The hidden figures across species boundaries: the mitochondrial energetics behind mating signal divergence

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Abstract

The energy expenditure of mating signals is often divergent between species and mediates heterospecific mating, thus influencing the direction of gene flow across the species boundaries. The relative energetics of the mating signals can be underpinned by mitochondrial haplotype divergence between species, which contributes to hybrid mitonuclear incompatibility and speciation. Here, we discuss the connection between mitochondrial variation, mating signal energetics, and their impact on gene flow across the species boundaries. Using multiple case studies, we highlight the connections between mating signal energetics and gene flow across visual, acoustic, kinesthetic, and chemosensory signaling modalities. Integrating mitochondrial functions and mating signal energetics at the species boundaries will illuminate the organismal mechanism underlying the formation and maintenance of species boundaries.

Keywords: mating signals, sexual selection, mitochondria, mitonuclear, speciation, hybridization, energetics.

Introduction

Mating sexual signals are traits that lead to behavioral changes in the receivers that increase the mating success of the signalers (Endler, 1992; Darwin, 1871, Ryan, 2018). These signals often mediate gene flow across species boundaries in the speciation continuum, influencing breeding outcomes within and between species (McDonald et al. 2001; Veen et al. 2001; Blom et al. 2024; Schield et al. 2024). Sexual signals are often associated with excessive energy expenditures (Höglund et al. 1998; Somjee et al. 2018) besides the energy involved in the development, homeostasis, survival (Walsberg 1983; Maurer 1996), and post-mating reproductive efforts (Welcker et al. 2015).

Mitochondria, being the ATP-producing symbiont, empowered the origin and radiation of eukaryotic species (Schavemaker and Muñoz-Gómez 2022). Most mitochondrial energetic functions are encoded in the nuclear genomes, which have been coevolving with the mitochondrial genome every generation for billions of years of eukaryotic evolution (Sagan 1967; Boore 1999; Wang et al. 2021). Mitonuclear ancestry discordance often disrupts hybrid fitness and fundamentally contributes to speciation (Hill 2017; Burton 2022). The forms and functions underlying sexually selected signals among all the fitness-determining traits require mitonuclear synergy to generate ATP. Therefore, mate choice is expected to favor the signal variations that reflect mitonuclear compatibility or synergy, i.e., ‘mitonuclear mate choice’ (Hill 2018).

Energy penetrates all signal modalities, including pigments and tissue development in visual signals (Bennett et al. 1997; Ballentine and Hill 2003; Pincemy et al. 2009; Alonso et al. 2010), sound waves in acoustic signals (Searcy 1992; Tomaszycki and Adkins-Regan 2005; Nemeth et al. 2012), locomotion in kinesthetic signals (Taylor et al. 1982a; Alonso et al. 2010; Ota et al. 2015), and pheromonal compounds in chemosensory signals (Hagelin et al. 2003; Santos et al. 2018). This energy expenditure comes in multiple forms, such as the nutrients required to develop, deposit, and maintain pigments (Hill 1996; Jawor and Breitwisch 2003; Hill and McGraw 2006; Weaver et al. 2018), energetic courtship displays (Barske et al. 2011; Fuxjager et al. 2022), as well as the frequency and repertoires of courtship songs (Ryan 1988; Searcy 1992; Tomaszycki and Adkins-Regan 2005).

Mating signal energetics and gene flow

Higher expenditures are expected in honest signals within species (Grafen 1990), but the expectation across species boundaries remains elusive. In addition, the direct and indirect association between mitochondrial function and mating signal energetics awaits further characterization. Here, we discuss examples of signal energetics and how they predict the directionality of gene flow across avian species boundaries.

Visual signals

Visual signals are expressed in variable colorations (Cooney et al. 2019), sizes, and shapes of morphological features. The energetic costs associated with body size are relatively straightforward to assess, as a larger body mass generally requires more energy for sustained physiological activity and metabolism (Taylor et al. 1982b; Mcnab 1983). In contrast, the energetics of color signals are hierarchical composites of energetic expenditure involved in pigment synthesis, conversion, transportation, and deposition.

For example, the synthesis of melanic pigments requires ATP produced by mitochondria (Hill 2006; Maranduca et al. 2019). The distinct yellow and black pigmentation of the hybridizing sister species (Wang et al. 2019), *Setophaga townsendi* (STOW) and *S. occidentalis* (SOCC), are underpinned by the genotypic difference in ASIP, agouti signaling protein (Wang et al. 2020), which regulates MCR1 (melanocortin 1 receptor) to control the stoichiometry of the black eumelanin and yellow pheomelanin (Hida et al. 2009). The facial and flank pigmentations are shown to be mating signals, as the extent and intensity of the colorations are associated with male body size variation within species (de Zwaan et al. 2022). Hybrids with mismatched color patches display inferior territorial performance, while hybrids with concordant, more melanic patches reside in the peak of the performance landscape (Fig. 1). This reflects a slight asymmetric selection favoring the melanic appearance with greater territorial performance (Fig. 1 B) (de Zwaan et al. 2022). The hybridizing species also harbor divergent mitochondrial haplotypes (Wang et al. 2021), which can predispose the divergent signal energetics.

Carotenoid coloration, as seen in House finches (*Haemorhous mexicanus*), is linked to higher fitness and is sexually selected for (Hill 1999; McGraw 2000). Energy expenditure accrues as the carotenoids are acquired through the intake of specific nuts and fruits, processed, converted, transported, and deposited in the feathers (Brush 1990). The red carotenoid is preferred by females (Hill 1999) and is produced by oxidizing yellow versions of the same pigment, a process that has been linked to elevated mitochondrial function (increased respiration rates, membrane potential, and hydrogen peroxide production) in the liver (Hill et al. 2019).

The hybridization between house finches and domestic canaries (*Serinus canarius domesticus*) (Clement 2025) is likely influenced by the energetics of carotenoid signals. The canaries have white, yellow, or red carotenoid-based color morphs (Toomey et al. 2017). Canaries prefer the yellow and red morphs over the white morphs while remaining neutral for the red and yellow morphs (Koch and Hill 2019). The mate preference associated with carotenoid energetics can lead to asymmetric introgression at the species boundaries. Collectively, the examples underscore the linkage of mitochondrial function and mating signals' energetics mediating the extent and direction of gene flow across species boundaries.

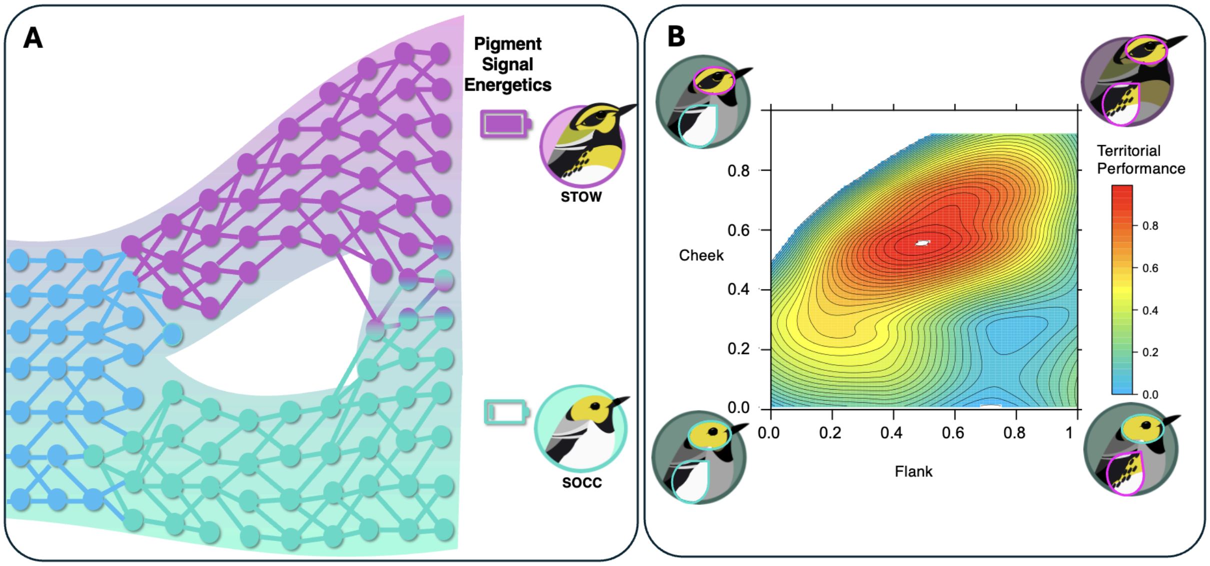

Fig. 1 Asymmetry of signal energetics and speciation in *Setophaga occidentalis* and *S. townsendi*. **A**, Illustration of speciation and hybridization in the sister species SOCC and STOW. **B**, Hybrids with more melanic plumage (as STOW) showed slightly greater territorial performance. Figure (B) adapted with permission from (de Zwaan et al. 2022).

Acoustic signals

Acoustic signals vary in energetics and complexity across species. Songs that contain 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). For example, Darwin's small tree finch (*Camarhynchus parvulus*), where songs with greater bandwidths and trill rates correlate with greater mating success (Christensen et al. 2006).

The hybridization between *C. parvulus* and its congener, the medium tree finch (*C. pauper*) in the Galapagos Islands (Peters et al. 2017) is modulated by their relative energetics of acoustic signaling. The songs of *C. pauper* had a slower trill rate, fewer syllables per song, broader frequency bandwidth, lower minimum frequency, and lower dominant frequency (Peters and Kleindorfer 2018), which converge to lower energetics. This relative acoustic energetic expenditure predicts greater mate attraction of *C. parvulus* males over *C. pauper* males. Indeed, *C. parvulus* males are preferred by females of both species, resulting in the disproportionate pairing of *C. pauper* females and *C. parvulus* males (Kleindorfer et al. 2014; Peters and Kleindorfer 2018). This initial heterospecific pairing pattern leads to the dominance of *C. parvulus* ancestry in hybrid populations (Dudaniec et al. 2025). The relative acoustic energetics can be linked to divergent mitochondrial functions in this species pair despite the limited mtDNA divergence (Sato et al. 1999; Metzger 2012).

More broadly, mitochondrial functions have been linked to the frequency of acoustic signals (Crino et al. 2022). However, mitochondrial efficiency is highly tissue-specific (Barbe et al. 2023), and avian vocalization involves the synergetic coordination of the respiratory-vocal and neuromuscular systems (Schmidt and Wild 2015). Future quantification of acoustic energetics requires a hierarchical understanding of mitochondrial functions.

Kinesthetic signals

A wide variety of signals are kinesthetic and involve ritualized locomotive displays and/or the construction of a courtship arena in the form of bowers or other architecture. In particular, kinesthetic signals can take the forms of courtship dances (Johnsgard 1965), aerial pair flights (Kilham 1960), or even the collection and arrangement of materials for a structural display (Doucet 2003). The neuromuscular coordination underlying these behaviors is influenced by mitochondrial functions, which support the cellular and physiological processes necessary for such complex actions (Koch and Hill 2018). Compromised mitochondrial function during development may impair neural pathway formation, whereas dysfunction in adulthood can hinder the execution of energy-intensive sexual traits.

More complex and prolonged displays are associated with greater energetic investment and signal higher individual quality. In satin bowerbirds (*Ptilonorhynchus violaceus*), males with well-constructed, highly decorated bowers are preferred by females (Borgia 1985) (Fig. 2). Building and maintaining these elaborate structures requires significant energy, both for gathering decorations and ensuring structural integrity with more resources. In contrast, their relatives, the regent bowerbirds (*Sericulus chrysocephalus*), build simple bowers, which are less energetically costly

(Fig. 2). The hybridization between these two species (Frith 2015) is likely influenced by their relative courtship energetics (Fig. 2).

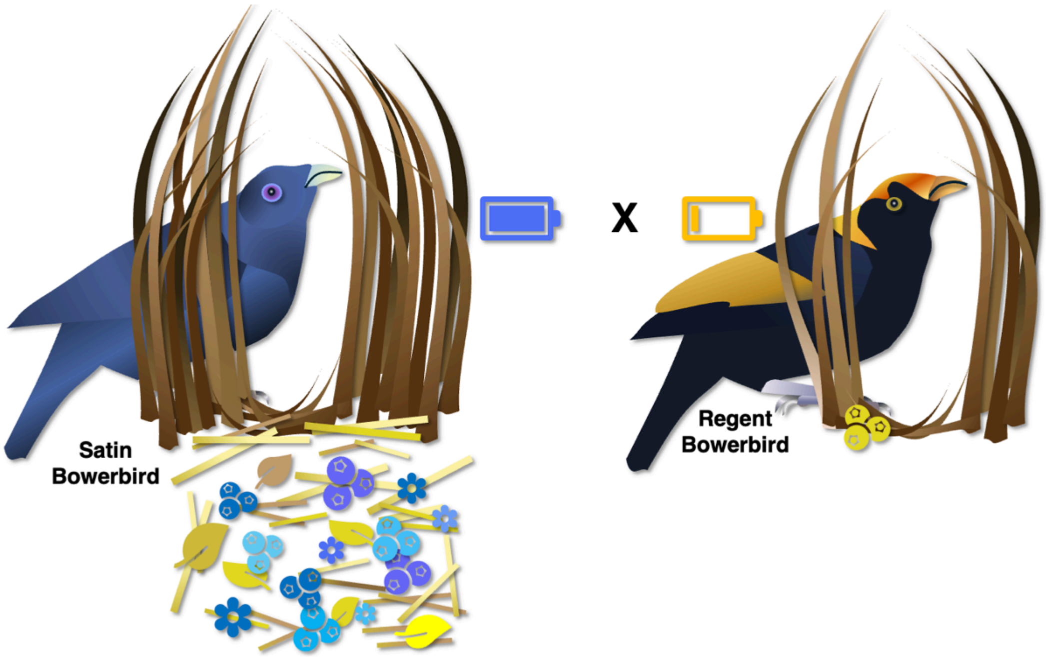

Fig. 2 Asymmetry of energetic expenditures of hybridizing bowerbirds.

Kinesthetic signals involving aerial displays have unique energetic demands, particularly in larger avian species. Flight muscles, rich in mitochondria, rely on aerobic metabolism to sustain display behaviors, with increasing muscle activity driving higher oxygen demand (Suarez et al. 1991). The energetics of these displays depend on altitude, duration, and maneuver complexity, as higher altitudes present greater oxygen limitations and increased costs for flapping flight (Butler 2016).

In birds of prey, such energetically costly displays remain understudied. The Bald Eagle (*Haliaeetus leucocephalus*) and Steller's Sea Eagle (*Haliaeetus pelagicus*), two hybridizing raptors, perform distinct aerial courtship displays that likely have energetic implications. Bald eagles engage in chases with maneuvers such as inverted flight to display talons and "roller-coaster" dives, where they plunge at high speeds before ascending again (Stalmaster 1987). Pairs may also interlock talons midair, releasing just before hitting the ground, often preceding copulation (Stalmaster 1987; Potapav 2015). In contrast, male Steller's Sea Eagles circle above females before diving sharply toward them, leading to copulation (Potapav 2015). These ritualized displays require substantial energy investment, particularly given the large body masses of both species, which increases the metabolic cost of maintaining altitude and executing flapping-intensive maneuvers (Butler 2016).

While direct studies on *Haliaeetus* flight energetics are absent, broader avian research provides relevant insights. Mitochondrial requirements for the pectoralis muscle are estimated at 1 mL of mitochondria per 1 watt of power output (Pennycuick and Rezende 1984), with flight power demands varying by speed. Takeoff and high-speed maneuvers require significantly more energy than moderate-speed cruising (Biewener 2011). Given that both *Haliaeetus* species engage in rapid, energetically demanding courtship flights, these displays likely reflect mitochondrial performance and serve as direct indicators of fitness.

Chemosensory signals

Chemosensory signaling remains the most understudied modality. Among the limited studies, several suggest that chemosensory signals mediate conspecific mate recognition in birds (Van Huynh and Rice 2019; Krause et al. 2023), which highlights their significance in reproductive isolation and speciation. Less is known in terms of the relative energy expenditures among variants of chemosensory signals, though the synthesis and perception of this modality of signals cost energy. For example, the production of urinary peptides that are heavily used in chemosensory signaling for territoriality and mate attraction in mice requires complex biochemical pathways (Brennan and Kendrick 2006) that require ATP generated by mitochondria. Additionally, olfactory sensory neurons rely on ATP to mobilize Ca^{2+}, a process essential for accurate odor detection and signal processing in various animals (Fluegge et al. 2012). The mammalian chemosensory signaling energetics may extend to mating systems of other animals. Future studies that quantify the relative energy expenditure among signal variants would shed light on the cause of chemosensory energetics and their consequence in speciation.

Multi-modal mating contexts across species boundaries

Heterospecific interactions often involve multiple modalities simultaneously. For example, in the hybridizing species complex of *Setophaga occidentalis* and *Setophaga townsendi*, both acoustic and color signals (Love and Goller 2021; de Zwaan et al. 2022) influence the extent and direction of gene flow. Similarly, satin bowerbirds (*Ptilorhynchus violaceus*) select mates based on a combination of intricate bower constructions, decorations, and plumage coloration (Fig. 2) (Doucet 2003). Moreover, multimodal signals are often interconnected, as higher call frequencies were linked to lower mitochondrial efficiency and smaller body mass (Crino et al. 2022). Meanwhile, body mass itself is a key signal for mate choice, as it can indicate overall condition, competitive ability, and reproductive potential (Davis and Darby 1990; Peters et al. 2017; Coster et al. 2018). Given the complex layering of energetic and selection contributions across different modalities, future studies should adopt both reductionist and holistic approaches for understanding the independent and synergistic mating signal energetics and their impact on species boundaries.

Future Directions

Here, we highlight the future directions that would advance the understanding of mating signal energetics and their mediation of species boundaries.

(1) Studies that quantify and examine energy input into the production or maintenance of signals are fundamental to energy costs required for mating signaling. In particular, hierarchical tissue-specific mitochondrial energy production underlying composite signals are needed.

(2) Among signaling modalities, understanding the energy allocation, compensation, and synergy would be necessary to infer the emergent energetics of mating signals.

(3) The synergistic effects of hybridization across modalities are often difficult to determine. Multiple modalities may overlap during courtship displays, and the individual effects of each modality are difficult to determine. We suggest studies that focus on understanding the independent and interactive effects of signal modalities on hybridization. Specifically, experimental studies masking specific signal modalities could be illuminating.

(4) The direct quantification of relative energetics expenditure along signal divergence remains understudied. The production and maintenance of distinct character states of divergent signals likely incur distinct energy levels. Studies that link the relative energy expenditure of divergent signals and mating outcomes can inform the effect of mating signal energetics on hybridization.

(5) There is limited understanding of mating signals in hybridizing species and even less about the physiological underpinnings of mating signal energetics. More behavioral physiological studies are needed for a diverse array of hybridizing organisms. Further comparative study on mating signal energetics across hybridizing species can inform energetic regularity behind the diverse forms and function across the tree of life.

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