, 105–113.
- *KODRIC-BROWN, A. (1985). Female preference and sexual selection for male coloration in the guppy (*Poecilia reticulata*). *Behavioral Ecology and Sociobiology* **17**, 199–205.
- *KODRIC-BROWN, A. (1996). Role of male–male competition and female choice in the development of breeding coloration in pupfish (*Cyprinodon pecosensis*). *Behavioral Ecology* **7**, 431–437.
- *KODRIC-BROWN, A. & NICOLETTO, P. F. (2001). Female choice in the guppy (*Poecilia reticulata*): the interaction between male color and display. *Behavioral Ecology and Sociobiology* **50**, 346–351.
- *KOH, T. H., SEAH, W. K., YAP, L.-M. Y. & LI, D. (2009). Pheromone-based female mate choice and its effect on reproductive investment in a spitting spider. *Behavioral Ecology and Sociobiology* **63**, 923–930.
- *KOJIMA, W. & LIN, C.-P. (2017). It takes two to tango: functional roles, sexual selection and allometry of multiple male weapons in the flower beetle *Dicranocephalus wallachii bourgoini*. *Biological Journal of the Linnean Society* **121**, 514–529.
- KOKKO, H. & RANKIN, D. J. (2006). Lonely hearts or sex in the city? Density-dependent effects in mating systems. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* **361**, 319–334.
- KOKKO, H., KLUG, H. & JENNIONS, M. D. (2012). Unifying cornerstones of sexual selection: operational sex ratio, Bateman gradient and the scope for competitive investment. *Ecology Letters* **15**, 1340–1351.
- *KOLM, N., AMCOFF, M., MANN, R. P. & ARNVIST, G. (2012). Diversification of a food-mimicking male ornament via sensory drive. *Current Biology* **22**, 1440–1443.
- *KOREN, L., MOKADY, O. & GEFFEN, E. (2008). Social status and cortisol levels in singing rock hyraxes. *Hormones and Behavior* **54**, 212–216.
- *KORTET, R. & HEDRICK, A. (2005). The scent of dominance: female field crickets use odour to predict the outcome of male competition. *Behavioral Ecology and Sociobiology* **59**, 77–83.
- *KOTIAHO, J. S. (2002). Sexual selection and condition dependence of courtship display in three species of horned dung beetles. *Behavioral Ecology* **13**, 791–799.
- *KOTIAHO, J., ALATALO, R. V., MAPPE, J. & PARRI, S. (1996). Sexual selection in a wolf spider: male drumming activity, body size, and viability. *Evolution* **50**, 1977–1981.
- *KOTIAHO, J. S., SIMMONS, L. W. & TOMKINS, J. L. (2001). Towards a resolution of the lek paradox. *Nature* **410**, 684–686.
- *KRAAIJEVELD, K., GREGURKE, J., HALL, C., KOMDEUR, J. & MULDER, R. A. (2004). Mutual ornamentation, sexual selection, and social dominance in the black swan. *Behavioral Ecology* **15**, 380–389.
- *KREBS, E. A., HUNTE, W. & GREEN, D. J. (2004). Plumage variation, breeding performance and extra-pair copulations in the cattle egret. *Behaviour* **141**, 479–499.

- KRONFELD-SCHOR, N. & DAYAN, T. (2003). Partitioning of time as an ecological resource. *Annual Review of Ecology, Evolution, and Systematics* **34**, 153–181.
- KVARNEMO, C. & AHNEJO, I. (1996). The dynamics of operational sex ratios and competition for mates. *Trends in Ecology & Evolution* **11**, 404–408.
- *LADICH, F. (1990). Vocalization during agonistic behaviour in *Cottus gobio* L. (Cottidae): an acoustic threat display. *Ethology* **84**, 193–201.
- *LADICH, F. (1998). Sound characteristics and outcome of contests in male croaking gouramis (Teleostei). *Ethology* **104**, 517–529.
- *LANDRY, C., GARANT, D., DUCHESNE, P. & BERNATCHEZ, L. (2001). ‘Good genes as heterozygosity’: the major histocompatibility complex and mate choice in Atlantic salmon (*Salmo salar*). *Proceedings of the Royal Society of London B: Biological Sciences* **268**, 1279–1285.
- *LECLAIRE, S., STRANDH, M., MARDON, J., WESTERDAHL, H. & BONADONNA, F. (2017). Odour-based discrimination of similarity at the major histocompatibility complex in birds. *Proceedings of the Royal Society of London B: Biological Sciences* **284**, 20162466.
- *LEDERHOUSE, R. C. & SCRIBER, J. M. (2017). Intrasexual selection constrains the evolution of the dorsal color pattern of male black swallowtail butterflies, *Papilio polyxenes*. *Evolution* **50**, 717–722.
- *LEMASTER, M. P. & MASON, R. T. (2002). Variation in a female sexual attractiveness pheromone controls male mate choice in garter snakes. *Journal of Chemical Ecology* **28**, 1269–1285.
- *LEONARD, M. L. & HORN, A. G. (1995). Crowing in relation to status in roosters. *Animal Behaviour* **49**, 1283–1290.
- *LI, J., ZHANG, Z., LIU, F., LIU, Q., GAN, W., CHEN, J., LIM, M. L. M. & LI, D. (2008). UVB-based mate-choice cues used by females of the jumping spider *Phintella vittata*. *Current Biology* **18**, 699–703.
- *LIGON, J. D., THORNHILL, R., ZUK, M. & JOHNSON, K. (1990). Male-male competition, ornamentation and the role of testosterone in sexual selection in red jungle fowl. *Animal Behaviour* **40**, 367–373.
- *LIM, M. L. M., LI, J. & LI, D. (2008). Effect of UV-reflecting markings on female mate-choice decisions in *Cosmophasis umbratica*, a jumping spider from Singapore. *Behavioral Ecology* **19**, 61–66.
- LIMAN, E. R. & INMAN, H. (2003). Relaxed selective pressure on an essential component of pheromone transduction in primate evolution. *Proceedings of the National Academy of Sciences of the United States of America* **100**, 3328–3332.
- *LIU, X., HAYASHI, F., LAVINE, L. C. & YANG, D. (2015). Is diversification in male reproductive traits driven by evolutionary trade-offs between weapons and nuptial gifts? *Proceedings of the Royal Society of London B: Biological Sciences* **282**, 20150247.
- *LOCATELLO, L., PIZZOLON, M. & RASOTTO, M. B. (2012). One trait, many signals: different information on male quality is enclosed within the same trait in a blenny fish. *Naturwissenschaften* **99**, 863–867.
- *LONGAIR, R. W. (2004). Tusked males, male dimorphism and nesting behavior in a subsocial afrotopical wasp, *Synagris cornuta*, and weapons and dimorphism in the genus (Hymenoptera: Vespidae: Eumeninae). *Journal of the Kansas Entomological Society* **77**, 528–557.
- *LÓPEZ, P., ARAGÓN, P. & MARTÍN, J. (2003). Responses of female lizards, *Lacerta monticola*, to males’ chemical cues reflect their mating preference for older males. *Behavioral Ecology and Sociobiology* **55**, 73–79.
- *LOYAU, A., GOMEZ, D., MOUREAU, B., THÉRY, M., HART, N. S., JALME, M. S., BENNETT, A. T. D. & SORCI, G. (2007). Iridescent structurally based coloration of eyespots correlates with mating success in the peacock. *Behavioral Ecology* **18**, 1123–1131.
- *LYONS, S. & MORRIS, M. (2008). Headstands: a sexually selected signal in the swordtail fish *Xiphophorus nezahualcoyotl*. *Behaviour* **145**, 1247–1262.
- *MAAN, M. E. & CUMMINGS, M. E. (2009). Sexual dimorphism and directional sexual selection on aposematic signals in a poison frog. *Proceedings of the National Academy of Sciences of the United States of America* **106**, 19072–19077.
- MAAN, M. E. & SEFC, K. M. (2013). Colour variation in cichlid fish: developmental mechanisms, selective pressures and evolutionary consequences. *Seminars in Cell and Developmental Biology* **24**, 516–528.
- *MAAN, M. E., SEEHAUSEN, O., SÖDERBERG, L., JOHNSON, L., RIPMEESTER, E. A. P., MROSSO, H. D. J., TAYLOR, M. I., VAN DOOREN, T. J. M. & VAN ALPHEN, J. J. M. (2004). Intraspecific sexual selection on a speciation trait, male coloration, in the Lake Victoria cichlid *Pundamilia nyererei*. *Proceedings of the Royal Society of London B: Biological Sciences* **271**, 2445–2452.
- *MACHNIK, P. & KRAMER, B. (2008). Female choice by electric pulse duration: attractiveness of the males’ communication signal assessed by female bulldog fish, *Marcusenius pongolensis* (Mormyridae, Teleostei). *Journal of Experimental Biology* **211**, 1969–1977.
- *MACLAREN, R. D., ROWLAND, W. J. & MORGAN, N. (2004). Female preferences for sailfin and body size in the sailfin molly, *Poecilia latipinna*. *Ethology* **110**, 363–379.
- *MADSEN, T. & SHINE, R. (1993). Male mating success and body size in European grass snakes. *Copeia* **1993**, 561–564.
- *MADSEN, V., DABELSTEEN, T., OSORIO, D. & OSORNO, J. L. (2007). Morphology and ornamentation in male magnificent frigatebirds: variation with age class and mating status. *The American Naturalist* **169**, S93–S111.
- *MAGANA, M., ALONSO, J. C. & PALACÍN, C. (2011). Age-related dominance helps reduce male aggressiveness in great bustard leks. *Animal Behaviour* **82**, 203–211.
- *MAGER, J. N., WALCOTT, C. & PIPER, W. H. (2007). Male common loons, *Gavia immer*, communicate body mass and condition through dominant frequencies of territorial yodels. *Animal Behaviour* **73**, 683–690.
- *MAGER, J. N., WALCOTT, C. & PIPER, W. H. (2012). Male common loons signal greater aggressive motivation by lengthening territorial yodels. *The Wilson Journal of Ornithology* **124**, 73–80.
- *MAJERUS, M., O’DONALD, P. & WEIR, J. (1982). Evidence for preferential mating in *Adalia bipunctata*. *Heredity* **49**, 37–49.
- MANK, J. E., HALL, D. W., KIRKPATRICK, M. & AVISE, J. C. (2006). Sex chromosomes and male ornaments: a comparative evaluation in ray-finned fishes. *Proceedings of the Royal Society of London B: Biological Sciences* **273**, 233–236.
- *MARCO, A., CHIVERS, D. P., KIESECKER, J. M. & BLAUSTEIN, A. R. (1998). Mate choice by chemical cues in western redback (*Plethodon vehiculum*) and Dunn’s (*P. dunni*) salamanders. *Ethology* **104**, 781–788.
- *MARKS, E. J., RODRIGO, A. G. & BRUNTON, D. H. (2010). Ecstatic display calls of the Adélie penguin honestly predict male condition and breeding success. *Behaviour* **147**, 165–184.
- *MARTIN, C. & GENNER, M. (2009). A role for male bower size as an intrasexual signal in a Lake Malawi cichlid fish. *Behaviour* **146**, 963–978.
- *MARTIN, J. & LÓPEZ, P. (2007). Scent may signal fighting ability in male Iberian rock lizards. *Biology Letters* **3**, 125–127.
- *MARTIN, J., MOREIRA, P. L. & LÓPEZ, P. (2007). Status-signalling chemical badges in male Iberian rock lizards. *Functional Ecology* **21**, 568–576.
- *MARTÍN-VIVALDI, M., PALOMINO, J. J., SOLER, M. & MARTÍNEZ, J. G. (1999). Song strophe-length and reproductive success in a non-passerine bird, the Hoopoe *Upupa epops*. *Ibis* **141**, 670–679.
- *MARTÍN-VIVALDI, M., PALOMINO, J. J. & SOLER, M. (2000). Attraction of Hoopoe *Upupa epops* females and males by means of song playback in the field: influence of strophe length. *Journal of Avian Biology* **31**, 351–359.
- MASON, N. A., SHULTZ, A. J. & BURNS, K. J. (2014). Elaborate visual and acoustic signals evolve independently in a large, phenotypically diverse radiation of songbirds. *Proceedings of the Royal Society of London B: Biological Sciences* **281**, 20140967.
- *MASSA, R., GALANTI, V. & BOTTONI, L. (1996). Mate choice and reproductive success in the domesticated budgerigar, *Melopsittacus undulatus*. *Italian Journal of Zoology* **63**, 243–246.
- *MASSARO, M., DAVIS, L. S. & DARBY, J. T. (2003). Carotenoid-derived ornaments reflect parental quality in male and female yellow-eyed penguins (*Megadyptes antipodes*). *Behavioral Ecology and Sociobiology* **55**, 169–175.
- *MATEOS, C. & CARRANZA, J. (1995). Female choice for morphological features of male ring-necked pheasants. *Animal Behaviour* **49**, 737–748.
- *MATEOS, C. & CARRANZA, J. (1996). On the intersexual selection for spurs in the ring-necked pheasant. *Behavioral Ecology* **7**, 362–369.
- *MATEOS, C. & CARRANZA, J. (1997a). The role of bright plumage in male–male interactions in the ring-necked pheasant. *Animal Behaviour* **54**, 1205–1214.
- *MATEOS, C. & CARRANZA, J. (1997b). Signals in intra-sexual competition between ring-necked pheasant males. *Animal Behaviour* **53**, 471–485.
- *MATHEWS, L. M. (2003). Tests of the mate-guarding hypothesis for social monogamy: male snapping shrimp prefer to associate with high-value females. *Behavioral Ecology* **14**, 63–67.
- *MATHIS, A. (1990). Territorial salamanders assess sexual and competitive information using chemical signals. *Animal Behaviour* **40**, 953–962.
- *MCCLINTOCK, W. J. & UETZ, G. W. (1996). Female choice and pre-existing bias: visual cues during courtship in two *Schizocosa* wolf spiders (Araneae: Lycosidae). *Animal Behaviour* **52**, 167–181.
- *MCCOMB, K. E. (1991). Female choice for high roaring rates in red deer, *Cervus elaphus*. *Animal Behaviour* **41**, 79–88.
- MCCULLOUGH, E. L., MILLER, C. W. & EMLEN, D. J. (2016). Why sexually selected ornaments are not weapons. *Trends in Ecology & Evolution* **31**, 742–751.
- *MCDONALD, D. B. (1989). Correlates of male mating success in a lekking bird with male-male cooperation. *Animal Behaviour* **37**, 1007–1022.
- *MCKIBBEN, J. R. & BASS, A. H. (1998). Behavioral assessment of acoustic parameters relevant to signal recognition and preference in a vocal fish. *The Journal of the Acoustical Society of America* **104**, 3520–3533.
- *MILINSKI, M. & BAKKER, T. C. M. (1990). Female sticklebacks use male coloration in mate choice and hence avoid parasitized males. *Nature* **344**, 330–333.
- *MILINSKI, M., GRIFFITHS, S., WEGNER, K. M., REUSCH, T. B. H., HAAS-ASSENBAUM, A. & BOEHM, T. (2005). Mate choice decisions of stickleback females predictably modified by MHC peptide ligands. *Proceedings of the National Academy of Sciences of the United States of America* **102**, 4414–4418.
- *MILLER, S. J. & INOUE, D. W. (1983). Roles of the wing whistle in the territorial behaviour of male broad-tailed hummingbirds (*Selasphorus platycircus*). *Animal Behaviour* **31**, 689–700.
- *MILLER, E. J., ELDRIDGE, M. D. B., COOPER, D. W. & HERBERT, C. A. (2010). Dominance, body size and internal relatedness influence male reproductive success

- in eastern grey kangaroos (*Macropus giganteus*). *Reproduction, Fertility and Development* **22**, 539–549.
- *MISOF, B., LIU, S., MEUSEMANN, K., PETERS, R. S., DONATH, A., MAYER, C., FRANDSEN, P. B., WARE, J., FLOURI, T., BEUTEL, R. G., NIEHUIS, O., PETERSEN, M., IZQUIERDO-CARRASCO, F., WAPPLER, T., RUST, J., ABERER, A. J., ASPOCK, U., ASPOCK, H., BARTEL, D., BLANKE, A., BERGER, S., BOHM, A., BUCKLEY, T. R., CALCOTT, B., CHEN, J., FRIEDRICH, F., FUKUI, M., FUJITA, M., GREVE, C., GROBE, P., GU, S., HUANG, Y., JERMIIN, L. S., KAWAHARA, A. Y., KROGMANN, L., KUBIAK, M., LANFEAR, R., LETSCH, H., LI, Y., LI, Z., LI, J., LU, H., MACHIDA, R., MASHIMO, Y., KAPLI, P., MCKENNA, D. D., MENG, G., NAKAGAKI, Y., NAVARRETE-HEREDIA, J. L., OTT, M., OU, Y., PASS, G., PODSIADLOWSKI, L., POHL, H., VON REUMONT, B. M., SCHUTTE, K., SEKIYA, K., SHIMIZU, S., SLIPINSKI, A., STAMATAKIS, A., SONG, W., SU, X., SZUCSICH, N. U., TAN, M., TAN, X., TANG, M., TANG, J., TIMELTHALER, G., TOMIZUKA, S., TRAUTWEIN, M., TONG, X., UCHIFUNE, T., WALLZ, M. G., WIEGMANN, B. M., WILBRANDT, J., WIPFLER, B., WONG, T. K. F., WU, Q., WU, G., XIE, Y., YANG, S., YANG, Q., YEATES, D. K., YOSHIZAWA, K., ZHANG, Q., ZHANG, R., ZHANG, W., ZHANG, Y., ZHAO, J., ZHOU, C., ZHOU, L., ZIESMANN, T., ZOU, S., LI, Y., XU, X., ZHANG, Y., YANG, H., WANG, J., WANG, J., KJER, K. M. & ZHOU, X. (2014). Phylogenomics resolves the timing and pattern of insect evolution. *Science* **346**, 763–767.
- *MIYATAKE, T. (1997). Functional morphology of the hind legs as weapons for male contests in *Leptoglossus australis* (Heteroptera: Coreidae). *Journal of Insect Behavior* **10**, 727–735.
- *MIYAZAKI, M. & WAAS, J. R. (2003). Acoustic properties of male advertisement and their impact on female responsiveness in little penguins *Eudyptula minor*. *Journal of Avian Biology* **34**, 229–232.
- *MØLLER, A. P. (1988). Female choice selects for male sexual tail ornaments in the monogamous swallow. *Nature* **332**, 640–642.
- MØLLER, A. P. & POMIANKOWSKI, A. (1993). Why have birds got multiple sexual ornaments? *Behavioral Ecology and Sociobiology* **32**, 167–176.
- *MØLLER, A. P., FLENNSTED-JENSEN, E. & MARDAL, W. (2007). Black beak tip coloration as a signal of phenotypic quality in a migratory seabird. *Behavioral Ecology and Sociobiology* **61**, 1561–1571.
- *MOORE, A. J. (1990). The evolution of sexual dimorphism by sexual selection: the separate effects of intrasexual and intersexual selection. *Evolution* **44**, 315–331.
- *MOORE, A. J. & MOORE, P. J. (1999). Balancing sexual selection through opposing mate choice and male competition. *Proceedings of the Royal Society of London B: Biological Sciences* **266**, 711–716.
- *MOORE, P. J., REAGAN-WALLIN, N. L., HAYNES, K. F. & MOORE, A. J. (1997). Odour conveys status on cockroaches. *Nature* **389**, 25.
- *MORAVEC, M. L., STRIEDTER, G. F. & BURLEY, N. T. (2006). Assortative pairing based on contact call similarity in budgerigars, *Melopsittacus undulatus*. *Ethology* **112**, 1108–1116.
- *MORINA, D. L., DEMARAIS, S., STRICKLAND, B. K. & LARSON, J. E. (2018). While males fight, females choose: male phenotypic quality informs female mate choice in mammals. *Animal Behaviour* **138**, 69–74.
- *MORRIS, M. R., MUSSEL, M. & RYAN, M. J. (1995). Vertical bars on male *Xiphophorus multilineatus*: a signal that deters rival males and attracts females. *Behavioral Ecology* **6**, 274–279.
- MORRIS, M. R., TUDOR, M. S. & DUBOIS, N. S. (2007). Sexually selected signal attracted females before deterring aggression in rival males. *Animal Behaviour* **74**, 1189–1197.
- *MOSS, R., KOLB, H. H., MARQUISS, M., WATSON, A., TRECA, B., WATT, D. & GLENNIE, W. (1979). Aggressiveness and dominance in captive cock red grouse. *Aggressive Behavior* **5**, 59–84.
- MUÑOZ, M. M., CRAWFORD, N. G., MCGREEVY, T. J. JR., MESSANA, N. J., TARVIN, R. D., REVELL, L. J., ZANDVLIET, R. M., HOPWOOD, J. M., MOCK, E., SCHNEIDER, A. L. & SCHNEIDER, C. J. (2013). Divergence in coloration and ecological speciation in the *Anolis marmoratus* species complex. *Molecular Ecology* **22**, 2668–2682.
- *MURAI, M. & BACKWELL, P. R. Y. (2006). A conspicuous courtship signal in a fiddler crab *Uca perplexa*: female choice based on display structure. *Behavioral Ecology and Sociobiology* **60**, 736–741.
- *MURPHY, T. G. (2007). Racketed tail of the male and female turquoise-browed motmot. *Behavioral Ecology and Sociobiology* **61**, 911–918.
- *NAKANO, R., ISHIKAWA, Y., TATSUKI, S., SURLYKKE, A., SKALS, N. & TAKANASHI, T. (2006). Ultrasonic courtship song in the Asian corn borer moth, *Ostrinia furnacalis*. *Naturewissenschaften* **93**, 292–296.
- NICHOLSON, K. E., HARMON, L. J. & LOSOS, J. B. (2007). Evolution of *Anolis* lizard dewlap diversity. *PLoS ONE* **2**, e274.
- *O'BRIEN, D. M., KATSUKI, M. & EMLEN, D. J. (2017). Selection on an extreme weapon in the frog-legged leaf beetle (*Sagra femorata*). *Evolution* **71**, 2584–2598.
- *OMLAND, K. E. (1996). Female mallard mating preferences for multiple male ornaments. *Behavioral Ecology and Sociobiology* **39**, 361–366.
- ORD, T. J. & STUART-FOX, D. (2006). Ornament evolution in dragon lizards: multiple gains and widespread losses reveal a complex history of evolutionary change. *Journal of Evolutionary Biology* **19**, 797–808.
- ORNELAS, J. F., GONZÁLEZ, C. & ESPINOSA DE LOS MONTEROS, A. (2009). Uncorrelated evolution between vocal and plumage coloration traits in the trogons: a comparative study. *Journal of Evolutionary Biology* **22**, 471–484.
- *OSAWA, N. & NISHIDA, T. (1992). Seasonal variation in elytral colour polymorphism in *Harmonia axyridis* (the ladybird beetle): the role of non-random mating. *Heredity* **69**, 297–307.
- *ÖSTLUND-NILSSON, S. & HOLMLUND, M. (2003). The artistic three-spined stickleback (*Gasterosteus aculeatus*). *Behavioral Ecology and Sociobiology* **53**, 214–220.
- OTTE, D. (1992). Evolution of cricket songs. *Journal of Orthoptera Research* **1**, 25–49.
- *OWENS, I. P. F., BURKE, T. & THOMPSON, D. B. A. (1994). Extraordinary sex roles in the Eurasian Dotterel: female mating arenas, female-female competition, and female mate choice. *American Naturalist* **144**, 76–100.
- PAGEL, M. (1994). Detecting correlated evolution on phylogenies: a general method for the comparative analysis of discrete characters. *Proceedings of the Royal Society of London B: Biological Sciences* **255**, 37–45.
- *PAINTING, C. J. & HOLWELL, G. I. (2014). Exaggerated rostra as weapons and the competitive assessment strategy of male giraffe weevils. *Behavioral Ecology* **25**, 1223–1232.
- *PALESTIS, B. G., NISBET, I. C. T., HATCH, J. J., ARNOLD, J. M. & SZCZYS, P. (2012). Tail length and sexual selection in a monogamous, monomorphic species, the roseate tern *Sterna dougallii*. *Journal of Ornithology* **153**, 1153–1163.
- *PANHUIS, T. M. & WILKINSON, G. S. (1999). Exaggerated male eye span influences contest outcome in stalk-eyed flies (Diopsidae). *Behavioral Ecology and Sociobiology* **46**, 221–227.
- *PAPKE, R. S., KEMP, D. J. & RUTOWSKI, R. L. (2007). Multimodal signalling: structural ultraviolet reflectance predicts male mating success better than pheromones in the butterfly *Colias eurytheme* L. (Pieridae). *Animal Behaviour* **73**, 47–54.
- *PARRI, S., ALATALO, R. V., KOTIAHO, J. & MAPPE, J. (1997). Female choice for male drumming in the wolf spider *Hygrolycosa rubrofasciata*. *Animal Behaviour* **53**, 305–312.
- *PARROTT, M. L., WARD, S. J. & TEMPLE-SMITH, P. D. (2006). Genetic similarity, not male size, influences female mate choice in the agile antechinus (*Antechinus agilis*). *Australian Journal of Zoology* **54**, 319–323.
- *PARROTT, M. L., WARD, S. J. & TEMPLE-SMITH, P. D. (2007). Olfactory cues, genetic relatedness and female mate choice in the agile antechinus (*Antechinus agilis*). *Behavioral Ecology and Sociobiology* **61**, 1075–1079.
- *PASCH, B., GEORGE, A. S., CAMPBELL, P. & PHELPS, S. M. (2011a). Androgen-dependent male vocal performance influences female preference in Neotropical singing mice. *Animal Behaviour* **82**, 177–183.
- *PASCH, B., GEORGE, A. S., HAMLIN, H. J., GUILLETTE, L. J. & PHELPS, S. M. (2011b). Androgens modulate song effort and aggression in Neotropical singing mice. *Hormones and Behavior* **59**, 90–97.
- *PEARNS, S. M., BENNETT, A. T. & CUTHILL, I. C. (2001). Ultraviolet vision, fluorescence and mate choice in a parrot, the budgerigar *Melopsittacus undulatus*. *Proceedings of the Royal Society of London B: Biological Sciences* **268**, 2273–2279.
- *PENTERIANI, V. (2003). Breeding density affects the honesty of bird vocal displays as possible indicators of male/territory quality. *Ibis* **145**, E127–E135.
- *PENTERIANI, V., DEL MAR DELGADO, M., ALONSO-ALVAREZ, C. & SÉRGIO, F. (2007). The importance of visual cues for nocturnal species. *Behavioral Ecology* **18**, 143–147.
- *PEREIRA, R., RISMONDO, S., CAIANO, M., PEDROSO, S. S., FONSECA, P. J. & AMORIM, M. C. P. (2014). The role of agonistic sounds in male nest defence in the painted goby *Pomatoschistus pictus*. *Ethology* **120**, 53–63.
- *PERROT, C., BÉCHET, A., HANZEN, C., ARNAUD, A., PRADEL, R. & CÉZILLY, F. (2016). Sexual display complexity varies non-linearly with age and predicts breeding status in greater flamingos. *Scientific Reports* **6**, 36242.
- *PINCENY, G., DOBSON, F. S. & JOUVENIN, P. (2009). Experiments on colour ornaments and mate choice in king penguins. *Animal Behaviour* **78**, 1247–1253.
- *POLAK, M., STARMER, W. T. & WOLF, L. L. (2007). Sexual selection for size and symmetry in a diversifying secondary sexual character in *Drosophila bipunctinata* (Diptera: Drosophilidae). *Evolution* **58**, 597–607.
- POLLUX, B. J. A., MEREDITH, R. W., SPRINGER, M. S., GARLAND, T. & REZNICK, D. N. (2014). The evolution of the placenta drives a shift in sexual selection in livebearing fish. *Nature* **513**, 233–236.
- *POOLE, J. H. (1999). Signals and assessment in African elephants: evidence from playback experiments. *Animal Behaviour* **58**, 185–193.
- POPPER, A. N. & FAY, R. (1997). Evolution of the ear and hearing: issues and questions. *Brain, Behavior and Evolution* **50**, 213–221.
- POUGH, F. H., ANDREWS, R. M., CRUMP, M. L., SAVITZKY, A. H., WELLS, K. D. & BRANDLEY, M. C. (2016). *Herpetology*, Fourth Edition. Sinauer Associates, Sunderland.
- PRADHAN, G. R. & VAN SCHAIK, C. P. (2009). Why do females find ornaments attractive? The coercion-avoidance hypothesis. *Biological Journal of the Linnean Society* **96**, 372–382.
- PRICE, T. D. (2017). Sensory drive, color, and color vision. *American Naturalist* **190**, 157–170.
- *PROCTER, D. S., MOORE, A. J. & MILLER, C. W. (2012). The form of sexual selection arising from male-male competition depends on the presence of females in the social environment. *Journal of Evolutionary Biology* **25**, 803–812.
- *PRUETT-JONES, S. G. & PRUETT-JONES, M. A. (1990). Sexual selection through female choice in Lawes' Parotia, a lek-mating bird of paradise. *Evolution* **44**, 486–501.

- *PRYKE, S. R. & ANDERSSON, S. (2003). Carotenoid-based epaulettes reveal male competitive ability. *Animal Behaviour* **66**, 217–224.
- *PUECHMALLE, S. J., BORISSOV, I. M., ZSEBOK, S., ALLEGRI, B., HIZEM, M., KUENZEL, S., SCHUCHMANN, M., TEELING, E. C. & SIEMERS, B. M. (2014). Female mate choice can drive the evolution of high frequency echolocation in bats: a case study with *Rhinolophus mehelyi*. *PLoS ONE* **9**, e103452.
- *RADESÄTER, T. & HALLDÖRSÐÓTTIR, H. (1993). Two male types of the common earwig: male-male competition and mating success. *Ethology* **95**, 89–96.
- *RADWAN, J. & KLIMAS, M. (2001). Male dimorphism in the bulb mite, *Rhizoglyphus robini*: fighters survive better. *Ethology Ecology & Evolution* **13**, 69–79.
- *RANTALA, M. J., JOKINEN, I., KORTET, R., VAINIKKA, A. & SUHONEN, J. (2002). Do pheromones reveal male immunocompetence? *Proceedings of the Royal Society of London B: Biological Sciences* **269**, 1681–1685.
- *RASMUSSEN, L. E. L. & SCHULTE, B. A. (1998). Chemical signals in the reproduction of Asian (*Elephas maximus*) and African (*Loxodonta africana*) elephants. *Animal Reproduction Science* **53**, 19–34.
- *REANEY, L. T. (2009). Female preference for male phenotypic traits in a fiddler crab: do females use absolute or comparative evaluation? *Animal Behaviour* **77**, 139–143.
- *REBY, D., MCCOMB, K., CARGNELUTTI, B., DARWIN, C., FITCH, W. T. & CLUTTON-BROCK, T. (2005). Red deer stags use formants as assessment cues during intrasexual agonistic interactions. *Proceedings of the Royal Society of London B: Biological Sciences* **272**, 941–947.
- *REECE-ENGEL, C. (1988). Female choice of resident male rabbits *Oryctolagus cuniculus*. *Animal Behaviour* **36**, 1241–1242.
- REEVE, H. K. & PFENNIG, D. W. (2003). Genetic biases for showy males: are some genetic systems especially conducive to sexual selection? *Proceedings of the National Academy of Sciences of the United States of America* **100**, 1089–1094.
- *REGIER, J. C., SHULTZ, J. W., ZWICK, A., HUSSEY, A., BALL, B., WETZER, R., MARTIN, J. W. & CUNNINGHAM, C. W. (2010). Arthropod relationships revealed by phylogenomic analysis of nuclear protein-coding sequences. *Nature* **463**, 1079–1083.
- *REID, J. M., ARCESE, P., CASSIDY, A. L. E. V., HIEBERT, S. M., SMITH, J. N. M., STODDARD, P. K., MARR, A. B. & KELLER, L. F. (2004). Song repertoire size predicts initial mating success in male song sparrows, *Melospiza melodia*. *Animal Behaviour* **68**, 1055–1063.
- *REUSCH, T. B. H., HÄBERLI, M. A., AESCHLIMANN, P. B. & MILINSKI, M. (2001). Female sticklebacks count alleles in a strategy of sexual selection explaining MHC polymorphism. *Nature* **414**, 300–302.
- *RICHARDS, H. L., GRUETER, C. C. & MILNE, N. (2015). Strong arm tactics: sexual dimorphism in macropodid limb proportions. *Journal of Zoology* **297**, 123–131.
- *RICK, I. P. & BAKKER, T. C. M. (2008). Males do not see only red: UV wavelengths and male territorial aggression in the three-spined stickleback (*Gasterosteus aculeatus*). *Naturwissenschaften* **95**, 631–638.
- *RICK, I. P., MODARRESSE, R. & BAKKER, T. C. M. (2006). UV wavelengths affect female mate choice in three-spined sticklebacks. *Animal Behaviour* **71**, 307–313.
- *RICO-GUEVARA, A. & ARAYA-SALAS, M. (2015). Bills as daggers? *Behavioral Ecology* **26**, 21–29.
- RICO-GUEVARA, A. & HURME, K. J. (2019). Intrasexually selected weapons. *Biological Reviews* **94**, 60–101.
- *RIEGER, N. S. & MARLER, C. A. (2018). The function of ultrasonic vocalizations during territorial defence by pair-bonded male and female California mice. *Animal Behaviour* **135**, 97–108.
- *RITCHIE, M. G., TOWNHILL, R. M. & HOIKKALA, A. (1998). Female preference for fly song: playback experiments confirm the targets of sexual selection. *Animal Behaviour* **56**, 713–717.
- *ROBERTS, J. A. & UETZ, G. W. (2005). Information content of female chemical signals in the wolf spider, *Schizocosa ocreata*: male discrimination of reproductive state and receptivity. *Animal Behaviour* **70**, 217–223.
- *ROBINSON, M. R. & KRUUK, L. E. (2007). Function of weaponry in females: the use of horns in intrasexual competition for resources in female Soay sheep. *Biology Letters* **3**, 651–654.
- *ROSENQVIST, G. (1990). Male mate choice and female-female competition for mates in the pipefish *Nerophis ophidion*. *Animal Behaviour* **39**, 1110–1115.
- *ROTH, O., SUNDIN, J., BERGLUND, A., ROSENQVIST, G. & WEGNER, K. M. (2014). Male mate choice relies on major histocompatibility complex class I in a sex-role-reversed pipefish. *Journal of Evolutionary Biology* **27**, 929–938.
- *ROULIN, A. (1999). Nonrandom pairing by male barn owls (*Tyto alba*) with respect to a female plumage trait. *Behavioral Ecology* **10**, 688–695.
- *ROWE, S. & HUTCHINGS, J. A. (2008). A link between sound producing musculature and mating success in Atlantic cod. *Journal of Fish Biology* **72**, 500–511.
- *ROWE, S., HUTCHINGS, J. A., SKJERAASEN, J. & BEZANSON, L. (2008). Morphological and behavioural correlates of reproductive success in Atlantic cod *Gadus morhua*. *Marine Ecology Progress Series* **354**, 257–265.
- *ROWLAND, W. J. (1995). Do female stickleback care about male courtship vigour? Manipulation of display tempo using video playback. *Behaviour* **132**, 951–961.
- RYAN, M. J. (1985). *The Tungara Frog: A Study in Sexual Selection and Communication*. University of Chicago Press, Chicago.
- *RYAN, M. J. & RAND, A. S. (1990). The sensory basis of sexual selection for complex calls in the tungara frog, *Physalaemus pustulosus* (sexual selection for sensory exploitation). *Evolution* **44**, 305–314.
- *VON SCHANTZ, T., GÖRANSSON, G., ANDERSSON, G., FRÖBERG, I., GRAHN, M., HELGÉE, A. & WITZELL, H. (1989). Female choice selects for a viability-based male trait in pheasants. *Nature* **337**, 166–169.
- *SCHMIDT, R., KUNC, H. P., AMRHEIN, V. & NAGUIB, M. (2008). Aggressive responses to broadband trills are related to subsequent pairing success in nightingales. *Behavioral Ecology* **19**, 635–641.
- *SCHNEIDER, R. A. Z., HUBER, R. & MOORE, P. (2001). Individual and status recognition in the crayfish *Orconectes rusticus*: the effects of urine release on fight dynamics. *Behaviour* **138**, 137–153.
- *SCHNELL, A. K., SMITH, C. L., HANLON, R. T., HALL, K. C. & HARCOURT, R. (2016). Cuttlefish perform multiple agonistic displays to communicate a hierarchy of threats. *Behavioral Ecology and Sociobiology* **70**, 1643–1655.
- *SEDDON, N., BUTCHART, S. & ODLING-SMEE, L. (2002). Duetting in the subdesert mesite *Momias benschi*. *Behavioral Ecology and Sociobiology* **52**, 7–16.
- *SEDDON, N., AMOS, W., MULDER, R. A. & TOBIAS, J. A. (2004). Male heterozygosity predicts territory size, song structure and reproductive success in a cooperatively breeding bird. *Proceedings of the Royal Society of London B: Biological Sciences* **271**, 1823–1829.
- *SEEHAUSEN, O., VAN ALPHEN, J. J. M. & WITTE, F. (1997). Cichlid fish diversity threatened by eutrophication that curbs sexual selection. *Science* **277**, 1808–1811.
- SEEHAUSEN, O., TERAI, Y., MAGALHAES, I. S., CARLETON, K. L., MROSSO, H. D. J., MIYAGI, R., VAN DER SLUIS, I., SCHNEIDER, M. V., MAAN, M. E., TACHIDA, H., IMAI, H. & OKADA, N. (2008). Speciation through sensory drive in cichlid fish. *Nature* **455**, 620–626.
- *SENAR, J. C. (2006). Color displays as intrasexual signals of aggression and dominance. In *Bird Coloration* (Volume 2, eds G. E. Hill and K. J. McGraw), pp. 87–136. Harvard University Press, Cambridge.
- *SETCHELL, J. M. (2005). Do female mandrills prefer brightly colored males? *International Journal of Primatology* **26**, 715–735.
- *SETCHELL, J. M. & DIXON, A. F. (2001). Changes in the secondary sexual adornments of male mandrills (*Mandrillus sphinx*) are associated with gain and loss of alpha status. *Hormones and Behavior* **39**, 177–184.
- *SHAMBLE, P. S., WILGERS, D. J., SWOBODA, K. A. & HEBETS, E. A. (2009). Courtship effort is a better predictor of mating success than ornamentation for male wolf spiders. *Behavioral Ecology* **20**, 1242–1251.
- *SHINE, R., OLSSON, M. M., MOORE, I. T., LEMASTER, M. P. & MASON, R. T. (1999). Why do male snakes have longer tails than females? *Proceedings of the Royal Society of London B: Biological Sciences* **266**, 2147–2151.
- *SHINE, R., OLSSON, M. M., MOORE, I. T., LEMASTER, M. P. & MASON, R. T. (2000). Body size enhances mating success in male garter snakes. *Animal Behaviour* **59**, F4–F11.
- *SHINE, R. & SHETTY, S. (2001). The influence of natural selection and sexual selection on the tails of sea-snakes (*Laticauda colubrina*). *Biological Journal of the Linnean Society* **74**, 121–129.
- *SHIPLEY, C., HINES, M. & BUCHWALD, J. S. (1981). Individual differences in threat calls of northern elephant seal bulls. *Animal Behaviour* **29**, 12–19.
- *SIGMUND, W. R. (1983). Female preference for *Anolis carolinensis* males as a function of dewlap color and background coloration. *Journal of Herpetology* **17**, 137–143.
- *SIMMONS, L. W. (1986). Inter-male competition and mating success in the field cricket, *Gryllus bimaculatus* (De Geer). *Animal Behaviour* **34**, 567–579.
- *SIMMONS, L. W. (1988a). The calling song of the field cricket, *Gryllus bimaculatus* (De Geer): constraints on transmission and its role in intermale competition and female choice. *Animal Behaviour* **36**, 380–394.
- *SIMMONS, R. (1988b). Honest advertising, sexual selection, courtship displays, and body condition of polygynous male harriers. *The Auk* **105**, 303–307.
- SIMMONS, L. W. (2001). *Sperm Competition and its Evolutionary Consequences in the Insects*. Princeton University Press, Princeton.
- *SIMMONS, R. E. & SCHEEPERS, L. (1996). Winning by a neck: sexual selection in the evolution of giraffe. *The American Naturalist* **148**, 771–786.
- SIMMONS, L. W., LÜPOLD, S. & FITZPATRICK, J. L. (2017). Trade-off between male expenditure on secondary sexual traits and ejaculates. *Trends in Ecology & Evolution* **32**, 964–976.
- *SIMON, V. B. (2011). Communication signal rates predict interaction outcome in the brown anole lizard, *Anolis sagrei*. *Copeia* **2011**, 38–45.
- *SIVA-JOTHY, M. T. (1999). Male wing pigmentation may affect reproductive success via female choice in a calopterygid damselfly (Zygoptera). *Behaviour* **136**, 1365–1377.
- *SLABBEKOORN, H. & CATE, C. (1997). Stronger territorial responses to frequency modulated coos in collared doves. *Animal Behaviour* **54**, 955–965.
- *SLABBEKOORN, H. & CATE, C. (1998). Perceptual tuning to frequency characteristics of territorial signals in collared doves. *Animal Behaviour* **56**, 847–857.
- *SNEDDEN, W. A. (1990). Determinants of male mating success in the temperate crayfish *Orconectes rusticus*: chela size and sperm competition. *Behaviour* **115**, 100–113.

- *SNEDDON, L. U., HUNTINGFORD, F. A. & TAYLOR, A. C. (1997). Weapon size versus body size as a predictor of winning in fights between shore crabs, *Carcinus maenas* (L.). *Behavioral Ecology and Sociobiology* **41**, 237–242.
- *SNELL, T. W., KIM, J., ZELAYA, E. & RESOP, R. (2007). Mate choice and sexual conflict in *Brachionus plicatilis* (Rotifera). *Hydrobiologia* **593**, 151–157.
- *SORENSEN, L. G. & DERRICKSON, S. R. (1994). Sexual selection in the northern pintail (*Anas acuta*): the importance of female choice versus male-male competition in the evolution of sexually-selected traits. *Behavioral Ecology and Sociobiology* **35**, 389–400.
- *SOUTH, S. H. & ARNQVIST, G. (2011). Male, but not female, preference for an ornament expressed in both sexes of the polygynous mosquito *Sabethes cyaneus*. *Animal Behaviour* **81**, 645–651.
- *STÅLHANDSKE, P. (2001). Nuptial gift in the spider *Psaura mirabilis* maintained by sexual selection. *Behavioral Ecology* **12**, 691–697.
- *STAUFFER, J. R., KELLOGG, K. A. & MCKAY, K. R. (2005). Experimental evidence of female choice in Lake Malawi cichlids. *Copeia* **2005**, 657–660.
- *STEELE, R. H. (1986). Courtship feeding in *Drosophila subobscura* II. Courtship feeding by males influences female mate choice. *Animal Behaviour* **34**, 1099–1108.
- *STEFFEN, J. E. & GUYER, C. C. (2014). Display behaviour and dewlap colour as predictors of contest success in brown anoles. *Biological Journal of the Linnean Society* **111**, 646–655.
- *STILES, F. G. (1982). Aggressive and courtship displays of the male Anna's hummingbird. *The Condor* **84**, 208–225.
- *STRANDH, M., WESTERDAHL, H., PONTARP, M., CANBÄCK, B., DUBOIS, M.-P., MIQUEL, C., TABERLET, P. & BONADONNA, F. (2012). Major histocompatibility complex class II compatibility, but not class I, predicts mate choice in a bird with highly developed olfaction. *Proceedings of the Royal Society B: Biological Sciences* **279**, 4457–4463.
- *STUART-FOX, D. M., FIRTH, D., MOUSSALLI, A. & WHITING, M. J. (2006). Multiple signals in chameleon contests: designing and analysing animal contests as a tournament. *Animal Behaviour* **71**, 1263–1271.
- *SUBLETT, C. (2012). Observations on the mating behavior of a South American species of the genus *Corydalus* (Megaloptera: Corydalidae). *Entomological News* **122**, 372–375.
- *SUK, H. Y. & CHOE, J. C. (2002). Females prefer males with larger first dorsal fins in the common freshwater goby. *Journal of Fish Biology* **61**, 899–914.
- *SVENSSON, B. G., PETERSSON, E. & FRISK, M. (1990). Nuptial gift size prolongs copulation duration in the dance fly *Empis borealis*. *Ecological Entomology* **15**, 225–229.
- TAFF, C. C., STEINBERGER, D., CLARK, C., BELINSKY, K., SACKS, H., FREEMAN-GALLANT, C. R., DUNN, P. O. & WHITTINGHAM, L. A. (2012). Multimodal sexual selection in a warbler: plumage and song are related to different fitness components. *Animal Behaviour* **84**, 813–821.
- *TAMM, S. (1985). Breeding territory quality and agonistic behavior: effects of energy availability and intruder pressure in hummingbirds. *Behavioral Ecology and Sociobiology* **16**, 203–207.
- *TAMM, S., ARMSTRONG, D. P. & TOOZE, Z. J. (1989). Display behavior of male calliope hummingbirds during the breeding season. *The Condor* **91**, 272–279.
- *TAROF, S. A., DUNN, P. O. & WHITTINGHAM, L. A. (2005). Dual functions of a melanin-based ornament in the common yellowthroat. *Proceedings of the Royal Society of London B: Biological Sciences* **272**, 1121–1127.
- *TERRY, L. I. & DYRESON, E. (1996). Behavior of *Frankliniella occidentalis* (Thysanoptera: Thripidae) within aggregations, and morphometric correlates of fighting. *Annals of the Entomological Society of America* **89**, 589–602.
- *THORNHILL, R. (1976). Sexual selection and nuptial feeding behavior in *Bittacus apicalis* (Insecta: Mecoptera). *The American Naturalist* **110**, 529–548.
- *THORNHILL, R. (1980). Mate choice in *Hylobittacus apicalis* (Insecta: Mecoptera) and its relation to some models of female choice. *Evolution* **34**, 519–538.
- *THORNHILL, R. (1992). Female preference for the pheromone of males with low fluctuating asymmetry in the Japanese scorpionfly (*Panorpa japonica*: Mecoptera). *Behavioral Ecology* **3**, 277–283.
- *THÜNKEN, T., BALDAUF, S. A., KULLMANN, H., SCHULD, J., HESSE, S. & BAKKER, T. C. M. (2011). Size-related inbreeding preference and competitiveness in male *Pelvicachromis taeniatus* (Cichlidae). *Behavioral Ecology* **22**, 358–362.
- *THÜNKEN, T., BAKKER, T. C. M. & BALDAUF, S. A. (2014). "Armpit effect" in an African cichlid fish: self-referent kin recognition in mating decisions of male *Pelvicachromis taeniatus*. *Behavioral Ecology and Sociobiology* **68**, 99–104.
- *TIGREROS, N., MOWERY, M. A. & LEWIS, S. M. (2014). Male mate choice favors more colorful females in the gift-giving cabbage butterfly. *Behavioral Ecology and Sociobiology* **68**, 1539–1547.
- TINGHITTELLA, R. M., LACKEY, A. C. R., MARTIN, M., DIJKSTRA, P. D., DRURY, J. P., HEATHCOTE, R., SCORDATO, E. S. C. & TYERS, A. M. (2018). On the role of male competition in speciation: a review and research agenda. *Behavioral Ecology* **29**, 783–797.
- *TOMKINS, J. L. & SIMMONS, L. W. (1998). Female choice and manipulations of forceps size and symmetry in the earwig *Forficula auricularia* L. *Animal Behaviour* **56**, 347–356.
- *TORRES, R. & VELANDO, A. (2003). A dynamic trait affects continuous pair assessment in the blue-footed booby, *Sula nebouxi*. *Behavioral Ecology and Sociobiology* **55**, 65–72.
- *TORRES, R. & VELANDO, A. (2005). Male preference for female foot colour in the socially monogamous blue-footed booby, *Sula nebouxi*. *Animal Behaviour* **69**, 59–65.
- *VASCONCELOS, R. O., SIMÕES, J. M., ALMADA, V. C., FONSECA, P. J. & AMORIM, M. C. P. (2010). Vocal behavior during territorial intrusions in the Lusitanian toadfish: boatwhistles also function as territorial 'keep-out' signals. *Ethology* **116**, 155–165.
- *VÁSQUEZ, T. & PFENNIG, K. S. (2007). Looking on the bright side: females prefer coloration indicative of male size and condition in the sexually dichromatic spadefoot toad, *Scaphiopus couchii*. *Behavioral Ecology and Sociobiology* **62**, 127–135.
- *VEIT, A. J. & JONES, I. L. (2003). Function of tail streamers of red-tailed tropicbirds (*Phaethon rubricauda*) as inferred from patterns of variation. *The Auk* **120**, 1033–1043.
- *VERZIJDEN, M. N., VAN HEUSDEN, J., BOUTON, N., WITTE, F., TEN CATE, C. & SLABBEKOORN, H. (2010). Sounds of male Lake Victoria cichlids vary within and between species and affect female mate preferences. *Behavioral Ecology* **21**, 548–555.
- *VIERA, V. M., NOLAN, P. M., CÔTÉ, S. D., JOUVENTIN, P. & GROSCOLAS, R. (2008). Is territory defence related to plumage ornaments in the king penguin *Aptenodytes patagonicus*? *Ethology* **114**, 146–153.
- *VITT, L. J. & COOPER, W. E. (1985). The evolution of sexual dimorphism in the skink *Eumeces laticeps*: an example of sexual selection. *Canadian Journal of Zoology* **63**, 995–1002.
- *WALLS, S. C., MATHIS, A., JAEGER, R. G. & GERGITS, W. F. (1989). Male salamanders with high-quality diets have faeces attractive to females. *Animal Behaviour* **38**, 546–548.
- *WARNER, R. R. & SCHULTZ, E. T. (1992). Sexual selection and male characteristics in the bluehead wrasse, *Thalassoma bifasciatum*: mating site acquisition, mating site defense, and female choice. *Evolution* **46**, 1421–1442.
- *WATSON, N. L. & SIMMONS, L. W. (2010). Reproductive competition promotes the evolution of female weaponry. *Proceedings of the Royal Society of London B: Biological Sciences* **277**, 2035–2040.
- *WEDEKIND, C., SEEBECK, T., BETTENS, F. & PAEPKE, A. J. (1995). MHC-dependent mate preferences in humans. *Proceedings of the Royal Society of London B: Biological Sciences* **260**, 245–249.
- *WEISS, S. L. (2002). Reproductive signals of female lizards: pattern of trait expression and male response. *Ethology* **108**, 793–813.
- *WELLMORN, G. A. & BARTHOLF, S. E. (2005). Ecological context and the importance of body and gnathopod size for pairing success in two amphipod ecomorphs. *Oecologia* **143**, 308–316.
- *WEST, P. M. & PACKER, C. (2002). Sexual selection, temperature, and the lion's mane. *Science* **297**, 1339–1343.
- *WHITING, M. J., STUART-FOX, D. M., O'CONNOR, D., FIRTH, D., BENNETT, N. C. & BLOMBERG, S. P. (2006). Ultraviolet signals ultra-aggression in a lizard. *Animal Behaviour* **72**, 353–363.
- *WIAŁEK, J. (2004). Sky-dancing as an honest criterion of mate choice in Montagu's Harrier *Circus pygargus*. In *Raptors Worldwide: Proceedings of the VI World Conference on Birds of Prey and Owls* (eds R. E. CHANCELLOR and B.-U. MEYBURG), pp. 845–848. WWGBP/MME/Birdlife Hungary, Berlin and Budapest.
- *WIEBE, K. L. (2000). Assortative mating by color in a population of hybrid Northern Flickers. *The Auk* **117**, 525–529.
- *WIEBE, K. L. & VITOUSEK, M. N. (2015). Melanin plumage ornaments in both sexes of Northern Flicker are associated with body condition and predict reproductive output independent of age. *The Auk* **132**, 507–517.
- WIENS, J. J. (1999). Phylogenetic evidence for multiple losses of a sexually selected character in phrynosomatid lizards. *Proceedings of the Royal Society of London B: Biological Sciences* **266**, 1529–1535.
- WIENS, J. J. (2001). Widespread loss of sexually selected traits: how the peacock lost its spots. *Trends in Ecology & Evolution* **16**, 517–523.
- WIENS, J. J. (2015). Faster diversification on land than sea helps explain global biodiversity patterns among habitats and animal phyla. *Ecology Letters* **18**, 1234–1241.
- WIENS, J. J., REEDER, T. W. & NIETO MONTES DE OCA, A. (1999). Molecular phylogenetics and evolution of sexual dichromatism among populations of the Yarrow's spiny lizard (*Sceloporus jarrovi*). *Evolution* **53**, 1884–1897.
- *WILKINSON, G. S. & DODSON, G. N. (1997). Function and evolution of antlers and eye stalks in flies. In *The Evolution of Mating Systems in Insects and Arachnids* (eds J. C. CHOE and B. J. CRESPI), pp. 310–328. Cambridge University Press, Cambridge.
- *WILKINSON, G. S. & REILLO, P. R. (1994). Female choice response to artificial selection on an exaggerated male trait in a stalk-eyed fly. *Proceedings of the Royal Society of London B: Biological Sciences* **255**, 1–6.
- *WILLEMART, R. H., OSSES, F., CHELINI, M. C., MACÍAS-ORDÓÑEZ, R. & MACHADO, G. (2009). Sexually dimorphic legs in a neotropical harvestman (Arachnida, Opiliones): ornament or weapon? *Behavioural Processes* **80**, 51–59.
- YAGER, D. D. (1999). Structure, development, and evolution of insect auditory systems. *Microscopy Research and Technique* **47**, 380–400.
- *ZAMPIGA, E., GAIBANI, G. & CSERMELY, D. (2008). Ultraviolet reflectance and female mating preferences in the common kestrel (*Falco tinnunculus*). *Canadian Journal of Zoology* **86**, 479–483.

- *ZEH, D. W. (1987). Aggression, density, and sexual dimorphism in chernetid pseudoscorpions (Arachnida: Pseudoscorpionida). *Evolution* **41**, 1072–1087.
- *ZEH, D. W., ZEH, J. A. & TAVAKILIAN, G. (1992). Sexual selection and sexual dimorphism in the harlequin beetle *Acrocinus longimanus*. *Biotropica* **24**, 86–96.
- *ZHAO, X., JIANG, T., GU, H., LIU, H., SUN, C., LIU, Y. & FENG, J. (2018). Are aggressive vocalizations the honest signals of body size and quality in female Asian particoloured bats? *Behavioral Ecology and Sociobiology* **72**, 96.
- ZHENG, Y. & WIENS, J. J. (2016). Combining phylogenomic and supermatrix approaches, and a time-calibrated phylogeny for squamate reptiles (lizards and snakes) based on 52 genes and 4162 species. *Molecular Phylogenetics and Evolution* **94**, 537–547.
- ZUK, M. & SIMMONS, L. W. (1997). Reproductive strategies of the crickets (Orthoptera: Gryllidae). In *The Evolution of Mating Systems in Insects and Arachnids* (eds J. C. CHOE and B. J. CRESPI), pp. 89–109. Cambridge University Press, Cambridge.
- *ZUK, M., THORNHILL, R., LIGON, J. D., JOHNSON, K., AUSTAD, S., LIGON, S. H., THORNHILL, N. W. & COSTIN, C. (1990). The role of male ornaments and courtship behavior in female mate choice of red jungle fowl. *The American Naturalist* **136**, 459–473.
- *ZURI, I., SU, W. & HALPERN, M. (2003). Conspecific odor investigation by gray short-tailed opossums (*Monodelphis domestica*). *Physiology & Behavior* **80**, 225–232.

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VIII. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Methods for systematic review of sexually selected traits.

Appendix S2. Summary of sexually selected traits across animal clades.

Appendix S3. References used in review of sexually selected traits.

Appendix S4. Comparing frequencies of traits used in mate choice *versus* contests.

Appendix S5. Examples of sexually selected traits used in both contest competition and mate choice.

Appendix S6. Orders of insects and birds that appear to lack sexually selected traits.