












SYMPOSIUM ARTICLE

Sexual Selection, Energetics and Ecological Innovation: How Sexual Selection Diversifies the Landscape of Behavior, Morphology and Physiology

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Synopsis Sexual selection drives the evolution of a broad diversity of traits, such as the enlarged claws of fiddler crabs, the high-energy behavioral displays of hummingbirds, the bright red plumage of house finches, the elaborated antennae of moths, the wing “snapping” displays of manakins and the calculated calls of túngara frogs. A majority of work in sexual selection has aimed to measure the magnitude of these traits. Yet, we know surprisingly little about the physiology shaping such a diversity of sexually selected behavior and supportive morphology. The energetic properties underlying sexual signals are ultimately fueled by metabolic machinery at multiple scales, from mitochondrial properties and enzymatic activity to hormonal regulation and the modification of muscular and neural tissues. However, different organisms have different physiological constraints and face various ecological selection pressures; thus, selection operates and interacts at multiple scales to shape sexually selected traits and behavior. In this perspective piece, we describe illustrative case studies in different organisms to emphasize that understanding the physiological and energetic mechanisms that shape sexual traits may be critical to understanding their evolution and ramifications with ecological selection. We discuss (1) the way sexual selection shapes multiple integrated components of physiology, behavior, and morphology, (2) the way that sexually selected carotenoid pigments may reflect some aspects of cellular processes, (3) the relationship between sexually selected modalities and energetics, (4) the hormone ecdysone and its role in shaping sex-specific phenotypes in insects, (5) the way varied interaction patterns and social contexts select for signaling strategies that are responsive to social scenes, and (6) the role that sexual selection may have in the exploitation of novel thermal niches. Our major objective is to describe how sexually selected behavior, physiology, and ecology are shaped in diverse organisms so that we may develop a deeper and more integrated understanding of sexual trait evolution and its ecological consequences.

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Introduction

Sexual selection drives the evolution of elaborate morphology and diverse behavior that often pushes animals to physiological extremes (Anderson 1994; Emlen 2008; Ryan 2018; Harrison et al. 2022). The enlarged claws of male fiddler crabs used as weapons and displays can account for up to 50% of body mass (Allen and Levinton 2007; Tullis and Straube 2017), and the extremely rapid wing “snapping” display of manakins requires specialized integration of neuromuscular physiology (Fuxjager et al. 2022; Pease et al. 2022). Sexually selected signals are known to impose ecological fitness costs on the organisms that bear them, such as increasing their risk of predation (Estrada and Jiggins 2008; Hegyi et al. 2022), reducing their ability to feed efficiently (Valiela et al. 1974), and increasing the energetic costs of routine behavior (Basolo and Alcaraz 2003; Goyens et al. 2015; Van Wassenbergh et al. 2015). The large and conspicuous traits shaped by sexual selection and increased energy expenditure that organisms allocate to sexual traits and behavior have often puzzled evolutionary biologists (Darwin 1871; Anderson 1994). Large and conspicuous sexually selected traits are predicted to lead to trade-offs with traits under ecological selection (Hegyi et al. 2022; Somjee et al. 2024).

Many studies have revealed that sexually selected traits may impose high energetic costs (Ryan 1988), yet a growing body of evidence also suggests that animals have evolved physiological mechanisms to transmit signals highly efficiently, while incurring surprisingly low energetic costs relative to their body size (McCullough and Emlen 2013; McCullough and Tobalske 2013; Glazier 2014; Glazier et al. 2016; Somjee et al. 2018, 2021; Somjee 2021; Dinh 2022; Chen et al. 2024). In this way, sexual selection drives the evolution of exaggerated traits that may differ in their relative metabolic costs within a population, yet evolve as a suite of highly integrated systems associated with mitochondrial respiration, morphological development, and neuromuscular physiology (Lindsay et al. 2015; Fuxjager et al. 2022).

The adaptations associated with sexual traits and behavior occur at multiple levels and may lead to extreme differences in body size (Somjee et al. 2024) and differences in the relative allocation to both pre- and post-copulatory traits (Somjee et al. 2015, 2017). However, sexual traits are highly integrated with sub-cellular mitochondrial respiration, tissue-specific development, and whole organism metabolism (Hill et al. 2019; Somjee et al. 2021). Despite changes to animal physiology and ecology shaped by sexual selection, the idea that such adaptations play roles in other ecological life-history functions has received relatively little attention (Cornwallis and Uller 2010; Bonduriansky 2012; Koch and Hill 2018; Koch et al. 2021). For example,

elaborate moth antennae can function to enhance mate searching in male moths, but elaborate antennae can also be used for ecological functions, such as locating host plants in both sexes.

Sexual selection does not occur in isolation but in the context of multiple ecological selection pressures. In this perspective piece, we examine several case studies in different organisms to shed light on the integrated avenues by which sexual selection can shape physiology, behavior, and life-history. Together, these case studies and perspectives highlight the symposium “Energetics, sexual selection, and ecological innovation,” which was part of the 2025 annual meeting of the Society of Integrative and Comparative Biology. We explore the idea that variation in physiology generated by sexual selection interacts with the environment in novel and complex ways, often driven by changes in energetics. This approach aims to identify shared patterns shaping the diversity of sexual trait evolution and its interactions with ecological selection pressures. To gain a deeper understanding of the effects of sexual selection on ecological evolution, we suggest examining gene-expression patterns underlying complex physiology (Pease et al. 2022), the gains and losses of sexually selected traits over evolutionary time-scales (Miles and Fuxjager 2019), and the consequences of sexual selection across biological levels of organization (Carroll 2005; Koch and Hill 2018; Dixit 2024).

Sexually selected traits are shaped by the concurrent evolution of multiple physiological traits

Sexual selection for elaborate traits and reproductive behavior can facilitate the concurrent evolution of supportive mechanisms in neural, endocrine, and musculoskeletal systems (Lailvaux and Irschick 2006; Husak and Swallow 2011; Fuxjager et al. 2022). One way to conceptualize the effects of sexual selection on the evolution of physiology is by considering an organism's broader performance landscape. We can think of this landscape as the theoretical topography that encompasses how species can behave in their natural environment. By favoring a novel trait, sexual selection can push the boundaries of this landscape to expand an organism's behavioral limits (Bonduriansky 2011, 2012). These effects can be extreme, with selection directing the emergence of behavioral abilities that are spectacular and that expand our basic understanding of animal form and function. An illustrative example comes from a bird called the western grebe (*Aechmophorus occidentalis*). Individuals of this species weigh roughly 1–2 kg, and they inhabit lakes and marshes in western and central North America. As part of the courtship routine

between males and females, pairs run for multiple meters in tandem across the water's surface (Nuechterlein and Storer 1982). Indeed, selection for this ability, which is otherwise impossible for birds of this size, is supported by the emergence of numerous morphological and physiological modifications to the species, which enable an unusually swift hindlimb stride (Clifton et al. 2015). Indeed, courtship behavior is associated with exceptional physiological modifications in many bird species (Murphy 2007; Fuxjager et al. 2015; Santema et al. 2023). Thus, sexual selection may appear to shape traits freely. Yet, this process almost certainly occurs in balance with a wide range of other factors that influence phenotypic change through time. Foremost among these factors is the imprint of history.

A species' ancestral states can play a major role in determining which traits are more or less likely to evolve. Yet, at the same time shared selection patterns may result in convergence of the molecular pathways shaping behavior and morphology in different ways (Lipshutz et al. 2025). Thus, to begin to understand the evolution of such complex sexual behavior, it is important to understand the historical sequence of contingent processes that lead to these behaviors (Miles and Fuxjager 2019; Mangiamele et al. 2024). Recent work in manakin birds, for instance, explores the phylogenetic history of gene expression evolution in a specific wing muscle that is specialized to activate extremely rapid courtship gestures. The ability of this muscle to perform such maneuvering comes from the tissue's capacity to repeatedly contract and relax at rates that are roughly 3x faster than the wingbeat frequency associated with flight (Fuxjager et al. 2016; Miles et al. 2018). A number of genes (likely hundreds) are potentially involved in this process, and thus behavioral performance is likely dependent on an appropriate expression profile of these genes (Pease et al. 2022). Yet, this expression profile does not emerge at the same time as the behavior appears in the bird's lineage. Instead, changes in the expression of genes linked to this bird's display arise at different points across the species' evolution in a layered manner (Pease et al. 2022). The novel performance capacity to support rapid wing movements was contingent upon the slow accumulation of these changes during evolution.

Sexually selected signals may be related to vital cellular energetic processes

Sexual selection is a form of social selection, where intra-specific competition can lead to more constant and stronger selection compared to many forms of ecological selection (West-Eberhard 1983, 2014; Webster et al. 2018). In addition, Fisherian selection for arbitrary traits, which may drive extreme elaboration of signal-

ing structures, is also an important feature of sexual selection (Lande 1981; Kirkpatrick 1982). However, sexual signals are also often dependent on various metrics of condition (Cotton et al. 2006; Dougherty 2021), suggesting that such signals may serve as indicators of individual health, vigor, or other physiological features (Zahavi 1975; Pomiankowski 1987; Rowe and Houle 1996).

Some evidence suggests that sexual signals reflect some aspects of sub-cellular physiological processes. For example, the amount of bright red pigmentation in the wings of the damselfly, *Hetaerina americana*, reflects an individual's detoxification ability (G-Santoyo et al. 2021). Red carotenoid pigments as signals used in mate choice in birds have been a focus of many studies (Hill 2011; Koch et al. 2017; Hill et al. 2019). There is accumulating evidence that mitochondrial function may be reflected in sexually selected carotenoid pigment traits found in some bird species (Hill et al. 2002; Hill 2011; Koch et al. 2017). These findings suggest that the brightness of the red plumage in a male bird may provide females with information about that individual's health and vitality. However, it is unclear how a simple trait like feather hue can link to fundamental aspects of individual quality. In most bird species, the red carotenoid pigments used in coloration are produced from yellow dietary carotenoids via metabolic enzymes (Toomey et al. 2022); studies have shown that this metabolic transformation appears sensitive to mitochondrial characteristics (Hill et al. 2019). This suggests that the redness of carotenoid-colored ornaments may directly reflect some aspects of mitochondrial function (Hill 2011; Hill et al. 2019). However, this explanation does not account for different enzyme systems, with different species of red birds having different cellular locations of pigment production. In this issue, Koch et al. (2025) examine the different enzyme systems that relate to red carotenoid pigments in birds. Their findings suggest that understanding the molecular mechanisms underlying such signal evolution may be crucial to understanding the evolution of red carotenoid pigmentation in birds.

Visually conspicuous signals are just one small component of the diverse array of mating signals found in birds. Many mating signals are parts of complex multi-modal traits associated with behaviors that are shaped by competition for mating opportunities (Endler 1992; West-Eberhard 2014; Ryan 2018). Mating signals are not only important for reproduction within species but also play a role in speciation, as signals can mediate gene flow at the species boundaries, directing the evolutionary trajectories of distinct lineages (Mayr 1982; McDonald et al. 2001; Veen et al. 2001; Wang et al. 2020; Blom et al. 2024; Schield et al. 2024). These mating signals channel many sensory modalities, includ-

ing visual (Bennett et al. 1997; Ballentine and Hill 2003; Alonso et al. 2010), acoustic (Searcy 1992; Tomaszycki and Adkins-Regan 2005; Nemeth et al. 2012), kinaesthetic (Taylor et al. 1982; Alonso et al. 2010; Ota et al. 2015), and chemosensory signaling (Hirai et al. 1978).

Mating signals often require significant energy input to be maintained (Somjee et al. 2018) in addition to the already extensive energetic costs of growth, survival (Maurer 1996), and post-mating reproductive efforts (Welcker et al. 2015). The energetic requirements for diverse mating signals of all modalities are ultimately fueled by adenosine triphosphate, the energy-carrying molecule produced mainly by mitochondria. Yet, the sex-specific nature of mitochondrial inheritance complicates the avenues by which selection can act on mitochondrial characters (Nagarajan-Radha et al. 2020). Mitochondria have likely been coevolving with nuclear genomes for billions of years (Sagan 1967; Boore 1999; Wang et al. 2021), and incompatibilities between mitochondrial and nuclear genomes often lead to fitness decreases, especially in hybrid offspring (Hill 2017; Burton 2022). Thus, the mitochondrial genome and its co-functioning nuclear genes are predicted to co-segregate at species boundaries with selection that favors compatibility. Given the energy input required for mating displays in many species, such displays may serve as signals of high-performing mitochondria, such that individuals with “matched” mitonuclear genomes may be able to produce sufficiently attractive signals. This concept is referred to as “mitonuclear mate choice” (Hill 2018). However, it remains unclear how such selection occurs, as animals employ many different sensory modalities as sexual signals.

One possibility is that signals that exploit different sensory modalities are shaped to reflect energetic properties in different ways. Yet, it remains unclear how selective individuals evaluate mitonuclear compatibility in potential mates. One example, highlighted by Eddo et al. (2025) in this issue, comes from acoustic signals, which are common in birds. In some bird species, songs with higher trill rates, amplitudes, and/or higher syllable diversity are considered more energetically costly (Ritschard et al. 2010; Darolová et al. 2012; Sierro et al. 2023). In accordance with the prediction that songs with higher energy expenditure are more attractive, females of both Small Tree Finches (*Camarhynchus parvulus*) and Medium Tree Finches (*C. pauper*), prefer the calls of male Small Tree Finches, which have greater bandwidths and trill rates compared to medium tree finches (Podos 1997; Peters et al. 2017; Peters and Kleindorfer 2018). In these species, females appear to prefer songs that signal individuals with high-performing cellular energetic processes, at the potential cost of choosing a

heterospecific mate with uncertain mitonuclear compatibility.

In this issue, Eddo et al. (2025) examine other signal modalities that differ from static visual appearance, such as kinesthetic signals, which include courtship dances (Johnsgard 1965), aerial displays (Kilham 1960), and even the collection of materials used for structural displays (Doucet and Montgomerie 2003). The coordination required for these displays and the energy required to fulfill them are often associated with mating preferences (Koch and Hill 2018). Satin Bowerbirds (*Ptilonorhynchus violaceus*) produce elaborate structures that require significant energy for gathering decorations and building the bowers (Borgia 1985). However, Regent Bowerbirds (*Sericulus chrysocephalus*) build relatively simple bowers, which are less energetically costly to construct. Hybridization between these two species does occur, likely due to female regent bowerbirds preferring the apparently higher-energy bowers of Satin Bowerbirds (Eddo et al. 2025). Similar to the tree finches described above, mate choice preference for signals of high individual performance may conflict with selection against potentially incompatible hybrids.

Importantly, not all signaling modalities need to be linked directly to energetics. Eddo et al. (2025) suggest that the energy expenditure of mating signals can be difficult to decipher when multiple mating signals are involved during heterospecific interactions, such as the combined use of colorful pigments and acoustic signals (Love and Goller 2021; de Zwaan et al. 2022). However, linking complex mating displays to energetic processes enables the formulation of predictions and testable hypotheses, contributing to a more integrated understanding of mating signal energetics and their mediation of species boundaries (Eddo et al. 2025).

Social costs in crowded signaling environments shape calling strategies in túngara frogs

In this issue, Larter and Ryan (2025) consider the effects of social context in shaping the signaling strategies of chorusing insects and frogs in light of recent findings in túngara frogs. In many taxa, males produce elaborate courtship displays to attract mate-searching females, with signal elaboration evolving as males compete for female attention (Rosenthal 2017). Courtship signals are typically sent within the context of communication networks consisting of multiple signalers and receivers within the communication range of one another (McGregor 2006), which profoundly influences the evolution of courtship and mate choice strategies. One important communication network effect is sig-

nal interference among nearby signalers; this is an especially acute challenge for acoustic signals, which are loud and far-reaching (Greenfield 2015). For instance, in the dense acoustic choruses formed by many frogs and insects, background chorus noise impedes female abilities to recognize and localize conspecific males and to exert preferences among them (Vélez et al. 2013). In addition, more specific forms of inter-signaler interference during signaling interactions can be important. Here, a key factor is the temporal associations of signals, which, due to female sensory biases, can greatly influence the relative attractiveness of calls (Greenfield et al. 1997). This selects for signal-timing strategies allowing males to place their calls at opportune times relative to rivals' calls, to avoid calling at disfavored temporal positions, and even to relegate rivals to disfavored positions as a form of signal competition (Greenfield 1994).

The functioning of call-timing mechanisms driving signaling interactions has primarily been studied in chorusing insects that synchronize their calls, but the resulting call-timing models have been suggested to underpin call-timing interactions in frogs, pending a few parameter adjustments. However, frogs differ from synchronizing insects in their communication ecologies, with frogs forming denser choruses and primarily alternating with rivals to avoid call interference, rather than synchronizing (Gerhardt and Huber 2002). These different social contexts and strategies have likely led to differences in call-timing mechanisms. Specifically, the highly structured interactions of synchronizing insects seem to have selected for "rigid" call-timing mechanisms that are largely unresponsive to local acoustic conditions, to facilitate consistent responses to rivals' calls. After all, synchrony is a precise interaction outcome, and excessive responsiveness of call-timing mechanisms to local conditions might cause interaction patterns to break down.

Conversely, recent work on túngara frogs and hints from other frogs point to parameters of frog call-timing mechanisms being more probabilistic and malleable in response to local acoustic fluctuations. For instance, call periods (durations elapsing between onsets of successive calls) are more variable in frogs than synchronizing insects (Narins 2021), and frogs exhibit more probabilistic responses to rivals' calls (Narins 2021; Larter and Ryan 2024a, 2024b). Furthermore, túngara frog call-timing decisions are not influenced solely by the calls of individual rivals but also by emergent fluctuations in the acoustic scene at the chorus, such as amplitude spikes stemming from chance synchronous calls by multiple rivals (Larter and Ryan 2024b). Finally, túngara frog call-timing responses are sensitive to short-term patterns of arousal experienced prior to each call; males increase their probability of overlapping rivals'

calls and decrease response latencies when experiencing more intense conspecific acoustic stimulation immediately prior to calling (Larter, Cushing, and Ryan, submitted).

Stochasticity and malleability in response to local acoustic fluctuations are consistent with frogs' strategy of broadly avoiding calling at times of high conspecific interference. This broader strategy allows more degrees of freedom regarding interaction patterns than the highly structured interactions of synchronizing insects. Furthermore, it demands greater responsiveness to local acoustic environments due to the nature of relatively interference-free periods differing across acoustic environments generated at different chorus densities. These comparisons suggest that differing selection pressures—such as those associated with signal alignment in synchronizing insects versus more generic avoidance of interference in frogs—shaped by varying social environments, like denser choruses in frogs, can profoundly influence the mechanisms underlying sexually selected interactions.

Hormonal regulation by ecdysone shapes sex-specific phenotypes in insects

The sexes share the vast majority of genetic information and expression, yet they often face sex-specific selection pressures, leading to potential conflicts between the optimal phenotypes expressed in females relative to males (Pennell and Morrow 2013; Pennell et al. 2024). Males and females in gonochoric organisms are often monomorphic in morphology, but sexual dimorphism sometimes enables each sex to express phenotypes that may more closely align with their sex-specific selection pressures (Mank 2017, 2023; Van Der Bijl and Mank 2023). Indeed, the differences in energetics and physiology shaped by sex-specific reproductive, social, and ecological selection may impose highly divergent selection pressures on each sex (Somjee et al. 2022). In sexually dimorphic insects, for example, the developmental hormone ecdysone plays an important physiological role in the expression of sex-specific traits (Yamanaka et al. 2013).

One example of an ecdysone-associated molecular mechanism can be seen in the wing ornamentation of the Squinting bush brown butterfly, *Bicyclus anynana*. In this species, eyespots deflect predator attacks (Prudic et al. 2015), but these eyespots are also used in mate choice (Prudic et al. 2011). Sexual dimorphism in eyespot size occurs in the dry season, with males having smaller eyespots, but sexual monomorphism of these eyespots is found in the wet season, where both males and females develop large eyespots (Brakefield et al. 1998). In the wet season, exposure to higher tempera-

tures during the wandering larval stage leads to higher and similar 20HE (20-hydroxyecdysone) titer in both sexes, hence large eyespots in both sexes (Koch 1996). However, exposure to low temperatures in the dry season results in smaller eyespots in males. In females, the 20HE titers are still high, from an unknown mechanism, leading to the formation of larger eyespots. Here, the sex-specific difference in 20HE titer leads to seasonal sexual dimorphism in wing ornamentation (Bhardwaj et al. 2020).

Adding even more complexity to this paradigm is the sex-specific modification of ecdysone in the malaria carrier mosquito, *Anopheles gambiae*. Males produce a male-specific oxidized variant of 20HE, known as 3-dehydro-20E (3D20E). When they mate, males transfer 3D20E to females, effectively preventing further female remating (Hun et al. 2022; Peng et al. 2022). Here, the modified ecdysone variant acts as a powerful molecular mechanism to ensure the transfer of genetic material, bias the population-level prevalence of specific traits, and pave the way for selection of these traits in successive generations (Pondeville et al. 2008, 2019; Baldini et al. 2013; Peng et al. 2022). This provides an example of a simple, yet effective way that ecdysone-driven sexual dimorphism could guide ecological innovations. The different aspects of the ecdysone-driven molecular mechanisms in sexual dimorphism show remarkable biological diversity. These hormonally mediated variations could further drive physiological and behavioral differences, thereby expanding population-level phenotypic diversity (Prudic et al. 2011) and potentially playing a part in shaping evolutionary trajectories.

The ways in which hormone-mediated growth and behavior can be modified by ecdysone provide numerous avenues to generate variation at different scales of biological organization; such variation may be important for ecological adaptation (Carscadden et al. 2023). Ecdysone also interacts with metabolism in complex ways, with recent studies suggesting a link between ecdysone and mitochondrial function (Bollenbacher et al. 1977; Llorens et al. 2015; Vafopoulou and Steel 2016; Zhang et al. 2025). Further, examples of likely ecdysone-mediated developmental variants include the polymorphisms found in dung beetles (Moczek 1997, 2023; Moczek et al. 2011), crickets (Nespolo et al. 2008), leaf-footed bugs (Emberts et al. 2017), and harvestmen (Buzatto et al. 2011; Buzatto and Machado 2014; Painting et al. 2015). The pleiotropic effects of ecdysone signals in arthropods provide a trove of possibilities to understand the links between sexual selection and ecological adaptation.

Sexual selection may lead to the exploitation of novel thermal niches

Sexual selection often leads to trait elaboration and energetically demanding behavioral displays that can drive organisms to expand into different thermal environments. Multiple lines of evidence suggest that sexual selection may play an underappreciated role in the diversification of thermal niches. The enlarged bodies, ornaments, and weapons often favored by mate choice and/or competition confer greater “thermal inertia,” resulting in slower heating and cooling rates (e.g., elephant seals and insects [Muramatsu et al. 2020]). Dark sexual coloration can additionally elevate body temperatures by absorbing excess heat from the sun (e.g., lions [West and Packer 2002] and insects [Punzalan et al. 2007; Moore et al. 2019; Svensson et al. 2020; Laakso et al. 2021]), and metabolic heat is a frequent byproduct of energetically vigorous courtship and combat (e.g., insects [Sanborn et al. 2003; Villet et al. 2003; Erregger et al. 2017] and elephant seals [Norris et al. 2010]). Given that mating activity and the efficacy of sexual communication are both highly sensitive to environmental temperature (García-Roa et al. 2020; Leith et al. 2022), sexual selection can directly favor certain ornaments and behaviors due to the thermoregulatory advantages they provide in maintaining the optimal temperatures for mate competition (Punzalan et al. 2008; Laakso et al. 2021). In this issue, Giacometti et al. (2025) demonstrate how sexual selection can change how weapons and ornaments interact with the thermal environment and ultimately change organismal thermal biology. They also gathered data on weapon size from different invertebrates and showed that sexually selected weapons are proportionally larger at higher latitudes in a few taxa. This suggests an interaction between sexual selection and environmental temperature that requires further exploration.

However, even beyond mate competition, the thermoregulatory functions of sexual traits can also be co-opted in ways that expand niche access in non-competitive contexts (Leith et al. 2022). For example, although waxy patches of pruinescence in dragonflies likely first evolved as an ultraviolet sexual signal, the physiological advantages of pruinescence for reduced heating and enhanced desiccation resistance also facilitate niche expansion for pruinose dragonflies into hotter and drier climates (Moore et al. 2024).

Beyond the ornaments, weapons, and behavioral displays favored by sexual selection, the microhabitats that are advantageous during mate competition often contain the most extreme temperatures that organisms en-

counter in their lifetimes. For example, male fiddler crabs must remain at the surface of thermally stressful intertidal zones to attract mates and fend off rivals (Darnell et al. 2015). These microhabitats used to compete for mates ultimately bias ecological niche diversification by providing a strong source of selection on eco-physiological traits (Leith et al. 2022). More generally, thermoregulatory effort and physiological performance play key roles in enhancing mate encounter rates within mating microhabitats (Willmer 1991; Wilde et al. 2018), and recent simulations suggest that sexual selection for such traits could facilitate colonization in novel environments and the expansion of species range limits (Tschol et al. 2024).

In summary, adaptation to novel thermal environments cannot occur without some underlying heritable variation in form, coloration, behavior, and physiology (Darnell et al. 2015; Leith et al. 2022; Moore et al. 2024). In this way, sexual selection as a generator of phenotypic variation may be especially important in adaptation to novel or changing thermal environments (Leith et al. 2022).

Conclusion

Sexual selection plays a fundamental role in shaping a wide array of physiological, behavioral, and morphological traits across diverse species (Emlen 2008; Ryan 2018; Fuxjager et al. 2022). The case studies presented here underscore the energetic, physiological, and social dimensions of sexual signals, as these perspectives provide critical insight into their evolution (Fuxjager et al. 2022; Pease et al. 2022). We emphasize that sexual traits are underpinned by metabolic, hormonal, and cellular machinery that fuels their development and maintenance. For instance, the energy-intensive signals produced by manakins and many species of frogs are products of highly specialized physiological adaptations (Ryan 1988; Pease et al. 2022). Sexually selected carotenoid pigment expression is underpinned by different molecular pathways in different species of birds (Koch et al. 2025), sex-specific phenotypes are shaped by the interaction of both hormonal and environmental effects and varied dynamics arising across social environments (Larter and Ryan 2024a, 2024c, 2025). Further, energetic processes that shape sexual signals, which comprise different modalities, may affect patterns of hybridization between closely related species (Eddo et al. 2025). Thus, understanding the mechanisms underlying the production and diversification of sexual signals may provide unique insights into cellular processes shaping trait evolution. As sexual traits evolve, they often interact with environmental challenges such as temperature (Giacometti et al. 2025) and

changes in social dynamics, leading to complex interactions between sexual selection and ecological selection. By examining the integrated relationship between sexual selection, physiology, and ecology, we may be able to develop a more comprehensive understanding of the role that sexual selection plays in shaping organismal diversity.

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