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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 (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).

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

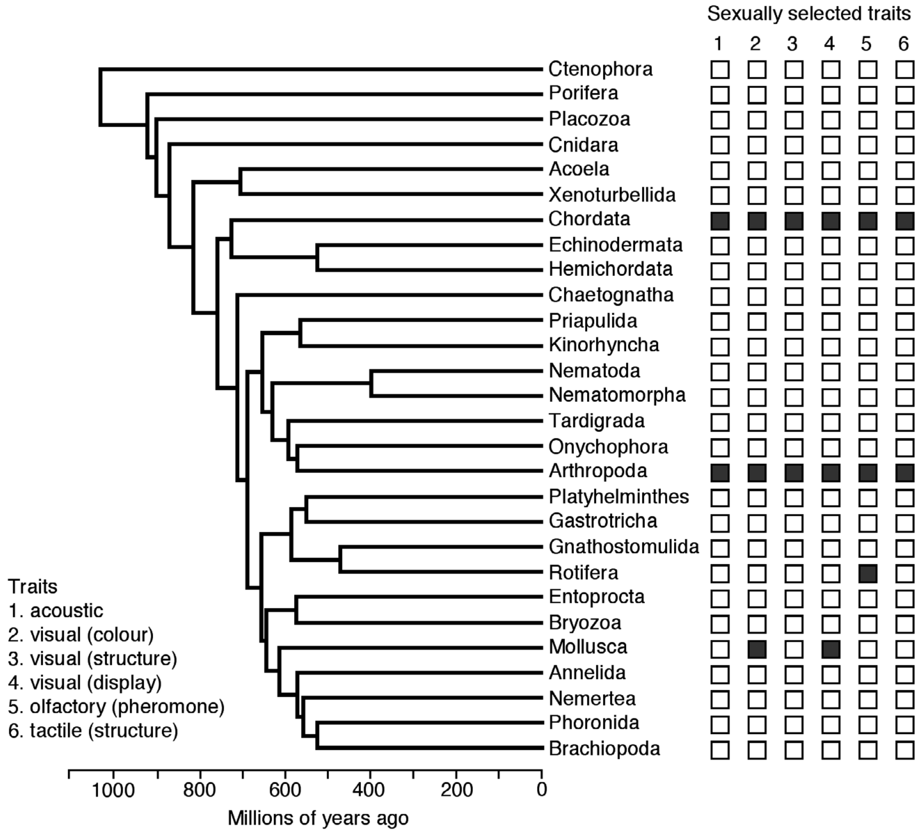

Fig. 2. The distribution of six major types of sexually selected traits among 28 animal phyla. Filled boxes indicate that a trait type is present in at least one species in that phylum (irrespective of prevalence), whereas open boxes indicate that the trait is absent from that phylum (as far as is currently 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 & Ahnesjo, 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 & Ahnesjo, 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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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.

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