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Woodpecker drum evolution: An analysis of covariation in elements of a multicomponent acoustic display among and within species

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Multicomponent signals are found throughout the animal kingdom, but how these elaborate displays evolve and diversify is still unclear. Here, we explore the evolution of the woodpecker drum display. Two components of this territorial sexually selected signal, drum speed and drum length, are used by territory holders to assess the threat level of an intruding drummer. We explore the coevolution of these display components both among and within species. Among species, we find evidence for strong coevolution of drum speed and length. Within species, we find that drum speed and length vary largely independent of each other. However, in some species, there is evidence of covariation in certain portions of the drum length distribution. The observed differences in component covariation at the macro- and microevolutionary scales highlight the importance of studying signal structure both among and within species. In all cases of covariation at both evolutionary scales, the relationship between drum speed and length is positive, indicating mutual elaboration of display components and not a performance trade-off.

KEY WORDS: Animal behavior, display design, multicomponent signal, sexual selection, trade-offs, woodpeckers.

Animal displays are used to mediate communication in a wide range of contexts including predator avoidance (Brown et al. 1999; Manser et al. 2002; Kim and Velando 2015; Wheeler et al. 2019), social cooperation (McConnell and Baylis 1985; Martin et al. 2017; Trapote et al. 2021), territory defense (Schuppe and Fuxjager 2018; Avendaño and Cadena 2021; Diniz et al. 2021), and mate choice (Elias et al. 2012; Borshagovski et al. 2020; Pham et al. 2021). As a result, biologists have spent decades trying to figure out how display traits arise in a population and diversify among taxa (Rowe 1999; Herberstein et al. 2014; Merwin et al. 2020). However, addressing this objective can be incredibly challenging, especially when display behavior is highly complex (Melo and Marroig 2015; Wilkins et al. 2015). Take multicomponent signals as an example—they are defined as display behaviors that incorporate two or more signal elements in the same sensory modality (Hölldobler 1995; Johnstone 1995; Rowe 1999). Components often differ in their function, in that they convey different meanings to different receivers (Beletsky 1983; Westcott 1992; Loyau et al. 2005; Ronald et al. 2018), fill different roles in different contexts (Pedroso et al. 2013; Zambre and Thaker 2017), and/or operate at different spatial and temporal scales (Gibson 1996; Mateos and Carranza 1999). This implies that these different components may evolve in response to unique selection regimens (Zambre and Thaker 2017), even if they all contribute to the display's overall functional aesthetic value. Yet, what the process of multicomponent signal evolution looks like remains unclear.

One challenge in understanding multicomponent signal evolution is disentangling signatures of correlated evolution within the signal trait. Whether components coevolve with each other in this regard depends on the degree to which they are interconnected. If, for example, the different components of a display are connected by shared functions and/or physiological mechanisms, such as the color of plumage on different areas of the body (Wilkins et al. 2015), then the components will likely covary (Monteiro et al. 2005; Porto et al. 2009; Dalziell et al. 2013). As a result, these components should coevolve even if selection is acting on only one of them (Melo and Marroig 2015; Penna et al. 2017). In contrast, when different components do not have a shared function or structure, then they are less likely to coevolve, as is the case with syllable length and repertoire diversity in barn swallow song (Wilkins et al. 2015; Hebets et al. 2016). Here, we analyze correlated evolution of signal components (which we call coevolution) by assessing the covariation between components at multiple evolutionary scales.

If components within a given species' signal have coevolved, then we would expect to see signatures of component covariation throughout the entire species distribution. By contrast, if signal components have not coevolved within a species, we would expect to see no correlation between individual signal components. Past work shows both patterns can occur in displays, with some studies showing evidence of component covariation and others not (Cardoso and Hu 2011; Girard et al. 2015; Miles et al. 2018, 2020). This question of within-species covariation is made additionally complex because of the many unknown factors that may influence the relationship between two components. We know that the performance of display components can vary among individuals (Keagy et al. 2012; Wilgers and Hebets 2012; Girard et al. 2015), across populations (Miller et al. 1998; Roach and Phillmore 2017), or in different contexts (DuVal 2007; Thomas et al. 2011; Vanderbilt et al. 2015; Schaedler et al. 2021). Importantly, the structural and/or functional mechanisms underlying component covariation within a species may be similarly influenced by contextual, individual, and population-level factors.

Combining studies of within-species display component covariation with broader phylogenetic patterning is especially important because multiscale comparisons may provide insight into how microevolutionary (within species) processes shape among species differences in display phenotype. However, there are very few studies that have taken such an approach to understanding display diversification. It can be difficult to detect coevolutionary signals at the macroevolutionary scale because oftentimes signals vary so much between species that signal components cannot be directly compared, even among closely related taxa. Studies of birdsong trill rate and frequency bandwidth, for example, are often limited to comparing component performance within a single species (but see Wilson et al. [2014] for notable exceptions).

Here, we address gaps in the field by studying patterns of component covariation in woodpecker drum displays, assessing signal evolution both across and within species. Nearly all woodpecker species drum to compete over nesting territories by rapidly hammering their bill on a tree, generating a loud percussive signal (Short 1974; Winkler and Short 1978; Bent 1992). The drum is fundamentally atonal and varies among individuals and across species in a variety of temporal measurements. Because all species' drums can be described using temporally measured components, the woodpecker system is uniquely suited to comparative studies of signal evolution. We characterize drum displays in terms of their rate of beat production ("speed," as measured by beats s^{-1}), total number of beats ("length"), and cadence and acceleration (together "rhythm," or Δ speed s^{-1}) (Stark et al. 1998; Schuppe and Fuxjager 2018; Miles et al. 2020).

In this study, we focus on two of these components: drum speed and drum length. One reason speed and length are well suited for this study is that previous work has shown that elaborating either of these components (i.e., drumming faster or longer) results in a more potent aggressive signal (Schuppe et al. 2016; Schuppe and Fuxjager 2018). This functional similarity in a territorial context may suggest that speed and length are subject to similar selective pressures. In theory, speed and length components should also be structurally linked because they are generated through the same mechanical mechanisms (Hebets et al. 2016; Schuppe et al. 2021). If the functional and/or physiological linkages between speed and length are strong, we would expect to see evidence of component coevolution within and among species. This is possibly most pronounced when signals are produced at or near a performance limit, such as with highly elaborate displays in which the extreme exaggeration of one component can influence other aspects of the signal (Ronald et al. 2017; Mitoyen et al. 2019; Goller 2022). On the other hand, we know that different drum components are under different biomechanical constraints, and as a result sexual selection has greatly elaborated one component (length) more than the other (speed) (Miles et al. 2018). The presence of different constraints on each component may suggest that speed and length do not coevolve.

At the within-species level, little is known about patterns of covariation between drum speed and length. One possibility is that there is a trade-off between these components. This is a particularly compelling explanation because performance indices such as speed and endurance (which would determine length) are often negatively related to each other (Vanhooydonck et al. 2001, 2014; Wilson et al. 2002; Wilson and James 2004). Some studies even suggest this trade-off is especially pronounced when animals perform high-speed displays that incorporate repetitive muscle movements, such as the drum (Miles et al. 2018). Another possible outcome is positive covariance between drum speed and length, indicating a pattern of mutual elaboration of components (Hebets and Papaj 2005; Girard et al. 2015). Alternatively, there may be no significant relationship between drum speed and length (Sorci et al. 1995). This finding would be consistent with independent signal components, allowing for flexible component performance (Ay et al. 2007). Notably, we may see multiple patterns throughout a given species, and other factors, such as component elaboration, may influence the relationship(s) (or lack thereof) between drum speed and length.

We start this study by examining the relationship between drum speed and length across much of the woodpecker family. We then explore the relationship between these components within eight focal species. Some of these species are closely related (within the same genus), whereas others are more distantly related, and thus separated by millions of years of evolution. For all analyses, we investigated the relationship between drum components using quantile regression, a statistical technique that allows us to assess the predictive relationship of one variable (speed) on another (length) at various percentiles of the dependent variable's distribution (various drum lengths). Quantile regression is particularly useful for studies of complex biological or ecological relationships because it calculates multiple slopes within a dataset, describing the relationship between variables at different portions of the distribution (Cade and Noon 2003). This differs from a standard linear regression, which describes the relationship between variables using only one rate of change (slope) calculated about the data's median. Here, we use quantile regression to determine if drum speed predicts drum length at different degrees of drum length elaboration. In other words, our current study explores variation in signal component performance as a function of component (length) elaboration across the clade to reveal whether drum speed and drum length are coevolving among woodpeckers.

Methods

STRUCTURE OF THE WOODPECKER DRUM

In this study, we focused on the metrics drum speed and drum length (Stark et al. 1998; Miles et al. 2018, 2020). As in Miles et al. (2018, 2020), drum speed is defined as the number of beats produced per second, which we calculate by measuring the full duration (seconds) of the drum and dividing by the total number of beats. Drum length is defined as the total number of separate beats (individual beak strikes) in a drum.

COMPONENT COVARIATION AMONG SPECIES

To understand component covariation in drumming behavior, we used phylogenetic quantile regression to assess the predictive relationship of drum speed on drum length in 126 woodpecker species (out of ≈230 total species). We used previously established average values for species' drum speed, drum length, and mass (log-transformed). For more details on the database of species measurements used in this study, see Miles et al. (2018). We chose quantile regression over phylogenetic generalized least squares (PGLS) because complex animal displays often exhibit unequal variance, resulting in substantial slope variability throughout the dataset (Cade et al. 1999; Wilson et al. 2014). Such effects can cloud the relationship between two variables, which may exist in robust measure for some portions of a distribution but not others. Indeed, by representing component covariation with a single linear relationship (slope), as in PGLS analyses, one can provide an overall average relationship between signal components. However, this approach is less useful for our purposes because it does not account for the potential influence of drum length elaboration on the drum speed-length relationship.

All quantile regression analyses were performed using the "quantreg" package in R (Koenker 2021). To account for the phylogenetic nonindependence of our data, we adapted methods outlined in Garland et al. (1992) and Jovani et al. (2016) to construct a phylogenetically controlled quantile regression. Using the "caper" package in R (Orme et al. 2018), we first ran a PGLS to determine the phylogenetic signal (λ) in our data. We then used this λ value to rescale our previously derived Picidae tree (Dufort 2016; Miles et al. 2018) to reflect the correct phylogenetic signal for our variables of interest. Next, we used the rescaled trees to create phylogenetic independent contrasts (PICs) for each of our three variables: drum speed, drum length, and mass. To control for body size, we "positivized" the contrasts for body size and then ran regressions through the origin (see below) for each component (speed and length PICs) on the "positivized" body size contrasts (Garland et al. 1992). We then calculated residuals from each linear regression and used those size-corrected residuals as our variables for the phylogenetic quantile regression (see Garland et al. [1992] and Garland and Janis [1993] for more detailed statistical methods). Due to the inherent ambiguous directionality of independent contrasts, the quantile regression analysis must be forced through the origin (Garland et al. 1992). To understand the predictive relationship of drum speed on drum length at all levels of the distribution, our model calculated a slope at every 10th percentile ($\tau = 0.1$–0.9). We calculated standard error and P-values for our model using the bootstrap method (boot.sims = 1000), and only considered percentile slope estimates to be significantly different from zero if $P < 0.05$ for five model iterations. It is not necessary to correct for multiple testing when using quantile regression because calculating slopes at multiple percentiles (τ values) is not repeated testing of the same statistical hypothesis (Spear and Mordecai 2018; Virta et al. 2019; Freestone et al. 2021).

COMPONENT COVARIATION WITHIN SPECIES

To determine whether the predictive relationship between drum speed and drum length exists within species, we selected eight focal taxa for within-species quantile regression analyses (Table 1). Focal species were chosen based on existing

Table 1. Summary statistics for each focal species. For a full list of recordings used, see Table S1.

Species	N	Mass (g) (Mean)	Drum Length (beats) (Mean ± SD)	Drum Speed (Hz) (Mean ± SD)
Campephilus melanoleucos	42	250	7 ± 2.3	15.44 ± 2.47
Dendrocopos leucotos	60	108	30 ± 6.67	18.86 ± 1.26
Dendrocopos major	320	79	12 ± 2.95	21.96 ± 1.81
Dryobates minor	151	23	21 ± 6.05	20.68 ± 2.09
Dryocopus martius	42	307	29 ± 7.6	17.26 ± 1.3
Dryocopus pileatus	40	299	26 ± 5.92	14.40 ± 0.93
Leuconotopicus villosus	63	61	27 ± 5.11	25.71 ± 2.14
Picoides tridactylus	81	63	18 ± 4.21	15.02 ± 1.71

acoustic data and to maximize the phylogenetic range of our analyses. Drum recordings were collected from the online databases, Xeno Canto (xeno-canto.org) and Macaulay Library (macaulaylibrary.org; Cornell University). We used Adobe Audition CC to measure spectrograms for each individual drummer and calculate drum speed and length. In cases where there were multiple drums from one individual on a recording, we calculated an average value for drum speed and drum length. Outliers were removed if the measurement for either drum speed or length was greater than three standard deviations from the species' mean, which likely indicates that the drumming bird was misidentified by the person who recorded the drum. We used a correlation power analysis ($\alpha = 0.05$, power = 0.8, Cohen's $w = 0.05$) to calculate the minimum required number of individual drummers per species (minimum = 40, median = 60, range = 40–320). The range of *Dendrocopos major* extends from Western Europe to Japan, but for the purposes of our study we only included data collected west of the Ural Mountains because the number of available recordings for the eastern population did not meet our minimum sample size requirement.

As above, we chose quantile regression to test the predictive relationship between drum speed and length at different percentiles (τ values) of each species' drum length distribution. We ran this model with average drum speed as the predictor variable and average drum length as the response. We did not correct drum measurements for body size in the within-species analyses because throughout the clade, intraspecies variation in body size is relatively small (≈12%–15%) compared to interspecies variation in size (≈51%–105%) (Gorman 2014). We ran the quantile regressions between drum speed and drum length at every 10th percentile ($\tau = 0.1$–0.9) to understand the predictive relationship throughout the species' drum length distribution. We calculated standard error and P-values for our model using the bootstrap method (boot.sims = 1000), and only considered percentile slope estimates to be significantly different from zero if $P < 0.05$ for five model iterations.

For some species, we ran additional analyses to explore the relationships between the available contextual metadata and individual drum performance. We calculated linear regressions for each species' drum speed and drum length (response variables) against time of day and day of year (predictor variables). We also considered the influence of geography on drum performance. We compared mean drum speed and mean drum length between different geographic regions, coarsely defined as "Nordic," "peninsular Europe," "western Europe," and "eastern Europe," using one-way ANOVA and Kruskal-Wallis tests. Significant findings were further explored by computing Tukey Honest Significant Difference and pairwise Wilcoxon Rank Sum Tests, respectively. See Table S1 for region assignments.

Table 2. Results of among species phylogenetically corrected quantile regression, showing the percentile of drum length (τ), relationship between drum speed and length (slope), standard error (SE), *t*-statistic, and *P*-value. Significant percentiles are denoted with an asterisk (*).

τ	Slope	SE	*t*-statistic	*P*-value
0.1*	0.58	0.21	2.73	0.0073
0.2*	0.59	0.19	3.11	0.0023
0.3*	0.67	0.16	4.13	<0.0001
0.4*	0.69	0.15	4.71	<0.0001
0.5*	0.72	0.09	7.70	<0.0001
0.6*	0.72	0.12	6.10	<0.0001
0.7*	0.73	0.16	4.57	<0.0001
0.8*	0.76	0.15	4.90	<0.0001
0.9*	0.76	0.18	4.11	<0.0001

Results

AMONG-SPECIES RELATIONSHIP

We first explored coevolutionary connectivity between drum speed and length across the woodpecker family. Our phylogenetically corrected quantile regression model showed that contrasts of these two display components are positively related to each other at all percentiles (τ values) across the entire clade's display distribution (Table 2; Fig. 1a; $\tau = 0.1$–0.9, $P < 0.01$). Moreover, slopes that describe the positive relationship between contrasts of

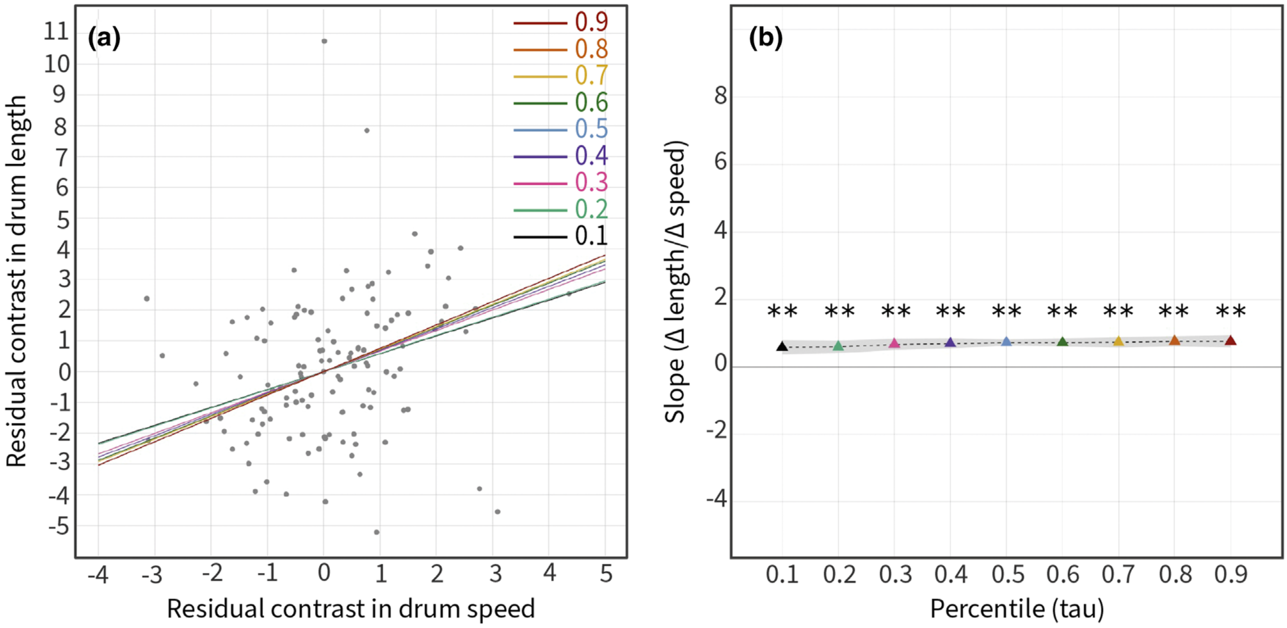

Figure 1. Phylogenetically corrected quantile regression showing variation among species in drum speed and length. (a) Data points represent residuals from regressions of PICs (see Garland et al. 1992; Garland and Janis 1993). Significant positive relationships between drum speed and drum length (corrected for mass using regression residuals) at all nine percentiles measured are represented by colored lines. Numbers to the right of their color-matched line segment indicate the percentile of drum length distribution (τ value). (b) Points represent the slope values reflecting the predictive relationship between drum speed and length as a function of percentile (τ). Colored triangles match the corresponding lines in panel (a), representing percentiles that differ significantly from zero ($P < 0.01$), also denoted by asterisks (**). Shading indicates the standard error for each slope. (See Table 2 for detailed statistics.)

drum speed and length did not appear to markedly differ from each other (Fig. 1b). Therefore, the degree to which drum speed predicts drum length is relatively uniform across woodpecker taxa.

WITHIN-SPECIES COMPARISONS

To explore the drum signal dynamics at the within species level, we assessed the relationship between drum speed and length in eight different focal species. These analyses revealed species-specific variation in the relationship between the two signal components (Fig. 2, Table S2). In some species, *Dryocopus martius* (Fig. 2c) and *Dryobates minor* (Fig. 2h), drum speed and length were positively related to each other only at the 90th percentile of drum length (*D. martius*: $\tau = 0.9$, slope $= 5.25 \pm 2.34$, $P = 0.030$; *D. minor*: $\tau = 0.9$, slope $= 1.18 \pm 0.47$, $P = 0.013$). By contrast, *Dendrocopos leucotos* (Fig. 2f) showed a positive predictive relationship between drum speed and length only at the lower-mid range of drum length, specifically, between the 20th and 50th percentiles ($\tau = 0.2$: slope $= 2.18 \pm 0.94$, $P = 0.024$; $\tau = 0.3$: slope $= 1.77 \pm 0.72$, $P = 0.017$; $\tau = 0.4$: slope $= 1.73 \pm 0.66$, $P = 0.011$; $\tau = 0.5$: slope $= 1.91 \pm 0.84$, $P = 0.026$). All other species in this analysis—*Campephilus melanoleucos* (Fig. 2a), *Dryocopus pileatus* (Fig. 2b), *Picoides tridactylus* (Fig. 2d), *Leuconotopicus villosus* (Fig. 2e), and *Dendrocopos major* (Fig. 2g)—showed no sign of a significant relationship between drum speed and length at any percentile of drum length elaboration. All these results, including the lack of any component covariation in five species, differ substantially from the among-species pattern of uniform, positive covariation of signal components.

For the three species that show a significant relationship between components at any percentile, we conducted additional analyses to explore the possible influence of underlying factors (time of day, day of year, and geography) on drum speed and length performance (Table S3). Of these tests, our geographical comparisons for *D. minor* were the only significant findings (Fig. 3). In this species, drum speed varies by geographic region (Kruskal-Wallis chi-squared = 56.28, $P < 0.001$) such that birds in peninsular Europe drum faster than those in the western European, Nordic, and eastern European regions (pairwise Wilcox test, adjusted $P < 0.001$) and western European birds drum faster than Nordic populations (pairwise Wilcox test, adjusted $P < 0.001$) (Fig. 3a). Additionally, a one-way ANOVA revealed that in *D. minor* drum length also varies by geography ($F(3,147) = 9.306$, $P < 0.0001$). Post hoc comparisons using Tukey HSD show that Nordic drums are shorter than both

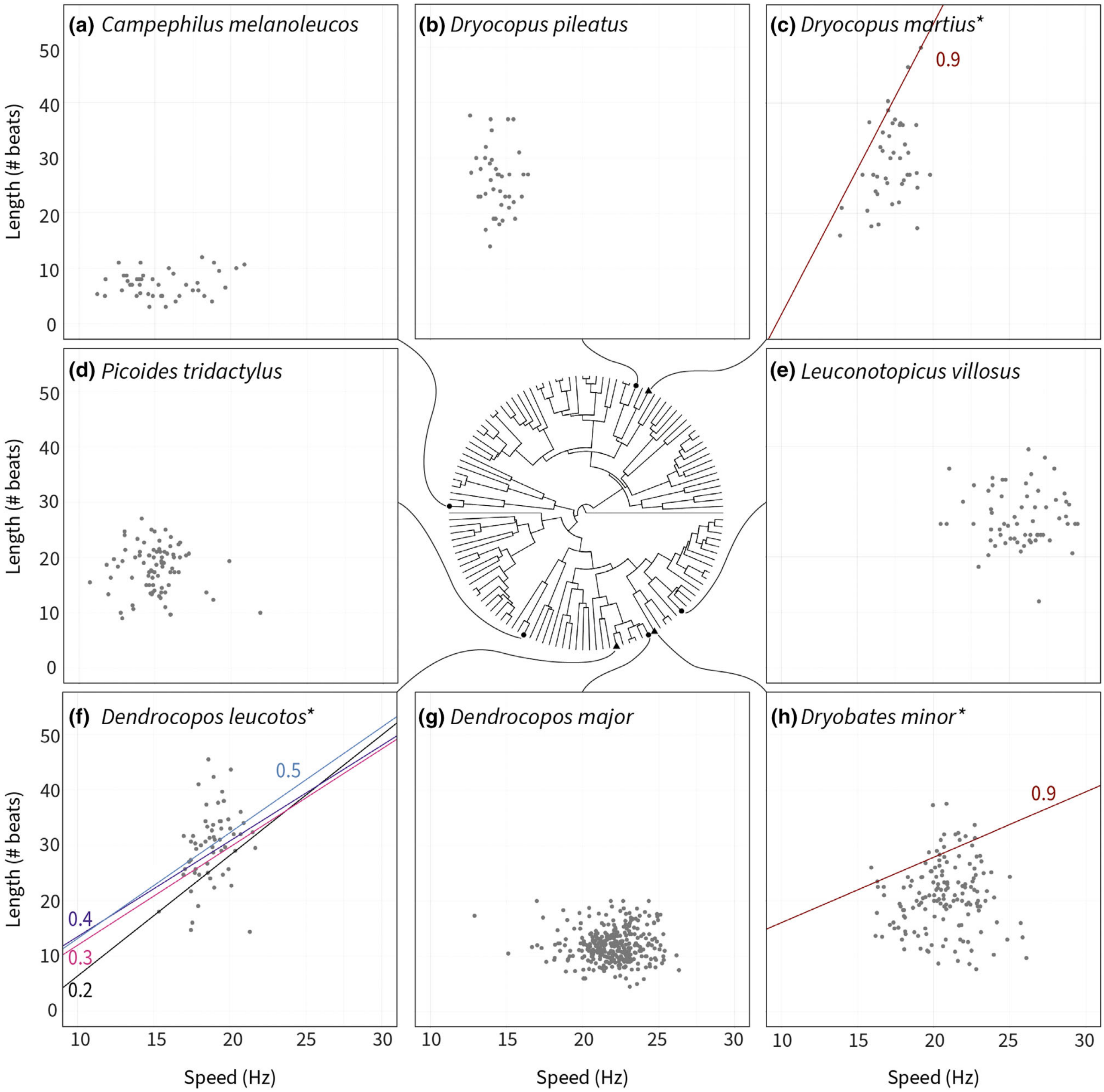

Figure 2. Within-species-level quantile regression results comparing drum speed and length, arranged around a woodpecker phylogeny. On the phylogeny, species that do not show any significant relationship between speed and length are represented by circles and those that do show a significant relationship are triangles. Data points represent individual drummers, and colored lines indicate percentiles (τ) with a significant predictive relationship of drum speed on drum length (see Table S2 for detailed statistics). (a) *Campephilus melanoleucos* ($\tau = 0.1$–0.9, $0.1 \leq P \leq 1$); (b) *Dryocopus pileatus* ($\tau = 0.1$–0.9, $0.3 \leq P \leq 0.9$); (c) *Dryocopus martius** ($\tau = 0.9$, $P = 0.03$); (d) *Picoides tridactylus* ($\tau = 0.1$–0.9, $0.3 \leq P \leq 1$); (e) *Leuconotopicus villosus* ($\tau = 0.1$–0.9, $0.3 \leq P \leq 1$); (f) *Dendrocopos leucotos** ($\tau = 0.2$, $P = 0.024$; $\tau = 0.3$, $P = 0.017$; $\tau = 0.4$, $P = 0.011$; $\tau = 0.5$, $P = 0.026$); (g) *Dendrocopos major* ($\tau = 0.1$–0.9, $0.3 \leq P \leq 0.8$); (h) *Dryobates minor** ($\tau = 0.9$, $P = 0.013$).

peninsular European (adjusted $P = 0.0012$) and western European (adjusted $P < 0.001$) drums, and western European drums are longer than eastern European drums (adjusted $P = 0.022$) (Fig. 3b). For full results of all nonsignificant tests, see Table S3.

Discussion

At the macroevolutionary level, we found strong evidence for coevolution between two signal components that make up the woodpecker drum display—speed and length. This means that

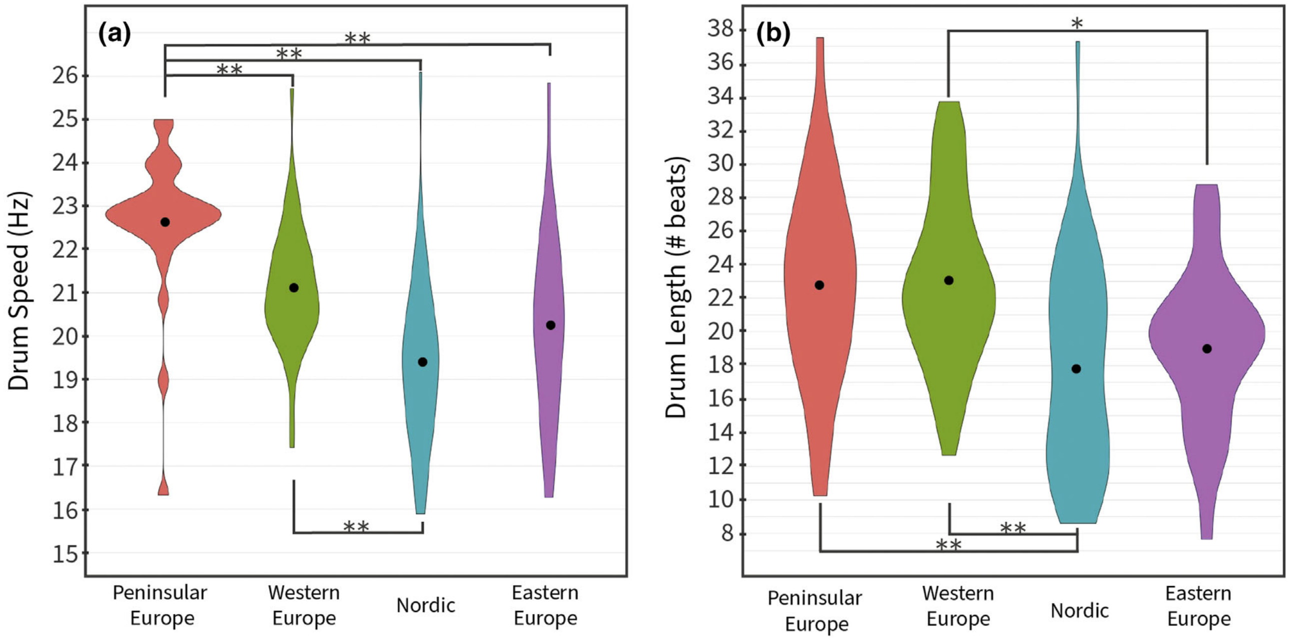

Figure 3. ***Dryobates minor*** **drum speed (a) and length (b) as functions of geographic region. (a) Kruskal-Wallis rank sum test (chi-squared = 56.28, df = 3, $P < 0.001$) followed by post hoc pairwise comparisons using Wilcoxon rank sum exact test shows differences in mean drum speed between Peninsular Europe and each of the other regions (adjusted $P < 0.001$) as well as between Western Europe and Nordic regions (adjusted $P < 0.001$). (b) A one-way analysis of variance ($F(3,147) = 9.306$, $P < 0.0001$) followed by post hoc Tukey multiple comparisons of means shows differences in mean drum length between Peninsular Europe and Nordic regions (adjusted $P = 0.0012$), Western Europe and Nordic regions (adjusted $P < 0.001$), and Western and Eastern Europe (adjusted $P < 0.05$).**

among woodpeckers, these components have undergone mutual elaboration resulting in faster, longer drums that likely provide a stronger territorial signal (Schuppe et al. 2016; Schuppe and Fuxjager 2018). However, the covariation found at the clade level is not reflected in kind by our within-species analyses. In fact, for individuals in most of our focal species, performance of drum speed and length are not correlated at all. There were, however, a few exceptions. In two species, we found a positive predictive relationship between drum speed and length at the 90th percentile of the drum length distribution. In one species, we found a relationship between these components at the 20th–50th percentiles. Together, these results suggest that covariation between drum speed and length is uncommon within any given woodpecker species, although when they do exist, patterns of component covariation appear to be species specific.

It is notable that in all species where there is a correlation between drum speed and drum length, we only found evidence supporting positive relationships. These findings are somewhat novel in the field of avian acoustic communication, where most work has focused on performance trade-offs in birdsong (Podos 1997; Illes et al. 2006; Cardoso et al. 2007; Janicke et al. 2008; Derryberry 2009; Sockman 2009; Cardoso and Hu 2011; Juola and Searcy 2011; Cramer 2013; Phillips and Derryberry 2017). Studies of signal evolution have often found evidence for a trade-off between traits in a unimodal multicomponent signal, whereby individuals have the potential to invest in the elaboration of either one component of the display or another, but not both (Manica et al. 2017). For example, in birdsong, the well-reported trade-off between frequency modulation and trill rate is believed to result from a combination of physiological constraints imposed by the multiple motor systems that are involved in respiration and vocalization (Goller 2022). Our positive results directly contrast with the negative relationship predicted by the trade-off hypothesis, indicating the mutual elaboration of these drum signal components in multiple species. In the woodpecker drum, the overwhelmingly positive relationship between components is consistent with the lack of a physiological or mechanistic constraint preventing an individual from drumming both fast and long.

SIGNAL COMPONENTS COEVOLVE ACROSS THE CLADE

The positive relationship between drum speed and length at the macroevolutionary level shows that these two signal components covary tightly across the clade. If forces like selection drive the elaboration of one display component over time, then the correlated component would also likely be elaborated. In fact, elaboration of the latter component may even occur in the absence of direct selection (Pigliucci 2003). This means that throughout woodpeckers, drum speed and length have likely coevolved, and may continue to respond to selection as a unit.

The mutual elaboration of these two display components could be adaptive or simply a by-product of the mechanical basis of the drum (see below). Several studies support the former view, showing that especially strong selection can drive evolution toward further display elaboration by incorporating additional signals or signal components (Møller and Pomiankowski 1993; Johnstone 1996; Wilson et al. 2013). In woodpeckers, it is thought that exaggerated drum length evolves in response to sexual selection by male-male competition. However, drum speed does not show a similar relationship to certain phenomenological signatures of strong selection (Miles et al. 2018). We therefore suspect that selection first elaborates length and then may secondarily elaborate speed. Previous work has shown that length is less constrained by body size or other associated physiological factors than speed (Miles et al. 2018, 2020; Schuppe et al. 2021). As a result, there is greater standing variation in a species' drum length compared to standing variation in drum speed (Miles et al. 2018). This means that overall, drum length may be more evolutionarily labile than drum speed (Miles et al. 2020).

Other potential influences on component coevolution are the organisms' physiology and how individual motivation manifests in display contexts. Less is known about the physiological or mechanical factors that might explain the observed relationships. The mechanistic basis of woodpecker drumming is only just becoming clear (see Schuppe et al. [2021] for a recent review), but it is possible that producing a longer drum physiologically necessitates drumming at a faster speed. Or perhaps an individual's functional motivation drives them to drum both longer and faster in a particular set of display circumstances. Of course, sexual selection, physiological mechanisms, and individual motivation could all be at play with respect to drum evolution, and thus further work is needed to fully understand their individual and collective influences on this process.

COVARIATION OF DISPLAY COMPONENTS WITHIN SPECIES

For most focal species in our study, we found no within-species relationship between drum speed and length. One explanation for this is that individual woodpeckers may flexibly adjust individual components of their drum to fit the current display context (Miller et al. 1998; Wilgers and Hebets 2011; Schuppe et al. 2016; Schaedler et al. 2021). Another possibility is that each individual's performance flexibility is low, but within the population there is substantial variation between each individual's speed and length performance abilities (Goller 2022). These two possibilities are not mutually exclusive, and some combination of both may therefore be present. Regardless, our results demonstrate that these display components can and do vary independently of each other in most species.

Interestingly, we do see a positive predictive relationship between drum speed and length components for the most exaggerated portion of drum length (90th percentile) in two species, *Dryocopus martius* and *Dryobates minor*. This suggests that for these taxa, individuals performing the longest drums are also performing the fastest drums. In this scenario, motivational, functional (i.e., territorial), and/or mechanistic factors may link the two display components together (see above). Functionally, increasing either drum speed or length can enhance the threat of a drum during territorial competition (Schuppe and Fuxjager 2018), so these data may reflect individuals who were recorded during territorial intrusions and are thus performing at an upper limit. In a third species, *Dendrocopos leucotos*, we see a positive relationship between drum speed and length in much of the species' distribution, namely, the 20th–50th percentiles of the drum length performance. This pattern is intriguing, and ripe for future work. Due to the limitations of our acoustic dataset for all species, we are unable to draw conclusions about the broader social context of these drums.

Environmental variation is another possible explanation for the observed within-species differences. Our coarse geographical analysis revealed that for *D. minor* both drum speed and length vary between regions. This variation could represent regional differences in the drumming substrate available to *D. minor*. In other words, perhaps peninsular Europe is characterized by trees that facilitate faster drumming than those in the rest of Europe, owing to variation in properties of the wood (resilience, stiffness, etc.) (Schuppe et al. 2021). However, if this were truly a reflection of substrate availability, we might expect to see a similar regional difference in other woodpecker species, because species often overlap in their resource utilization (Short 1971). Instead, we found no significant effect of geography on drum speed or length in *D. leucotos* or *D. martius*. Combined, these results may point to possible signal divergence among geographically distinct populations of *D. minor*. We encourage future work to explore the observed regional variation in drum component performance on a finer scale.

If physiological factors accounted for the coupling of drum speed and length, we would expect to see similar patterns of component covariation in closely related species. Yet, we see covariation at the 90th percentile of drum length in *D. martius* and no relationship between drum speed and length in its congener *D. pileatus*. Similarly, *D. leucotos*' congener *D. major* shows no relationship between drum speed and length, indicating that the explanation is likely not physiological. These findings are consistent with previous work on treefrog vocalizations that shows differences in the strength of component covariation among closely related species (Reichert and Höbel 2018). This study also reports that social context (function) does not explain these differences in covariation and instead attributes them to structural (mechanistic) factors. Taken together, we can conclude that closely related species may exhibit different patterns of signal component covariation, and the source of these differences can vary widely across systems.

Finally, within all three species, there is no apparent effect of time of day or day of year on either drum speed or length. The lack of temporal variation in drum performance differs from the widespread seasonal and diurnal variability observed in birdsong (Spector 1992). Similar temporal patterns of drumming have been reported previously in some woodpecker species (De Kiriline Lawrence 1967). As temporal patterns were not a primary goal of this study, we encourage future work to explore the potential of interspecies variation in drum performance cyclicity.

SYNTHESIZING PATTERNS OF MACRO- AND MICROEVOLUTION

Many studies explore macroevolutionary patterns to describe variation within a clade (Porto et al. 2009; Koyabu et al. 2014; Vanhooydonck et al. 2014; Miles et al. 2018, 2020; Merwin et al. 2020; Wylde and Bonduriansky 2020; Avendaño and Cadena 2021). Additionally, there is an equally robust body of literature characterizing phenotypic variation to understand how selection shapes individual diversity within a given species (Westcott 1992; Loyau et al. 2005; Derryberry 2009; Kim and Velando 2015; Vanderbilt et al. 2015). However, little research successfully bridges the gap between these two scales to fully describe how microevolution may or may not influence either the evolution of phenotypic differences among species or the process of speciation itself. Here, we incorporate two levels of analysis in an attempt to bridge this gap and understand how within-species variation in display component performance can contribute to the broader macro-level trends of a complex signal's evolution.

Although the coevolution of drum speed and length is clear when comparing species' average component performance, our within species results tell a different story. The lack of obvious within-species signal component covariation is intriguing, and the resulting variability may play an integral role in the broader evolution of this clade. Specifically, consider within-species variation of the less constrained signal component, drum length. *D. leucotos*, for example, exhibits noteworthy variation in drum length performance, with drums spanning 14–45 beats. To put this variability in context, this range includes drum lengths that are within one standard deviation of the mean for all but one (*C. melanoleucos*) of the other seven focal species included in this study. In other words, *D. leucotos* can and do produce drums that encompass the drum length phenotype space of many other woodpecker species. This level of resting variation in drum length performance offers a phenotypic landscape that is ripe for future signal diversification within the group. For example, if there is an event that results in reproductive isolation of different *D. leucotos* populations, the underlying variation in drum length provides a relatively easy route for selection to correspondingly adjust signal structure in a population-specific manner. We expect that this pattern applies to most woodpeckers, given that most species seem to perform drums in which speed and length do not covary. Collectively, our study illustrates the power of comparative studies that operate at both among-species and within-species levels to understand the evolution and diversification of complex signaling behavior.

Conclusions

Among species comparative analyses show a mutual elaboration of the signal components drum speed and drum length. In contrast, within individual species we found that these components are largely decoupled, with substantial species-specific variability in the performance and relatedness of drum speed and drum length. Together, we can conclude that signal component coevolution at a macroevolutionary level does not preclude independent component variation within species. There is no evidence, at any level, for a performance trade-off between drum speed and length.

AUTHOR CONTRIBUTIONS

MJF and NMM conceptualized the idea of the study, designed methodology, performed formal analysis, and wrote the manuscript. NMM and EKV collected and curated the data. MJF performed supervision and acquired funding.

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DATA ARCHIVING

Data available through Dryad (https://doi.org/10.5061/dryad.mgqnk991w).

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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Supporting Information

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

Table S1.xlxs
Table S2.xlxs
Table S3.xlxs
Table S1: Full list of audio recordings used in species level analyses. Note: the number of audio files does not equal the total sample size (N) for each species because some audio recordings included multiple drummers.
Table S2: Results of within species quantile regression, showing the percentile of drum length (τ), relationship between drum speed and length (slope), standard error, t-statistic, and p-value. Species with a significant relationship are denoted by an asterisk (*) and significant percentiles are shaded.
Table S3: Nonsignificant results of within species linear regression and analysis of variance models assessing the effects of time of day, day of year, and geography on drum speed and drum length for three focal species.