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# Testing the strength and direction of selection on vocal frequency using metabolic scaling theory

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**Abstract.** A major challenge for studies assessing drivers of phenotypic divergence is the statistical comparison of taxa with unique, often unknown, evolutionary histories, and for which there are no clear expected trait values. Because many traits are fundamentally constrained by energy availability, we suggest that trait values predicted by scaling theories such as the metabolic theory of ecology (MTE) can provide baseline expectations. Here, we introduce a metabolic scaling-based approach to test theory involving the direction and magnitude of ecological and sexual selection, using vocal frequency as an example target of selection. First, we demonstrate that MTE predicts the relationship between the natural log of body size and natural log of vocal frequency across 795 bird species, controlling for phylogeny. Family-wide deviations in slope and intercepts from MTE estimates reveal taxa with potentially important differences in physiology or natural history. Further, species-level frequency deviations from MTE expectations are predicted by factors related to ecological and sexual selection and, in some cases, provide evidence that differs from current understanding of the direction of selection and identity of ecological selective agents. For example, our approach lends additional support to the findings from many cross-habitat studies that suggest that dense vegetation selects for lower frequency signals. However, our analysis also suggests that birds in non-forested environments vocalize at frequencies higher than expected based on MTE, prompting intriguing questions about the selective forces in non-forest environments that may act on vocal frequency. Additionally, vocal frequency deviates more strongly from MTE expectations among species with smaller repertoires and those with low levels of sexual dichromatism, complicating the use of these common sexual selection surrogates. Broad application of our metabolic scaling approach might provide an important complementary approach to understanding how selection shapes phenotypic evolution by offering a common baseline across studies and taxa and providing the basis to explore evolutionary trade-offs within and among multicomponent and multimodal traits.

**Key words:** allometry; birdsong; ecological selection; metabolic theory of ecology; scaling laws; sexual selection; vocal evolution.

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## INTRODUCTION

An outstanding challenge for understanding drivers of phenotypic and species diversification is to assess the relative effects of sexual and ecological selection on trait evolution. This is largely because within systems, typically only one of these selective factors is considered (Maan and Seehausen 2011, Safran et al. 2013, Wilkins et al. 2013). Perhaps even more important, however, is the lack of baseline expectations for trait values across taxa to which observed trait values can be compared. To draw broader comparisons across studies and taxa, it would be useful to have a global set of predicted values for comparison that are independent of clade-specific phylogenetic contingencies of trait evolution. Like others before us (Valen 1976, Brown et al. 1993, Brown et al. 2004, Tomlinson et al. 2014), we suggest that energy—a fundamental currency of life—represents the key to linking many patterns and processes across scales, including the evolution of phenotypic traits. The Metabolic Theory of Ecology (MTE), and other metabolic scaling theories, such as Dynamic Energy Budget Theory (DEB), have become useful frameworks for identifying and testing general relationships among metabolism, temperature, size, and a variety of ecological patterns (reviewed in Brown et al. 2004, Glazier 2005, Glazier 2010, Maino et al. 2014). For example, MTE often predicts trait relationships among organisms that vary in mass by several orders of magnitude and live across broad temperature ranges (Sibly et al. 2012*a, b*). Despite its widespread use in explaining ecological phenomena, MTE is not often applied to evolutionary studies—except for explaining rates of molecular or phenotypic change (Gillooly et al. 2005, reviewed in Gittleman and Stephens 2012) or explaining variation in life histories among entire clades (Sibly and Brown 2007, Sibly et al. 2012*a, b*)—yet it has considerable potential to provide insights on other evolutionary processes.

Here, we argue that adopting a metabolic framework for studying evolution has the potential to provide a synthesis between ecological models based on units of energy and evolutionary models typically based on differences in phenotypes, genetics, or fitness. Whether a behavioral trait that depends on the availability of energy for

its expression or a morphological feature that requires energetic resources during ontogeny and maintenance, both are directly linked to metabolic rate. Thus, for any trait that varies with temperature and body size due to its dependence on metabolic power, metabolic scaling theories provide statistical expectations for trait values and bases for comparison across taxa.

There is considerable support for a central tendency of a 3/4-power-scaling relationship between metabolic rate and body mass across species (Kleiber 1932, Banavar et al. 2002, Isaac and Carbone 2010). The precise reasons for this relationship are not settled, with explanations deriving from limitations in how materials are transported through fractal networks of branching tubes (MTE, West 1997) or based on constraints on the ratio of cellular structure to energetic reserve as size increases (DEB, Kooijman 1986, Maino et al. 2014). Here, we focus on 3/4 power scaling that is consistent with MTE and DEB expectations for two primary reasons. First, MTE is the only metabolic theory which has previously been applied to variation in acoustic signaling within and among species (Gillooly and Ophir 2010, Ziegler et al. 2016). Second, within birds, metabolic rate appears to adhere quite closely to 3/4 scaling (Uyeda et al. 2017), suggesting it is the most appropriate scaling power for our purposes (see next two paragraphs).

For our worked example, we assume that vocal frequency is determined by metabolism. As outlined in Gillooly and Ophir (2010), animal vocal frequencies are largely determined by muscular contraction rates (Skoglund 1961, Elemans et al. 2008), both of which scale to the 1/4 power with body mass. Muscle contraction frequency is approximately equal to the frequency of the sound produced across vertebrates (Skoglund 1961, Martin 1971, Rome et al. 1996, Elemans et al. 2008), and muscular contraction rates are proportional to mass-specific metabolic rates (Prestwich 1994, Hempleman et al. 2005). An alternative explanation for  $-1/4$  power scaling of muscular contraction rates and vocal frequency is that geometric changes in body size inherently lead to 1/4 power scaling of the duration of a variety of physiological cycles and  $-1/4$  power scaling of their rates (reviewed in Lindstedt and

Calder 1981). More recently, Burger et al. (2020) presented  $1/4$  power scaling of time as a fourth dimension of life that, when integrated with static scaling of organisms to the third power, provides a more general model for the ubiquitous  $3/4$  power-scaling relationships. More work is necessary to integrate or exclude these alternative explanations. Importantly, the general analytical approach we outline below can be applied irrespective of the ultimate reason behind  $3/4$  power scaling or other scaling exponents.

Key to our worked example is that Gillooly and Ophir (2010) demonstrated wide support for metabolic scaling of signal rate, duration, and frequency across animals ranging from water bugs to whales that is consistent with  $3/4$  power metabolic scaling expectations. However, like numerous other studies, they showed significant variation in this relationship across taxa (McNab 2009, Glazier 2010, Isaac and Carbone 2010, Hudson et al. 2013). As suggested by Banavar et al. (2002), deviations from metabolic scaling predictions are expected to result from energetic inefficiency (i.e., weak selection for metabolic efficiency) and/or as a result of strong counteracting selection. Indeed, Sibly and Brown (2007) and Sibly et al. (2012*a, b*) interpreted relative differences in the intercept for the relationship between body mass and productivity among clades or species with different lifestyle traits as evidence for evolutionary innovations in ecology or physiology resulting from selection. Similarly, Fristoe et al. (2015) used residual variation in the allometric relationships of metabolic rate and thermal conductance with body mass to shed light on selection from thermal regimes. Thus, deviations from the statistical expectations generated from MTE, other metabolic theories, or other allometric relationships in general have the potential to provide a useful quantity for exploring the interplay between energetic or geometric constraint and other deterministic factors driving trait divergence.

In our metabolic framework for studying selection, we expect that selection for energetic efficiency, should maintain body size- and temperature-dependent trait values close to MTE's statistical expectations (blue line in Fig. 1). Thus, for metabolically constrained species, selection that changes body size or body temperature should result in a pleiotropic change in trait

expression to match the metabolic optimum (e.g., trait value for species "i" slides up or down the line in Fig. 1a). If, however, trait values are much higher or lower than MTE expectations for a species' body size or body temperature, this could mean the following: (1) There have been body size- or temperature-independent effects on metabolic rate or (2) counteracting selection has moved the trait value away from the metabolic optimum (e.g., trait value for species "ii" is far from the value predicted by MTE in Fig. 1). Previous work indicates that the first scenario, divergence in metabolic rate, could be driven by population density (DeLong et al. 2014) or numerous ecological factors such as feeding ecology, habitat, altitude, climate, and locomotion (McNab 2009). In general, the second scenario, trait evolution resulting from counteracting selection, has, as far as we are aware, received little or no attention. Therefore, we propose that deviations from MTE predictions for a variety of traits can be used to determine how different sources of selection explain phenotypic variation across species and other taxonomic levels (Box 1).

In terms of our trait of interest, peak frequency is a known target of both ecological and sexual selection (Boncoraglio and Saino 2007, Wilkins et al. 2013) and, along with several other features of acoustic communication, adheres quite closely to the MTE prediction that trait variation scales with body size according to the same power-law relationship as metabolism (Gillooly and Ophir 2010, Ziegler et al. 2016). These characteristics and widely available data make peak frequency ideal to evaluate the utility of our framework for providing insights on the direction and magnitude of ecological and sexual selection within a phylogenetic framework.

We compiled a dataset of 795 species, representing 18 orders and 74 families in class Aves, informed by the most recent species-level phylogeny for birds (Jetz et al. 2012). Our analyses encompass three taxonomic scales: class, family, and species. At the class level, we demonstrate that MTE can explain the relationship between body size and peak vocal frequency at both a smaller taxonomic scale and range of body sizes than the theory is typically applied (Brown and Sibly 2012, but see Ziegler et al. 2016 for an intraspecific example in frogs). We then explore

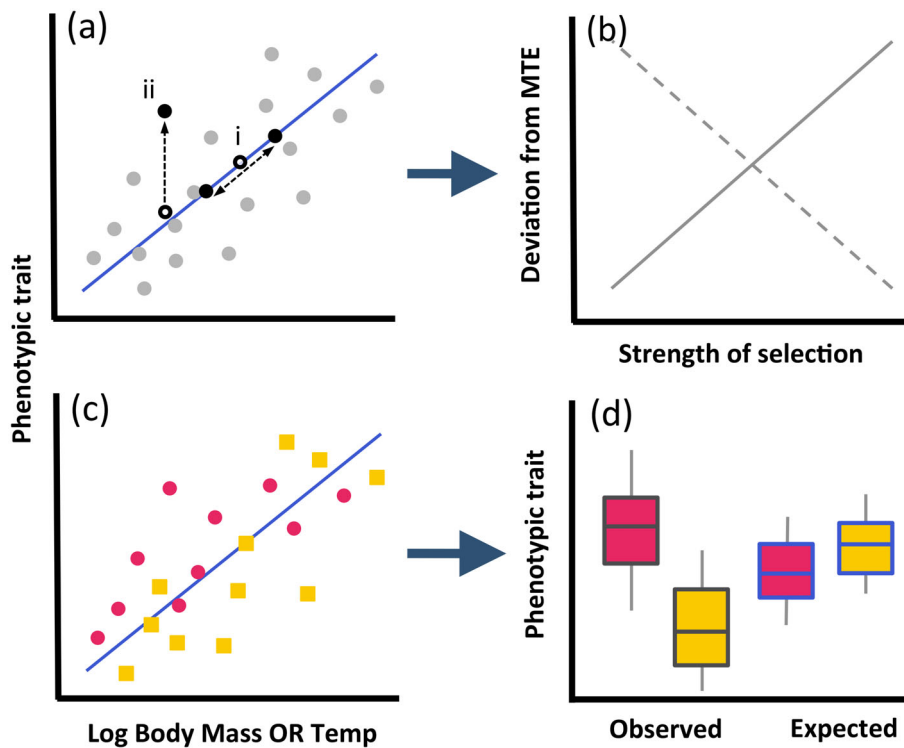


Fig. 1. Framework for using the metabolic theory of ecology (MTE) to test the direction and strength of selection. (a) Selection for resource transport efficiency should maintain trait values near or at the value predicted by MTE (denoted with an “i”); however, for species where expression of a trait is less metabolically constrained, selection could act on the trait such that it deviates from MTE expectations (denoted by “ii”). (b) The direction and distance a trait value differs from MTE expectations can be used to test theory about the forces shaping trait expression. Alternatively, if direction (i.e., higher or lower than expectations) is not required for a set of hypotheses and predictions, such as our worked example, the absolute value of the distance between observed and expected values can be used. (c) Observed values that correspond to two categories (red circles and yellow squares) can be compared with values expected from MTE (d) to determine whether there is evidence for selection operating on a trait in a predicted direction.

how the body size–frequency relationship varies across well-represented families in our dataset. Finally, we evaluated the influence of several indicators of ecological and sexual selection on avian peak frequency using two sets of phylogenetic generalized least squares (PGLS) analysis. First, we used frequency as the response variable and controlled for mass by including it as a covariate in each model. Second, we used the absolute value of the frequency deviation from MTE expectations as the response variable. To our knowledge, our study is the first to evaluate the strength and direction of phenotypic selection using power–law relationships derived from a metabolic perspective.

*Worked example background*

Our set of predictor variables were chosen due to their common usage as surrogate measures of natural and sexual selection. First, in our main test of natural selection, we tested the acoustic adaptation hypothesis, with different signaling environments (forested vs non-forested) as the sources of ecological selection that could influence vocal frequency divergence (Morton 1975). Specifically, because higher frequency sounds attenuate more strongly in closed relative to open habitats due to more sound absorption and scattering from foliage (Brumm and Naguib 2009), animals living in closed environments are predicted to vocalize at lower frequencies than

**Box 1.****Framework for using MTE or other metabolic scaling theories to study selection**

Trait values for metabolically constrained species should be highly predictable from MTE due to selection favoring energetic efficiency, and changes in trait values should arise primarily from changes to species' body size or body temperature (species "i" in Fig. 1a). However, an oft-cited criticism of MTE is that there is considerable residual variation around scaling relationships between temperature-corrected body mass or body mass-corrected temperature and various traits of interest (Horn 2004, DeLong et al. 2014, Fig. 1a,c). For many traits strongly influenced by metabolism, the difference between the observed trait and that expected by MTE may reflect *actual* differences in metabolism. That is, the observed metabolic rate for the species in question deviates from theoretical expectations, and the associated trait does not appear to be well explained by temperature-corrected body mass or body mass-corrected temperature (see main text; species "ii" in Fig. 1a). Alternatively, the distance from MTE's expectation (vertical dashed line in Fig. 1a) could reflect the influence of one or more counteracting agents of selection operating on the trait. Thus, the trait's distance from the expected value could convey information about selective pressures and used to test theory regarding the influence of selective agents on trait divergence (Fig. 1b). In many cases, researchers may predict greater deviation from MTE expectations with increases in the strength of selection (solid line in Fig. 1b). Alternatively, following the principle of allocation, if expression of a trait is predicted to trade-off with expression of one or more additional traits that experience strong selection, one might expect trait values to be closer to the metabolic optimum (dashed line in Fig. 1b). This may be especially true for composite traits (see Box 2).

Rather than comparing observed values across categories (e.g., clades or habitat types), which allows one to detect relative differences across categories, but does not identify the direction of selection, observed trait values (Fig. 1c) can also be compared with those expected from MTE (Fig. 1d). For such comparisons, MTE-derived values should represent the theoretical expectation for traits that have not experienced directional or disruptive selection from other agents. Comparisons of observed values to these "baseline" expectations can determine whether traits assumed to be under selection are actually different from what might be expected due to differences in metabolism alone and whether patterns of trait deviations correspond to measures of the strength and direction of selection. Finally, an important assumption inherent to both approaches is that while the slope for determining expected trait values is derived from theory, the intercept is derived empirically from data (see worked example). Because the sample can influence intercept estimates, researchers should restrict comparisons to the sample because only part of the expected values are derived from theory (i.e., using the slope).

those living in more open environments. Thus, in the context of using metabolic scaling theories to generate baseline values for comparison, we would expect birds living in forested environments to have signals that are lower in frequency than expected from MTE and that birds in non-forested environments would vocalize at frequencies that do not differ from MTE expectations.

We used several indices for the intensity of sexual selection, including avian plumage dichromatism, song repertoire size, a multimodal sexual selection index, and extra-pair paternity, as well as latitude as a measure of the combined effects of sexual and ecological selection. Avian plumage sexual dichromatism (henceforth, dichromatism) reflects the degree to which males and females differ in the color of their feathers. Investigators have used dichromatism as an index of the

intensity of sexual selection (Owens et al. 1999, Medina and Francis 2012, Seddon et al. 2013, Huang and Rabosky 2014) based on the notion that dichromatism evolved in response to female preferences and male-male competition (Andersson 1994). However, dichromatism may also result from ecological selection for crypsis in females, rather than increased elaboration in males (Burns 1998, Badyaev and Hill 2003), complicating interpretation of this variable. Moreover, the relationship between sexual dichromatism and speciation was shown to vary across bird families (Huang and Rabosky 2014), suggesting this metric likely underestimates the importance of sexual selection in monochromatic species, which may rely more on acoustic signals for mate choice. Song repertoire size is also thought to be driven by sexual selection (Maccougall-Shackleton 1997) either through female preference

(Catchpole and Slater 2003, Collins 2004) or through a combination of social factors, such as intrasexual competition (Byers and Kroodsmas 2009, Soma and Garamszegi 2011, Wilkins et al. 2015). Yet, similarly, this metric of sexual selection will be conservative for species with strong sexual selection but low repertoire size, a scenario which may be common (Snyder and Creanza 2019).

In general, due to differences in the spatial use of visual and acoustic signals (Uy and Safran 2013), these traits may often evolve under distinct selection pressures. Previous work demonstrates variable relationships between acoustic and visual complexity across taxa, with indications of positive (Medina and Francis 2012, Hebets et al. 2013, Santos et al. 2014), negative (Badyaev et al. 2002), or no relationship (Ornelas et al. 2009, Mason et al. 2014). Therefore, in order to provide an overall estimate of sexual selection, we created a multimodal index by averaging dichromatism scores with song repertoire quantile ranks. This metric should provide a better estimate of overall sexual selection strength across species.

Due to its clear and close link to fitness, our most direct measure of sexual selection was proportion of nests with extra-pair young (i.e., extra-pair paternity, henceforth, EPP). However, the relationship between EPP and the strength of sexual selection is not always straightforward (Schlicht and Kempenaers 2013).

Latitude has also been routinely linked to sexual selection intensity, based on the notion that animals at higher latitudes have shorter breeding seasons that lead to intense male–male competition and require rapid mate choices (Botero et al. 2009, Weir and Wheatcroft 2011). However, latitude also covaries with a number of factors, such as migratory behavior, cognitive ability, and the importance of female choice versus competition, which may affect the strength of sexual selection (reviewed in Singh and Price 2015). In addition, latitudinal variation in ecological factors such as proportion of open habitat and number of competitors for acoustic space could influence signal evolution, leading to higher pitched, more complex signals at higher latitudes (Ryan and Brenowitz 1985, Weir and Wheatcroft 2011, Greig et al. 2013, Singh and Price 2015). Song frequencies might also vary with latitude as a pleiotropic effect of gradients in body size (i.e., James' and

Bergmann's rules; Gaston et al. 2008) or bill size (i.e., Allen's rule; Danner and Greenberg 2015). Thus, latitude should serve as a reasonable proxy for the combined effects of ecological and sexual selection. Generally, we expect stronger selection at higher latitudes, where trait evolution (Weir and Wheatcroft 2011) and recent speciation rates (Weir and Schluter 2007, Schluter 2016) are thought to be higher for birds, though there is uncertainty about the generality of these findings (Tobias et al. 2008, Schluter 2016). Collectively, our set of predictors provides a nuanced view of the variety of factors that potentially influence vocal frequency and its deviation from metabolic expectations.

## MATERIALS AND METHODS

### Data

We created our dataset based on a detailed search of the literature, including papers that reported vocal peak frequency (the frequency with the most acoustic energy) for multiple species. This was completed by reviewing recent papers and reviews involving vocal frequency (Boncoraglio and Saino 2007, Ey and Fischer 2009, Tobias et al. 2010) and a Web of Science literature search for “acoustic adaptation hypothesis” and “bird or avian.” Ten papers met our criteria (Tubaro and Mahler 1998, Bertelli and Tubaro 2002, Rheindt 2003, Tubaro and Lijtmaer 2006, Hu and Cardoso 2009, Luther 2009, Cardoso 2010, Goodwin and Shriver 2010, Tobias et al. 2010, Francis et al. 2011). From residual plots from preliminary analyses, we identified spurious frequency values for several tinamou species in Bertelli and Tubaro (2002) and for *Cygnus olor* in Hu and Cardoso (2009). We therefore measured new peak frequencies from Xeno-Canto ([www.xeno-canto.org](http://www.xeno-canto.org)) recordings using seewave in R (Sueur et al. 2008) for the 35 species in question (see Appendix S1: Supplemental Methods for details). For the few source studies that did not present species body mass, we obtained body mass from Dunning (2008) using male mass if both male and female values were presented.

To characterize ecological selection and the influence of habitat structure on signal frequency, we compiled habitat affiliations from the Handbook of Birds of the World (Del Hoyo et al. 2013), categorized as either forested or

non-forested environments. We extracted minimum and maximum latitude of each species' breeding range (migratory species) or resident range (nonmigratory species) using data from (Bird Life International, 2018). From these latitudinal range limits, we used the absolute value of the smaller value as a proxy for the agents of ecological and sexual selection that vary along latitudinal gradients. This measure is a conservative proxy for these forces relative to the part of the range that is farthest from the equator, which might reflect the most environmentally extreme part of the range. It also never results in uninhabited point between two discontinuous ranges, which can be the case with the midpoint between the minimum and maximum latitudes of the range.

Recent studies have championed the use of spectrophotometry in studies of dichromatism (Armenta et al. 2008, Burns and Shultz 2012, Seddon et al. 2013), yet for a study of this scale, these methods were infeasible. Instead, and because human vision is a valid proxy for avian perception of non-UV sexual dichromatism (Armenta et al. 2008, Seddon et al. 2010), for all 795 species we used an index of dichromatism modified from Owens and Bennett (1994) and Dunn et al. (2001) using illustrations from Handbook of Birds of the World (Del Hoyo et al. 2013; see Appendix S1: Supplemental Methods for details). Although our index could underestimate dichromatism for species with UV-reflective plumage (Burns and Shultz 2012), recent research suggests that the resulting data structure from methods relying on human vision versus reflectance spectra is quite similar (Bergeron and Fuller 2018). Indeed, our index of dichromatism was strongly correlated with spectrally derived color discriminability for 295 species in common with the Armenta et al. (2008) dataset (Spearman's  $\rho = 0.781$ ,  $P < 0.001$ ), suggesting that our approach captured much of the variation in color. For a subset of species, we also collected information on song repertoire size from Read and Weary (1992) and Medina and Francis (2012). To calculate an index of multimodal sexual selection, we converted song-repertoire values to 11 quantiles (equivalent to dichromatism scores ranging from 0 to 10) and averaged these quantiles with dichromatism scores for each species with repertoire data

(mean: 3.93, SD: 2.25, range: 0.5–10). Lastly, we collected data on proportion of nests in a population with extra-pair young from Botero and Rubenstein (2012) and Liker et al. (2014). To improve normality, we applied transformations to two of our predictor variables: proportion of extra-pair paternity (arcsine square root) and song repertoire size (natural log). In order to directly compare models including continuous and categorical variables, we standardized all continuous variables by centering them around zero and scaling to 0.5 standard deviations (Grueber et al. 2011). Our sample sizes were as follows: habitat type = 795, extra-pair proportion = 95, song repertoire size = 101, dichromatism = 795, multimodal sexual selection index = 101, and breeding latitude = 789.

### Testing the metabolic theory of ecology

Metabolic theory of ecology predicts that vocal frequency (cycles/s) should have the same dependence on temperature and body size as mass-specific metabolic rate (Gillooly and Ophir 2010), which is as follows:

$$f = \frac{f_0 B}{M} = f_0 b_0 M^{-1/4} e^{-E/kT}, \quad (1)$$

where  $f_0$  represents the metabolic energy flux through a gram of tissue in cycles per joule ( $\text{cycle} \cdot \text{J}^{-1} \text{g}$ ),  $B$  is the whole-organism metabolic rate and  $M$  is body mass,  $b_0$  is the taxon-specific normalization constant and  $M^{-1/4}$  reflects the negative power scaling of *mass-specific metabolic rates* with body mass for taxa that show 3/4 power scaling of *whole-organism metabolic rate* with mass. Finally, frequency also has an exponential temperature dependence that is described by the Boltzmann-Arrhenius factor ( $e^{-E/kT}$ ). This reflects the exponential increase in biochemical reactions with temperature, where  $E$  is the energy required to activate the respiratory complex,  $k$  is Boltzmann's constant and  $T$  is absolute temperature. Because the range of body temperatures among endotherms only spans a few degrees (Clarke et al. 2010), body temperature variation is often ignored or treated as a class-wide constant in tests of MTE (Gillooly and Ophir 2010, Isaac and Carbone 2010). We also treated temperature as a constant in our analysis because body temperature has little variability in birds relative to mammals (Clarke



and Rothery 2008), which drops the Boltzmann-Arrhenius factor from the equation.

For our first (class-level) analysis, we determined whether MTE predicts the relationship between body mass and vocal frequency following best practices that account for phylogenetic non-independence (White et al. 2012). Specifically, we used phylogenetic generalized least squares (PGLS) to model the natural logarithm of vocal frequency as a linear function of the natural logarithm of body mass. Models were run in R v3.1.3 using “*phylolm*” from the package *phylolm* (Tung Ho and Ané 2014) and accounted for phylogenetic structure by estimating Pagel’s  $\lambda$  (Revell 2010).  $\lambda$  values equal to zero suggest the relationship between predictor and response variables is unrelated to evolutionary history and values at or approaching one indicate a strong correlation in the relationship between predictor and response variables for closely related species (i.e., high phylogenetic signal;  $\lambda = 1$  is a Brownian Motion Model). For our phylogenetic hypothesis, we used phylogenies developed by Jetz et al. (2012); however, due to some phylogenetic uncertainty in this set, we used 1000 randomly chosen phylogenies and ran each PGLS model 1000 times, averaging the resulting parameter estimates. We determined that the data failed to reject MTE predictions for the log–log mass–frequency relationship if the averaged 95% confidence intervals (95% CIs) overlapped the expected  $-0.25$  slope. We then replicated this procedure for 20 families with  $\geq 15$  species to evaluate how the mass–frequency relationship varies across different clades and to potentially identify distinct evolutionary lineages that deviate substantially from MTE expectations. That is, we wished to distinguish families with slope 95% CIs that excluded  $-0.25$  or intercept 95% CIs that excluded the overall intercept estimated from the entire dataset by fixing the slope at  $-0.25$ .

#### *Using metabolic scaling to test for selection*

We next used PGLS to test the influence of six selection metrics on vocal frequency in two ways: (1) a standard multiple regression approach, using mass as a covariate with each predictor and the natural log of frequency as the response, and (2) models testing each predictor’s effect on the deviation of the observed natural log of

frequency (Hz) from MTE-expected natural log values. We measured deviation from MTE as the absolute value of the difference between observed and expected natural log peak frequency (henceforth, frequency deviation), which is distinct from the residuals from the standard multiple regression approach. The first set of models ( $Y = \text{Natural Log Frequency}$ ,  $X = \text{Predictor} + \text{Natural Log Mass}$ ) are easier to compare to previous work and provide information about the potential direction of selection, while the second provides a novel test of how selective factors may drive vocal frequencies toward or away from those expected from MTE, regardless of whether selection favors high or low values. To calculate expected natural log frequency values from MTE, we first estimated the intercept from the data using the *nls* (nonlinear least squares) function in R by fixing the slope at  $-0.25$  and the natural log of mass as the predictor variable. We used this line to solve for MTE-expected natural log frequencies. We then calculated the frequency deviation for each species through the logarithmic subtraction of the expected natural log of frequency from the observed natural log of frequency, then taking the absolute value. As an example of how we might interpret these values, if latitude *positively* associated with frequency deviation, this could indicate that increased natural and sexual selection at high latitudes drive vocal frequency away from MTE expectations. Alternatively, if latitude *negatively* associated with frequency deviation, this could indicate that increased selection (on other phenotypes) at higher latitudes imposes greater metabolic constraints on frequency, causing them to be closer to MTE expectations.

Due to differences in sample sizes among our predictors, we evaluated the influence of each variable individually. As above, we iterated each PGLS model over 1000 randomly chosen phylogenies and averaged the resulting parameter estimates. In our models, peak frequency was natural log transformed and we further transformed frequency deviation by subtracting the minimum value and taking the square root to meet model assumptions of normality. We validated each model by confirming normality of residual histograms and qq plots for models using several randomly selected phylogenies. We concluded that there was little evidence for the

effect of a predictor variable on frequency deviation when the 95% CIs overlapped zero.

The approach detailed above represents a robust method for evaluating the influence of continuous variables on vocal frequency and its deviation from MTE expectations. For categorical variables with two levels, however, it can only provide inference as to whether the influence of one is stronger than the other. An alternative approach is to compare observed values in each signaling environment category to those expected from MTE using habitat type and observed versus expected values and an interaction between them as predictor variables in models. To do so, we used Bayesian generalized linear mixed-effect models in the R package MCMCglmm (Hadfield 2010) because the method allows multiple observations per tip in the phylogeny and the random effect of species to account for two records per species. We used uninformative priors for the variance component of the random effect (i.e.,  $V = 1$ ,  $\nu = 0.02$ ) to correspond to an inverse-Gamma distribution (Francis et al. 2018) and default priors for fixed effects. Estimates were based on 22,000 MCMC iterations with a thin rate of 20 following a burn-in of 2000. As with previous analyses, we ran models over 1000 phylogenies and interpreted a factor as having a strong effect if averaged 95% credible intervals (CrI) did not overlap zero. We estimated  $\lambda$  as the posterior mode from each model, which was also averaged across all iterations. We inspected trace and density plots of several model iterations to verify adequate mixing of the MCMC chain and to make sure that the autocorrelation of stored iterations was low (i.e.,  $<0.1$ ). Data supporting this paper are archived in FigShare (figshare.com; <https://doi.org/10.6084/m9.figshare.14977638>).

## RESULTS

### *Scaling relationship between body mass and frequency*

Our first analysis, including 795 bird species, suggests that the natural logarithm of frequency is a linear function of the natural logarithm of body mass, with a fitted slope ( $-0.215$ , 95% CI:  $-0.256$  to  $-0.174$  across 1000 trees) that is close to MTE's expected slope of  $-0.25$  (Fig. 2a). There was also a strong phylogenetic signal in the relationship between body mass and frequency

(mean  $\lambda = 0.868$ ). However, analysis across Aves provides neither insight on how the relationship between frequency and body mass differs across particular clades (shown in Fig. 2b), nor how  $\lambda$  varies within different clades.

Phylogenetically informed sub-analyses of 20 avian families revealed some heterogeneity in the relationship between body mass and frequency and the degree to which this relationship is phylogenetically structured (Fig. 3). Seventeen of 20 families had slope 95% CIs overlapping the slope expected from MTE. All three families that did not overlap MTE-expected slope (Emberizidae, Fringillidae, and Sylviidae) were passerines, with the first two having shallower slopes than  $-0.25$  (i.e., less decline in frequency with increased body mass), and the latter (Sylviidae), having a steeper slope.

Two of the three families with intercepts that differed from the whole-dataset estimate (Strigidae and Columbidae) were non-passerine families. Frequencies for these families were much lower. The only passerine family with a divergent intercept was Sylviidae. This family was the only one to show a significantly higher intercept and also the only family with both a divergent slope and intercept.  $\lambda$  estimates also varied considerably among families, suggesting high variation in the phylogenetic covariance between frequency and body mass across clades.

### *Influence of selection on vocal frequency and its deviation from MTE*

Consistent with the idea that strong sexual selection should favor lower frequencies, song repertoire size, dichromatism, and multimodal sexual selection index were negatively related to the natural log of frequency, after controlling for the natural log of mass in PGLS models (Fig. 4a:  $\beta_{\text{RepSize}} = -0.123$ , 95% CIs  $-0.237$ ,  $-0.009$ ,  $\lambda = 0.643$ ;  $\beta_{\text{Dichro}} = -0.098$ , 95% CIs  $-0.162$ ,  $-0.034$ ,  $\lambda = 0.864$ ;  $\beta_{\text{MMSSIndex}} = -0.143$ , 95% CIs  $-0.258$ ,  $-0.028$ ,  $\lambda = 0.620$ ). Mass effects were highly significant in all models (Appendix S1: Table S2).

The only strong predictors of frequency deviation from MTE expectations were repertoire size ( $\beta_{\text{RepSize}} = -0.142$ , 95% CIs  $-0.223$ ,  $-0.061$ ,  $\lambda = 0.286$ ; Fig. 4b) and our index of multimodal sexual selection ( $\beta_{\text{MMSSIndex}} = -0.094$ , 95% CIs  $-0.179$ ,  $-0.0101$ ,  $\lambda = 0.379$ ), indicating that species with the largest repertoires and more

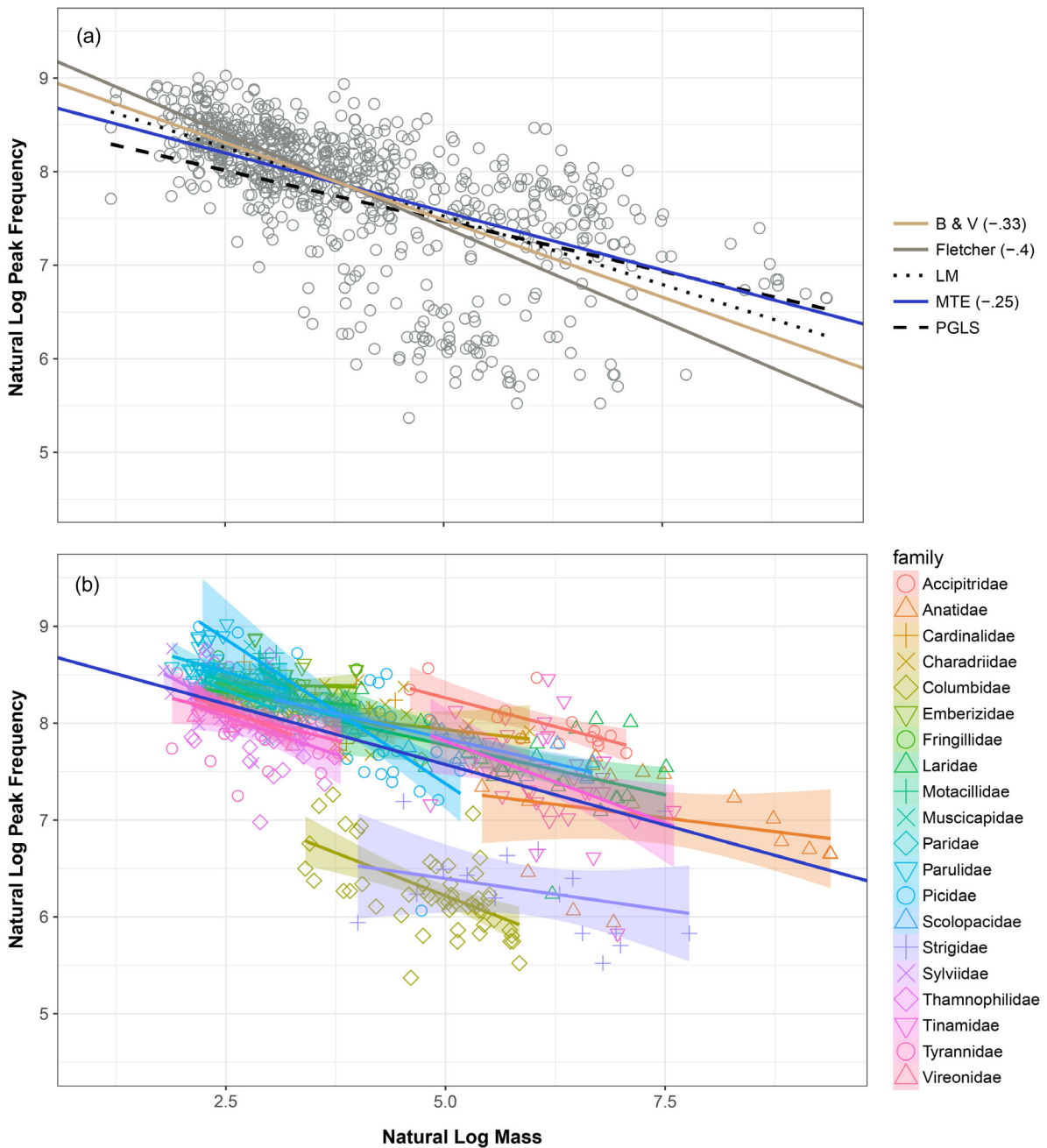


Fig. 2. Relationship between natural log peak frequency and natural log mass. Panel (a) includes 795 species, from 74 families. Solid lines represent theoretical expectations—tan = expectations from Bradbury and Vehrencamp (2011) ( $y = -0.33 + 9.09$ ); dark gray = expectations from Fletcher (2004) ( $y = -0.4 + 9.36$ ); and blue = MTE predictions ( $y = -0.25x + 8.82$ ). Dashed lines are best-fit models using simple linear regression (LM, dotted line,  $y = -0.29x + 8.99$ ) and phylogenetic least squares regression (PGLS, dashed line,  $y = -0.215x + 8.55$ ). Panel (b) shows the same relationship across 20 bird families for which at least 15 species were measured. The dark solid line again represents MTE-expected values. Each point represents estimates for one species, with different shape/color combinations indicating family. Linear regressions and 95% confidence intervals are shown for each family.

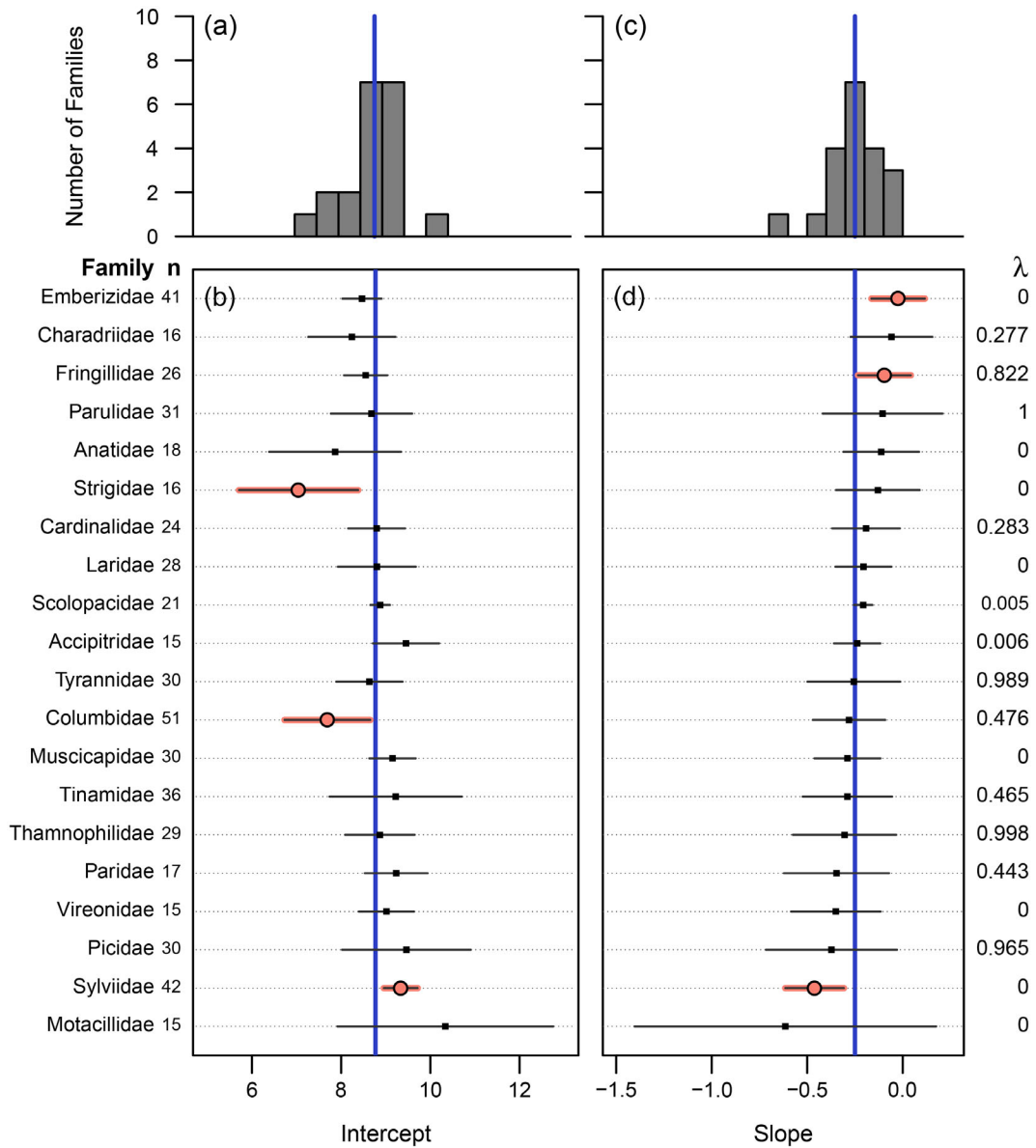


Fig. 3. Family level intercept and slope estimates. The distribution of phylogenetically informed log mass—log frequency (a) intercept and (c) slope estimates across bird families with a minimum 15 sampled species, calculated over 1000 trees. The dark blue lines represent the following: (a, b) the intercept estimated from the entire dataset when the slope was fixed at the MTE expectation of  $-0.25$ ; and (c, d) the expected slope ( $-0.25$ ), based on MTE-scaling. The (b) intercept and (d) slope estimates and confidence intervals are shown for the log mass—log frequency relationship across bird families. Families with confidence intervals that do not overlap the expected intercept or slope are highlighted in red. Thus, while the full dataset strongly conforms to MTE predictions, there is considerable variation from this within some families, indicating potentially interesting differences in physiology or selective pressures within these taxa.

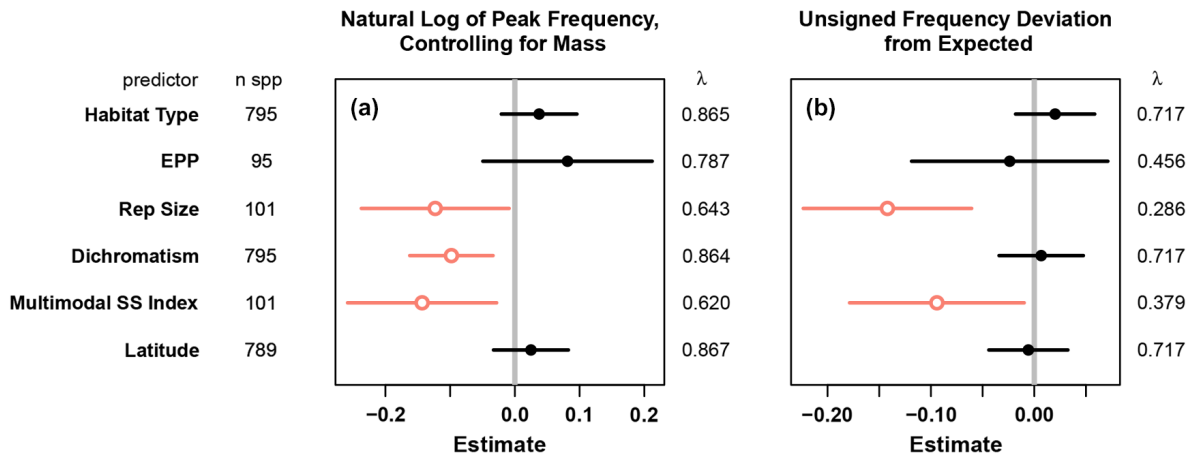


Fig. 4. Average PGLS estimates and 95% confidence intervals for the effects of six measures of selection on species-level (a) natural log of frequency, after accounting for body mass, and (b) unsigned frequency deviation (natural log scale) from MTE. Red, open circles do not overlap zero, while black, closed circles do overlap zero. The column labeled “n spp” indicates the number of species sampled. Average values for Pagel’s lambda for each analysis indicate estimates of phylogenetic signal. All continuous predictor variables were scaled to 0.5 standard deviations and centered around zero, allowing for estimate comparisons across continuous and categorical predictors.

dichromatic plumage tended to have vocal frequencies closer to the metabolic optimum (Fig. 5). However, because three families (Strigidae, Columbidae, and Sylviidae) had intercept estimates that differed substantially from the dataset as a whole (Fig. 3), we also performed our selection analysis without these families. Subanalysis results were effectively the same, except that dichromatism showed a significantly positive effect on frequency deviation, while the negative effect of multimodal sexual selection index was no longer apparent (Appendix S1: Fig. S2). Signaling environment (i.e., habitat type) failed to influence natural log of frequency or frequency deviation for both the full dataset and the subanalysis excluding families with divergent intercepts (Fig. 4; Appendix S1: Fig. S2), suggesting that ecological selection on vocal frequency is not stronger in forest versus non-forest environments. Latitude and EPP were unrelated to natural log of frequency or frequency deviation for either dataset.

In the analysis of expected versus observed values across signaling environments using all 795 species, phylogenetically informed models suggest that MTE-expected natural log frequencies were lower in non-forest environments than

forest environments ( $\beta_{\text{Non-forest}} = -0.085$ , 95% CrIs  $-0.146, -0.025$ ), reflecting the larger body sizes of our sample of non-forest bird species. Observed natural log frequencies in forests were lower than MTE-expected values ( $\beta_{\text{ObsForest}} = -0.084$ , 95% CrIs  $-0.130, -0.038$ ), while observed frequencies for non-forest birds were higher than MTE expectations ( $\beta_{\text{Obs}\times\text{Non-forest}} = 0.170$ , 95% CrIs  $0.105, 0.235$ ; whole model  $\lambda = 0.519$ ; Fig. 6). Results from sub-analyses excluding families with divergent intercepts were qualitatively similar except that observed and MTE-expected natural log frequencies were indistinguishable in forests (Appendix S1: Table S3).

## DISCUSSION

This study is the first to use metabolic scaling theory to test hypotheses regarding the strength and direction of selection. Although the large amount of residual variation around metabolic scaling relationships has been a source of criticism (Horn 2004, DeLong et al. 2014), we have shown that this presents an opportunity to explore the effect of different selective factors on trait values, using avian vocal frequency as an

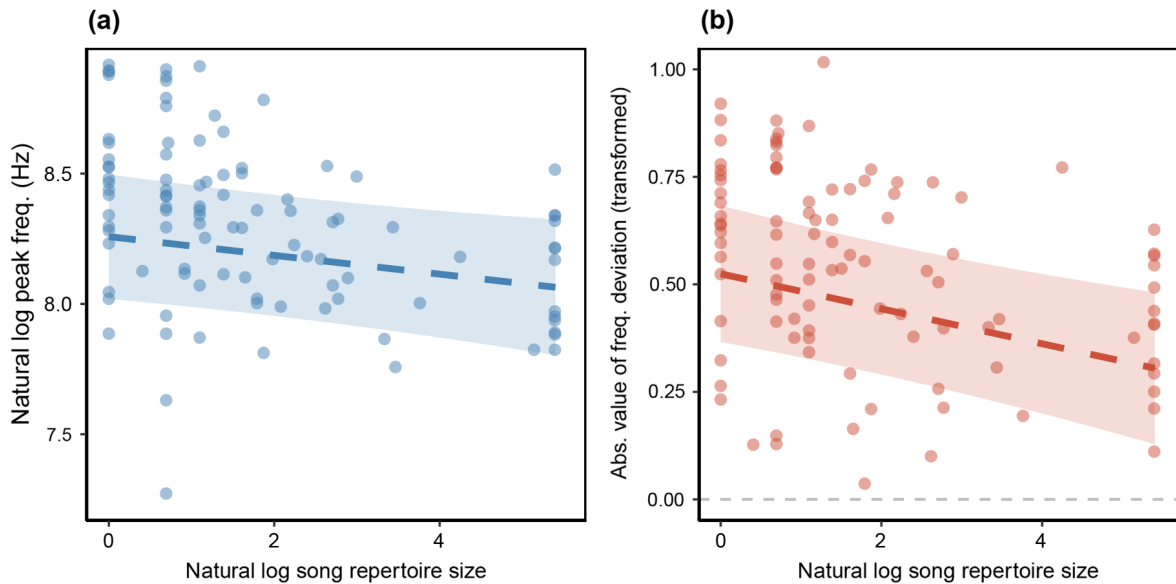


Fig. 5. (a) The natural log of peak frequency (Hz), after accounting for body mass, and (b) the absolute value of deviation of natural log of frequency from MTE expectations were both negatively related to the natural log of centered and scaled song repertoire size. Together, these findings suggest that species with smaller repertoires sing at higher peak frequency than expected. In panel (b), responses were transformed by subtracting the minimum value and taking the square root.

example. Overall, we found strong support for convergence on a log–log body mass–vocal frequency slope near  $-0.25$  across 795 bird species, ranging from 3 to 11,000 g. Our empirical slope estimate ( $-0.215$ ) is very close to the value ( $-0.21$ ) estimated in an analysis of signaling organisms spanning  $10^{-3}$  to  $10^8$  g (Gillooly and Ophir 2010), the coarse scale where MTE usually performs well (Sibly et al. 2012a, b). Although the 95% CI ( $-0.256$ ,  $-0.174$ ) did not exclude the power–law scaling exponent predicted by MTE (and DEB), it did exclude a slope of  $-0.33$ , the long-standing hypothesized scaling relationship between the natural logarithms of body mass and vocal frequency that is based on linear scaling (Bradbury and Vehrencamp 2011) or a proposed scaling exponent of  $-0.40$  that is based on linear scaling and additional morphological constraints (Fletcher 2004). Despite a slope near  $-0.25$  across most families, our sub-analyses revealed variation in the relationship between body mass and vocal frequency and identified highly divergent clades from expected values and patterns typical of other families.

Owls and doves had vocal frequencies that were well below those of most groups. Cardoso (2012) noted that among studies that have examined the relevance of sexual signals, most non-passerines appear to use low frequency signals as a signal of body size. Proximate explanations for the aberrant values in these groups include vocalizing with closed beaks and nares among doves (Riede et al. 2004), which may allow for the production of lower frequencies by the syrinx. In owls, despite males typically being smaller in body size than females, they have larger syringes (Johnsgard 1988), which is consistent with the notion that sexual selection favors low frequency vocalizations. These groups, as well as Sylviidae (which was the only family to diverge from expectations in intercept and slope), should be subjects of future research seeking to understand selection on vocal signals, including whether family or order-specific scaling expectations would more effectively reveal the influence of counteracting selective agents.

By using variation around scaling exponents predicted by MTE, we find vocal frequency and its deviation from MTE expectations are related

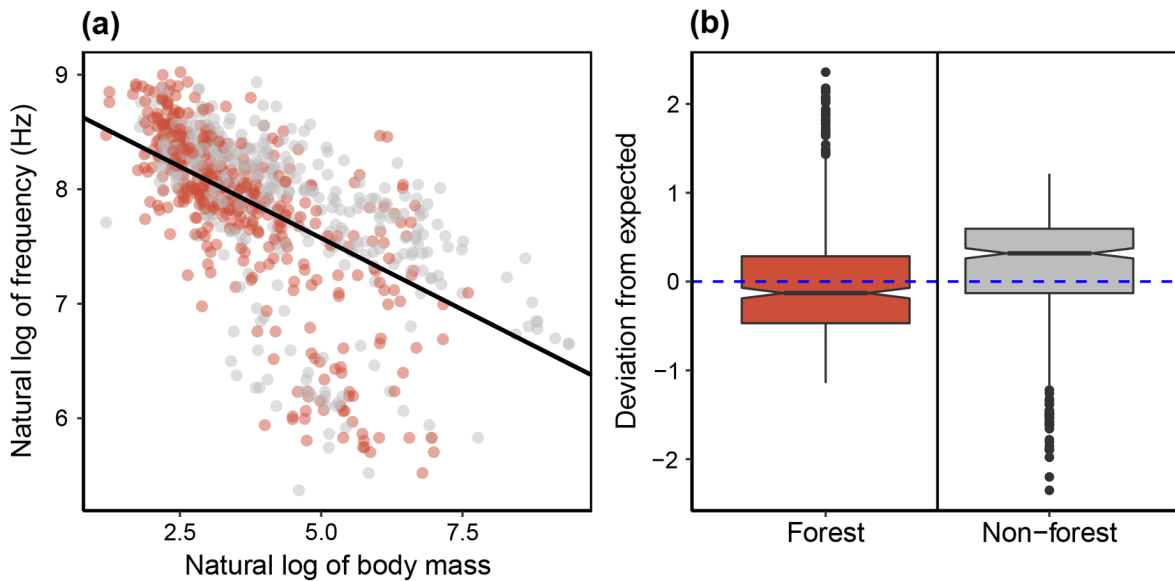


Fig. 6. (a) Plot of natural log peak frequency and natural log mass, where red points reflect forest birds and gray reflect non-forest birds. Black line denotes MTE expectations using the theoretically derived slope and the empirically derived intercept ( $y = -0.25x + 8.82$ ). (b) Observed frequencies were lower than expected in forested environments (left) and higher than expected in non-forest environments (right). Whisker plots show the natural log of vocal frequency plotted as the deviation from MTE-expected mean values. As the mean expected value was necessarily calculated for each habitat independently (each containing a separate sample of species with different body sizes), these boxplots should only be compared with the zero-deviation (blue-dashed) line, not to each other.

to several indices of sexual selection. However, the direction of relationships was not always consistent with theory. For example, our phylogenetically informed results comparing vocal frequencies to those expected by MTE generally support conclusions from previous studies suggesting that animals in densely vegetated environments have low frequency signals (reviewed in Boncoraglio and Saino 2007, Ey and Fischer 2009). Our results from the full dataset suggest that birds in forested environments vocalize at frequencies lower than expected by MTE, but the subanalysis excluding families with different intercepts reveal no such difference between expected and observed natural log of vocal frequency. However, analyses based on the full dataset and the subset excluding families with divergent intercepts also suggest that birds in non-forested environments signal at natural log frequencies higher than expected based on MTE. This finding provides a potentially different perspective from the long-held assumption in

acoustic adaptation hypothesis studies that ecological selection from dense vegetation is responsible for differences in frequency between animals in forested and non-forested environments by suggesting that selection may also shape frequency in open habitats.

**Ecological and sexual selection on vocal frequency**

Evidence for acoustic adaptation across animals is mixed, with many studies demonstrating lower mass-corrected vocal frequencies for species inhabiting dense vegetation compared with more open environments (Ryan and Brenowitz 1985, Boncoraglio and Saino 2007, Derryberry 2009, Ey and Fischer 2009, Kirschel et al. 2009, Tobias et al. 2010), and others showing limited evidence of habitat effects on acoustic signals (Daniel and Blumstein 1998, Jain and Balakrishnan 2011, Mason and Burns 2015, Tietze et al. 2015, Graham et al. 2016, Mikula et al. 2020). Implicit to most acoustic adaptation studies is the idea that a dense signaling environment

favors lower frequency signals; however, selection on vocal traits is often assumed to be relaxed in open environments (Ryan et al. 1990, Weir et al. 2012) or potential selective agents in non-forested areas are left unidentified.

Here, however, we provide evidence that the natural log of vocal frequency in non-forest environments is higher than expected by MTE and that it also tends to be lower than expected in forested environments. That there does appear to be separation between expected and observed values in forest and non-forest environments, and in opposite directions, supports the notion that vocal frequency, after accounting for mass, differs for birds in these two habitat categories. However, given the sensitivity of this analysis to the estimated MTE intercept from the sample (see Box 1), some caution in the interpretation is warranted. Nevertheless, assuming the empirically derived intercept for calculating expected values is not biased downward, selection appears to favor higher frequency signals in non-forested environments. Selective agents in open environments that could favor higher frequency signals include low frequency noise from moving water and wind (Brumm and Slabbekoorn 2005) or the ability of predators and natural enemies to localize lower frequency acoustic cues, and integrate them with visual cues in less-cluttered open areas. Higher frequencies in open habitat could also result from selection for broader frequency ranges, which may show increased signal propagation (but higher degradation) over long distances (Rek and Kwiatkowska 2016). Although we cannot identify the full suite of selective agents for acoustic adaptation in this study, the finding that greater natural log frequency deviation from MTE expectations occurs in open rather than closed environments should motivate research toward a more comprehensive understanding of habitat effects on acoustic signal properties, including re-examining assumptions about directionality of selection.

Many studies of acoustic signal evolution through sexual selection have emphasized the importance of directional female mate choice for lower frequency signals (Searcy and Andersson 1986, Ryan and Keddy-Hector 1992, Boul et al. 2007). However, some evidence suggests many bird species also prefer high frequency signals over low ones (Cardoso 2012) and that females

often prefer signals performed at the limits of an individual's physiological abilities (Byers et al. 2010), which could be low or high frequency. Thus, the direction that "should" be favored by sexual selection is unclear. Our results provide mixed support for the hypothesis that strongly sexually selected species should have signal frequencies that deviate further from MTE expectations. For dichromatism—our most robust proxy for sexual selection, measured for all species in the dataset—from our more traditional analysis of the natural log of frequency while controlling for the natural log of mass, more dichromatic species produced significantly lower vocal frequencies compared with monochromatic species (Fig. 4). This suggests that low frequency signals may be favored among highly dichromatic species, independent of mass. However, dichromatism was unrelated to deviation from MTE expectations, as the lower frequencies of more dichromatic species did not translate to consistently increasing distances from the predicted line (Appendix S1: Fig. S1a). Potential reasons for the discrepancy between the two analyses are not obvious. The discrepancy may involve species-specific differences in resource allocation to traits (see Box 2) or the relationship between dichromatism and frequency, after controlling for mass, is quite weak and could be spurious.

The influence of song repertoire and the multimodal index of sexual selection on deviation from MTE expectations were contrary to our predictions; increases in song repertoire size and the multimodal sexual selection index were associated with smaller deviations from MTE expectations. This finding raises important questions about energetic trade-offs that govern the elaboration of signals across different dimensions and may relate to differences in resource allocation across different trait axes (Fig. 7, Box 2). Curiously, for our subanalysis removing the three families with divergent intercepts, dichromatism showed a positive association with frequency deviation. Thus, our inability to detect an effect of increased dichromatism on frequency deviation from MTE expectations for the full dataset likely results from taxonomic heterogeneity—perhaps owing to differences in the physiological basis (and associated costs) of plumage color (Badyaev et al. 2002) or whether dichromatism is driven by increased elaboration in males versus



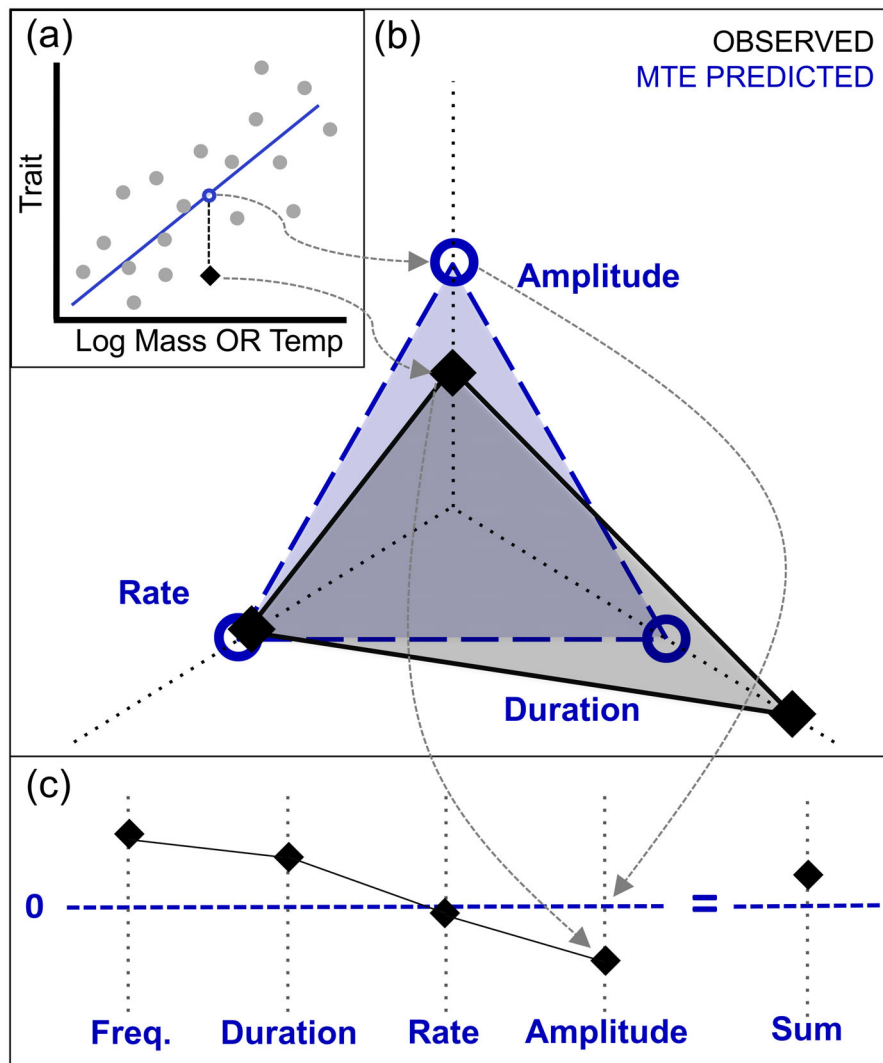


Fig. 7. Frameworks for evaluating trade-offs by comparing observed trait values to those expected based on MTE predictions for a given species. (a) Observed (black diamond) and expected values (open blue circle) can be standardized by conversion to a common scale and centered relative to scaling expectations to facilitate the visualization and analysis of trade-offs through (b) radar and (c) parallel coordinate plots. Radar plots (b) can be used to visualize the degree to which observed traits deviate from predicted values and, by comparing the area of polygons defined by vectors connecting expected or observed values. Frequency is not shown to highlight other axes of signal variation. Parallel coordinate plots (c) can also be useful to display deviation from expected values, especially when negative or positive changes in trait values from MTE expectations could represent increased metabolic costs. The sum of the deviations can provide information on how well MTE predicts composite traits or even the expression of traits in separate modalities, which can be compared across species or clades. Data in all panels are hypothetical.

crypsis in females within a particular taxon (Burns 1998, Badyaev and Hill 2003, Johnson et al. 2013, Wilkins et al. 2020). A potentially fruitful direction for future work would be to blend the

metabolic approach adopted here with techniques to identify correlated rate shifts in trait evolution, such as parallel increases in visual complexity and frequency deviation, or increases

**Box 2.****Using baseline expectations to evaluate trade-offs among traits**

The principle of allocation informs much of life history theory (Stearns 1989, Ricklefs and Wikelski 2002) and is also a key concept to metabolic scaling theory broadly and MTE in particular through the view that metabolic rate determines the rate of energy allocation to all processes within an organism (Sibly et al. 2012a, b). Examining trait expression through trade-off analyses that use a metabolic ecology lens could prove fruitful for understanding the expression of composite traits (i.e., complex traits comprising multiple components or phenotypic axes) or the expression of traits across different modalities. Using vocal signals as an example of the former, splitting finite resources across multiple dimensions could explain deviation from MTE (or other power-law scaling expectations) in the expression of one axis of a composite trait (e.g., frequency) and little deviation in other(s) (e.g., call rate). Trade-off analyses could be facilitated by the use of radar (spider) or parallel coordinate plots (Fig. 7), which allow one to compare observed multidimensional values to those predicted by MTE. In both approaches, both observed and expected values (Fig. 7a) would need to be transformed to a common scale, such as energy (joules), or expressed in terms of relative increases or decreases from metabolic scaling expectations. Radar plots have the advantage that, when all axes are standardized to a common scale, the area defined by vectors linking predicted and observed values on each axis can be directly compared (Fig. 7b). Consistently larger areas for observed values relative to expected could suggest metabolic expansion or, if metabolism is unchanged, that trait expression has largely diverged from MTE expectation due to counteracting selection. Smaller areas than expected could suggest that selection favors the expression of other traits at the expense of expression of the traits under consideration. Note, however, that the area for radar plots with greater than three axes will change depending on axis arrangement; thus, averaging areas from all possible arrangements would be necessary. In contrast, parallel coordinate plots may be advantageous when positive or negative deviations in one or more traits, such as vocal frequency, could be viewed as increasing metabolic costs (e.g., signaling at the margin of upper or lower physiological limits; Fig. 7c). Plotting transformed and scaled observed values relative to MTE expectations can provide information about possible trade-offs among traits and, by summing the deviations, insights as to whether composite trait expression deviates from MTE expectations. Trade-off analyses using these and other methods could provide key information on why ecological or sexual selection appears to strongly influence some trait axes, but not others and the field could benefit from development of these quantitative approaches.

in song elaboration or other measures of complexity with declines in frequency deviation.

Surprisingly, rates of EPP did not appear to significantly influence the natural log of frequency, while controlling for the natural log of mass, or frequency deviation. It is possible this is due to greater variability in rates of EPP among populations and over time (Bonier et al. 2014, Liu et al. 2015), compared with other measures of sexual selection. This possibility merits further investigation, as broad-scale studies such as this rely on appropriate measures of selection, and it would be useful to know more about the relative within versus among species variation in surrogate selection metrics. Latitude, our measure of the combined effects of ecological and sexual selection, had no influence on the natural log of frequency, while controlling for the natural log of mass, or frequency deviation from MTE expectations. The absence of an observed relationship may stem from a paucity of tropical species

(average latitude:  $22.26 \pm 14.46$  SD). Still, this result contrasts with previous work showing increasing vocal frequency with latitude (Weir et al. 2012, Tietze et al. 2015), suggesting additional research may be necessary to determine whether this relationship exists.

***Metabolic scaling theories and trade-offs***

Most phenotypes—and acoustic signals are no exception—are composite traits, comprising multiple distinct components. MTE predicts not only that frequency will scale with metabolic rate, but also that other acoustic attributes will as well, including signal duration, rate, and power (Gilluly and Ophir 2010, Ziegler et al. 2016). Additional components of acoustic signals may also be energetically costly, such as the complexity of vocalizations (Byers et al. 2010). Based on the principle of allocation, because vocal frequency deviates in a predictable manner with respect to signaling environment and indicators of sexual

selection, frequency changes may come with costs whereby the allocation of energy to one phenotypic axis reduces energy available to another (Fig. 7, Box 2). Such an allocation trade-off may explain the negative relationship between the frequency deviation from MTE expectations and song repertoire size, one measure of song complexity (Medina and Francis 2012). That is, the energetic costs associated with growing and maintaining neural tissue to learn large song repertoires (Nowicki et al. 1998, Laughlin 2001, Gil and Gahr 2002) and producing a variety of notes at different frequencies, rates, and modulations may leave little energy available for an individual to sing at a peak frequency different from that expected from scaling theory. Similarly, allocation of energy to pitch signals at frequencies better suited to environmental signaling conditions or in response to intra- and intersexual selection pressures could come with predictable trade-offs among other signal features. Trade-offs between energetically costly traits are well documented—a prime example for acoustic signals is the vocal performance trade-off between frequency bandwidth and trill rate (Podos 1997, Wilson et al. 2014). Depending on resource distributions (Shutler 2011), trade-offs may also occur across modalities, such as negative covariance between song complexity and carotenoid plumage ornamentation (Badyaev et al. 2002). As with cross-habitat comparisons of relative differences in signal features, many trade-off analyses suffer from no clear expectation for a trait value in the absence of selection, leaving the magnitude and direction of phenotypic changes ambiguous. By providing baseline expectations, a metabolic scaling framework represents an especially useful tool to examine trade-offs and has the promise to not only reveal which phenotypic traits have diverged strongly from expectations, but also help understand these patterns. Importantly, because expectations are generated based on a finite common currency (energy), this approach can be applied to trade-offs across modalities (e.g., vocal versus visual signaling rate) and may help explain wide variation in these relationships across taxa. This approach could easily be modified by incorporating statistical expectations for trait values generated from metabolic scaling theory with different power-law scaling exponents

than those used by MTE. A potentially fruitful application could explore whether predictions from different metabolic scaling theories provide contrasting interpretations of selection and adapt our approach to empirically test the alternatives.

## CONCLUSIONS

All patterns of animal behavior exist within a range of possibilities defined by physiology and ecology. Since these scale with size, the range of behavior must also do so... a knowledge of allometry might allow animal behaviorists a greater definition of the probable behavior a study animal might exhibit Robert H. Peters (1986)

Despite the intuitive appeal of Peters' observation, over 30 yr on we are only beginning to understand how physiological and ecological constraints affect the evolution of behavior, and more broadly, many other traits linked to metabolism. Although we have made considerable progress in applying MTE and other metabolic scaling theories to various ecological phenomena (Glazier 2005, Sibly et al. 2012a, b), evolutionary applications have lagged behind. We believe there is great promise in using scaling exponents based on metabolic theories and other allometries to define *probable* trait values, as this approach offers a meaningful null expectation for single-population studies, a common metric for comparative studies, and a vehicle for greater synthesis across taxa. Additionally, deviation from expectations generated from metabolic scaling theories provides a novel means for assessing the relative importance of different selective pressures and should direct researchers to understand how this deviation varies at different taxonomic levels (i.e., over short and long evolutionary timescales). We hope our approach and worked example will stimulate future studies of trait divergence that leverage the utility of metabolic scaling theories to gain new insights into selective processes.

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