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Original Article

Form–function relationships within species are uncoupled from those across species in swimming and jumping performance in arboreal frogs

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Abstract

Variation of form–function relationships within populations is the substrate for adaptation at higher levels. Therefore, assessing similarity in form–function relationships within and between species may help reveal the processes shaping functional diversity. Here, we test such similarity across three levels of anuran phenotypic divergence: within a population, among species in a single family (Hylidae; ~60 myr), and across a much broader sample of all anuran species using a single microhabitat (arboreal; ~120 myr). We expected less interspecific divergence to show higher similarity of form–function relationships with the intraspecific level. We analyzed the relationships between locomotor performance (in both swimming and jumping) and several hindlimb traits across these three evolutionary levels. While we found a positive correlation between swimming and jumping velocity at both intra- and interspecific levels, relationships between performance and body form did not match across levels. We suggest that different strengths of functional constraints or trade-offs may have produced more variation in form–function relationships across species, decoupling them from within-species patterns. We conclude that performance landscapes are likely qualitatively different across the different evolutionary scales, potentially reflecting changes in the relative importance of different behaviors across all arboreal species.

Keywords: Anura, intraspecific variation, functional diversity, locomotor performance, performance correlations, phylogenetic comparative methods

Introduction

Form–function relationships reflect the influence of mechanical properties on the functioning of organisms in their environments. Such relationships are therefore expected to be shaped by adaptation (Arnold, 1983, 2003). However, due to the complex and hierarchical nature of biological systems, the link between variation in form (the size and shape of organisms) and variation in functional properties and performance (e.g., muscle power output and sprinting velocity) may not be straightforward (Anderson, 2022; Simon & Moen, 2023; Taylor & Thomas, 2014; Wainwright, 2007). Biological systems are composed of multiple parts that interact with each other to influence more than one function (Arnold, 1983; Collar et al., 2014; Garland & Losos, 1994; Lauder, 1996). On one hand, this complexity raises the possibility of many morphological configurations producing similar levels of functional performance, often called many-to-one mapping (Wainwright et al., 2005). On the other hand, the same traits affecting performance in many functions may prevent the optimization of those functions simultaneously, revealing trade-offs (Anderson et al., 2014; Corn et al., 2021; Garland et al., 2022; Ghalambor et al., 2003; Wainwright, 2007). Moreover, the relationships between long-term evolution and diversity in form and function may be obscured by phylogenetic and other constraints (Simon & Moen, 2023a; Simon et al., 2025).

Faced with these challenges to study form–function diversity, an understanding of how and why morphology and functional performance vary within species may help reveal the processes shaping diversity across species (Grant, 1981; Emerson & Arnold, 1989; Grant & Grant, 2007). Differences among individuals may arise due to developmental plasticity or to microgeographic variation in resources and biotic interactions that may resemble larger-scale differences (Calsbeek, 2009; Calsbeek et al., 2006, 2007; Losos, 2000; Martin & Wainwright, 2013). For instance, in anole lizards, selection on limb length and locomotor performance associated with competition and habitat use within species is also implicated in divergence across species (e.g., Calsbeek, 2009; Calsbeek & Irschick, 2007; Losos, 2011; Losos & Sinervo, 1989). The key point is that variation among individuals within populations is the raw material for selection to act upon and eventually scale up those differences between populations and species (Calsbeek et al., 2006, 2007; Martin, 2016; Simpson, 1944; Taverne et al., 2021). Hence, finding similar form–function relationships within and between species would suggest similar processes shaping morphological and functional performance variation at different evolutionary scales.

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Here, we explore the similarity of relationships between hindlimb traits and jumping and swimming performance within and across species of arboreal frogs. We focus on a single type of organism and ecology, as we expect the relative importance of different functions (e.g., different types of locomotion) in shaping fitness to be similar within populations and across species belonging to the same microhabitat (Losos, 1990; Moen, 2019; Moen et al., 2016). Thus, we expect this approach to more likely show a clear link between intra- and interspecific variation than an analysis across many ecological types. Moreover, the relationship between morphology and performance in multiple locomotor modes in frogs has been mostly studied across species encompassing different microhabitats (e.g., Moen, 2019; Moen et al., 2013, 2016). Therefore, we do not know if form–function relationships at a finer ecological scale mirror the patterns found at a broader scale of frog diversity.

The kinematics of swimming in anurans has been described as "jumping in water," and generation of thrust may be similar in both behaviors (Kamel et al., 1996; Nauwelaerts et al., 2007; Peters et al., 1996), at least in nonaquatic species (Richards, 2010). Accordingly, across species of frogs, both jumping and swimming velocities show a correlation of ~2/3 (Moen, 2019). However, within species of frogs, no consistent relationship has been found (Nauwelaerts et al., 2007). Moreover, we may expect some differences in form–function relationships for swimming and jumping, given that the musculoskeletal system of hindlimbs has to act against very different media: fluid water versus solid ground, respectively (Nauwelaerts & Aerts, 2003; Richards & Sawicki, 2012). Frogs need to exert lower forces in water than on the ground, indicating that the optimal functional parameters for swimming may be different than for jumping (Richards & Sawicki, 2012). Yet, when several traits interact to perform different functions, as is the case with hindlimb traits in frogs, empirical evidence for clear-cut functional trade-offs can be elusive (Garland et al., 2022).

As the hindlimbs of frogs are a multitrait system, we might expect many-to-one mapping. For example, multiple combinations of foot size and muscle size can maximize muscle power in frog swimming (Richards & Clemente, 2013). Furthermore, even when multiple traits affect a function, they may show differential mechanical sensitivity: some traits will affect a specific function more than others (Anderson & Patek, 2015; Holzman et al., 2011; Muñoz et al., 2018). Within species, some muscles may contribute more to swimming or to jumping (Nauwelaerts et al., 2007), and mechanical behavior (e.g., timing of muscle shortening) and muscle activity patterns (e.g., duration of electromyographic activity) can differ for the same muscles depending on whether they are used for jumping or swimming (Gillis & Biewener, 2000). Across species, muscles that show stronger effects on locomotor performance may evolve faster, as shown in other systems (Holzman et al., 2012; Muñoz et al., 2018). Additionally, many-to-one mapping can alleviate functional trade-offs across multiple taxa (Dumont et al., 2014; Holzman et al., 2011; Pigot et al., 2020; Wainwright et al., 2005). Particularly in frogs, both longer and more muscular legs can enhance jumping and swimming performance, but species in different microhabitats differ in how they maximize performance (e.g., high muscle mass in swimming types; Moen et al., 2013, Moen, 2019). Nonetheless, a complicating factor when studying performance across species is that different kinematic strategies may be used in species with different ecologies (Corn et al., 2021), as has been shown for frog swimming (Richards, 2010; Robovska-Havelkova et al., 2014). Therefore, it is hard to predict whether intraspecific patterns of form–function relationships for swimming and jumping will match those across species.

We addressed these issues by studying the relationships between hindlimb traits and both jumping and swimming performance within a species of arboreal frog, *Hyla cinerea*, and among an additional 42 arboreal species from 20 genera across five families. Using this sampling design, we were able to test whether the relationships between morphology and locomotor performance matched at three different levels: within species, within the family Hylidae, and across all arboreal species (Figure 1). If the amount of divergence influences similarity between intra- and interspecific relationships, more recent phenotypic divergence (within Hylidae; ~60 myr of divergence) should show more similar form–function relationships between these levels than divergence accumulated over longer periods of time (across all five frog families; ~120 myr of divergence). Support for this prediction would suggest that evolutionary processes that have acted within populations also drove functional evolution across species. If this prediction is not supported, then form–function relationships may be shaped by distinct processes across these scales. Such processes might be related to functional trade-offs across species, given that the hindlimbs perform more than one locomotor task.

Material and methods

Specimens, species, and phylogeny

We collected 40 individuals of *H. cinerea* (eight females and 32 males) at Red Slough Wildlife Management Area (Oklahoma, USA) on June 24, 2023. *Hyla cinerea* is a hylid frog generally found during the breeding season on emergent vegetation in large, still water bodies (Dodd, 2023). Individuals jumped into the water to escape capture in the field, suggesting that this species uses swimming to evade predators when they are most exposed: calling for females in the water. Males were identified by the presence of nuptial pads and a distended throat sac, whereas females lacked these features; sex was verified by internal inspection of the gonads after we completed all work with live animals. This research was conducted under Oklahoma State University Institutional Animal Care and Use Committee (IACUC) protocol 20-09 and Oklahoma Department of Wildlife Conservation scientific collecting permit W2302.

The additional interspecific data from 38 arboreal and four semiarboreal species ($n = 177$; 1–8 individuals/species) were obtained from previously published data (Moen et al., 2013, 2021a, b). These species have a common ancestor estimated at 114.9 million years old (Portik et al. 2023), and they belong to five different families: Mantellidae ($n = 19$ species), Hylidae ($n = 14$), Microhylidae ($n = 5$), Hyperoliidae ($n = 2$), and Rhacophoridae ($n = 2$). For analyzing these interspecific data, we used the recent anuran phylogeny of Portik et al. (2023), who estimated the phylogeny with over 300 markers, calibrated branch lengths to units of time, and had the most comprehensive species sampling of anuran phylogenies to date. We thus pruned their maximum-likelihood tree to contain only the 43 species in this study (Figure 1).

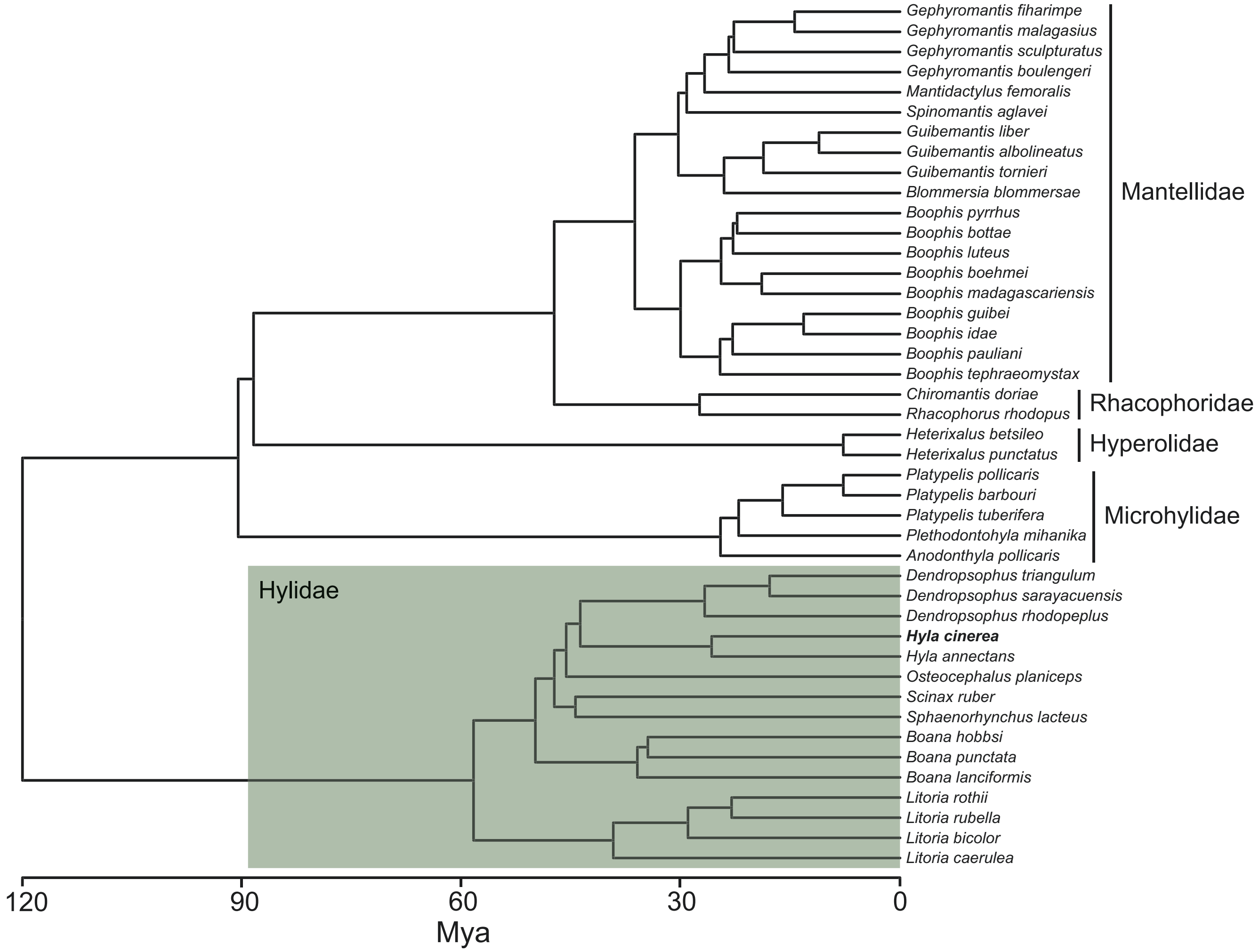

Figure 1. Phylogenetic relationships across all 43 arboreal frogs sampled for this study. The shaded clade is Hylidae, which includes *Hyla cinerea* (in bold). The remaining species are mostly from Mantellidae from Madagascar, as well as three other families that include arboreal taxa. Pruned from Portik et al. (2023).

Jumping and swimming trials

All specimens were measured for jumping and swimming performance by using a high-speed camera. We focused on peak performance in jumping and swimming, as most frogs use burst performance to catch prey and to avoid predation (Bulbert et al., 2015; Duellman & Trueb, 1994; Heinen & Hammond, 1997; Wells, 2019). Moreover, peak performance is expected to be highly relevant for anurans to effectively escape predators, both on land and in water, and should reflect past selection in the wild (Losos & Miles, 2002; Moen, 2019; Moen et al., 2021a). Because *H. cinerea*, our focus for intraspecific analyses, is arboreal (Dodd, 2023), we focused on arboreal species for interspecific analyses in order to study divergence and form–function relationships in taxa likely under similar selective pressures. We recognize that studying swimming in arboreal frogs—rather than another microhabitat type, such as semi-aquatic (e.g., Peters et al., 1996; Nauwelaerts et al., 2007)—may seem unconventional. However, although arboreal frogs are primarily climbers and jumpers, several species regularly swim in water to call (males) or lay eggs (females; Moen, 2019; Moen et al., 2013). Thus, their ability to swim may affect competition for mates and exposure to predators in aquatic environments, at least when breeding. Moreover, no studies have directly focused on the traits that affect swimming in arboreal frogs.

All details of performance trials, video capture, and video processing followed Moen et al. (2013, 2021a) and can be found in those papers. In brief, individuals performed both behaviors in several trials on different days, such that we could maximize our chance to collect the peak performance in both behaviors for each individual. Jumping take-off and burst swimming were recorded using high-speed cameras at 250 frames/second. In previous work (Moen et al., 2021a), we have found that this frame rate is the best compromise between reducing the digitizing error-to-signal ratio (favored by lower frame rates) and accurately capturing the full shape of the velocity and acceleration profiles (favored by the increased data density of higher frame rates). Nonetheless, we acknowledge that acceleration profiles, as the second derivative of our raw distance-by-time data (see below), will show more error than velocity profiles.

We then digitized the tip of each frog's snout during the take-off (jumping) or power stroke (swimming), converted the 2D coordinates into 1D displacement-by-time curves, smoothed those curves to reduce digitization error, and extracted velocity and acceleration profiles (i.e., the first and second derivatives of distance-by-time curves, respectively). For intraspecific analyses, we used jumping and swimming velocity and acceleration values of more than one trial (see below). For interspecific analyses, we extracted the individual peak values of performance in each behavior and then averaged values per species. After completion of trials, specimens were euthanized with benzocaine, fixed with 10% formalin, and preserved in 70% ethanol.

Morphological measurements

We collected five linear measurements on all preserved specimens using a digital caliper: femur length, tibiofibula length, tarsus length, and foot length on the left hindlimb, plus snout-to-vent length (SVL). We summed the hindlimb bone lengths to calculate the total leg length, which is relevant to both jumping and swimming performance (Moen, 2019). We also photographed the left foot pressed against a glass slide, then measured foot webbing areas between all digits and foot area (without webbing) in ImageJ (version 1.53e, Schneider et al., 2012). We summed these area measurements to calculate the total foot area, which should be relevant to swimming performance (Gal & Blake, 1988; Nauwelaerts et al., 2001; Richards, 2008, 2010). Finally, we dissected out all upper- and lower-leg muscles of the left hindlimb, removed excess surface ethanol by patting them dry, and weighed them on a scale with 0.0001 g precision. We then added all the muscle weights to calculate total leg muscle mass. These hindlimb muscles contain the major extensors relevant for jumping and swimming (Gillis & Biewener, 2000; James & Wilson, 2008; Nauwelaerts et al., 2007; Olson & Marsh, 1998; Prikryl et al., 2009), and their summed mass has been shown to strongly correlate with performance in both behaviors across frog species (Moen 2019; Moen et al. 2013). We logged performance and morphological variables for analyses to control for scaling effects. We also scaled and centered the morphological variables to test for form–function relationships (in regressions, see below), given that the traits have different units (leg length in mm, foot area in mm^2, and leg mass in g) that are incommensurate and complicate multivariate analyses (Adams & Collyer, 2019). This standardization assured that we could compare regression coefficients among the different morphological traits.

Intraspecific analyses

The motivation of individuals to perform in artificial conditions (i.e., in the laboratory) can vary, with some individuals much easier to motivate than others (Losos et al., 2002; Adolph & Pickering, 2008; Moen et al., 2013, 2021a). Moreover, individuals may perform better on some days than others. Thus, we first performed a repeatability analysis to examine whether variation between individuals was a substantial proportion of total variation (the sum of between- and within-individual variation). To estimate these components of variation, we analyzed repeated measurements of jumping and swimming performance variables (velocity and acceleration) of the same individuals across different trials in univariate mixed models (Dingemanse & Dochtermann, 2013). The repeated measures were peak performances for each individual per day extracted from digitized trials that showed qualitatively high performance relative to undigitized trials. While this criterion (to digitize a video or not) is undoubtedly subjective, it guarantees the removal of poor performance. This procedure generally resulted in two peak values for swimming performance and three peak values for jumping performance for each individual.

We ran the univariate mixed models in the R programming environment (version 4.3.2, R Core Team, 2023) using the package *lme4* (version 1.1-35.1, Bates et al. 2015), with individual [ID] as a random factor. We then calculated the repeatability of performance as the variation associated with the ID (between-individual) divided by total variation (sum of between- and within-individual variation).

Because repeatability analysis indicated substantial within-individual variation in performance variables (see Results), we opted to use multivariate mixed models to estimate the correlations between jumping and swimming performance within *H. cinerea*. These multivariate mixed models allow for the estimation of covariances between response variables while accounting for random-effects structure (Houslay & Wilson, (2017)). Particularly, these models can reveal between-individual correlations of performance variables that may be masked by within-individual variation (Careau & Wilson, 2017; Lailvaux et al., 2019). We ran a multivariate mixed model with all four performance variables (repeated measures of peak velocity and acceleration for both jumping and swimming) as response variables, scaled by their standard deviation (to account for unequal variances after logging), and ID as a random factor nested within performance type (swimming vs. jumping). We also included a two-way interaction between performance type and performance trait (acceleration vs. velocity) as a fixed factor. However, because in our experimental design, we tested jumping and swimming on different days for the same individuals, we could not estimate covariances between performance types within individuals (only within-individual covariances in acceleration and velocity within the same performance type; Dingemanse & Dochtermann, 2013). Yet, we could still estimate between-individual covariances between swimming and jumping while taking within-individual variation into account, by employing multivariate mixed models in a Bayesian framework using the package MCMCglmm (version 2.35, Hadfield, 2010). We ran the Markov chain Monte Carlo (MCMC) chains for 2,000,000 iterations with a 200,000 burn-in period, and we also sampled once every 1,000 iterations to estimate the posterior. We checked for autocorrelation and convergence using the R package *coda* (version 0.19-4.1, Plummer et al., 2006). Further details on these analyses are given in Supplementary Methods.

Finally, to estimate the form–function relationships within species (i.e., the partial regression slopes of performance on morphology), we added the fixed factors SVL, leg length, leg muscle mass, and foot area to the multivariate mixed model described above. All four predictor variables were mean centered and scaled by their standard deviations. One of the advantages of using repeated-measures Bayesian regression models is that all aspects of uncertainty of parameter estimates (e.g., variation within individuals across trials) are propagated in the model and displayed via their resulting posterior distributions (Hadfield, 2010). On the other hand, using just peak performance for each individual to estimate performance correlations has the advantage of eliminating what can be alternatively considered as experimental error, reflected in variation (across trials) to successfully motivate individuals to perform as they would in nature (see Discussion). Therefore, we also estimated the partial regression coefficients using just a single value of peak performance (i.e., velocity and acceleration) across all trials for each individual as response variables in an ordinary least squares (OLS) multivariate linear regression.

Interspecific analyses

We used species means of peak performance for all interspecific analyses; at this scale, within-individual variation should not obscure between-species performance correlations, given the typically high divergence among species (Mendoza et al., 2020; Moen et al., 2013, 2021a). Nevertheless, within-species variation (often in the form of measurement error) can strongly affect phylogenetic comparative analyses (Grabowski et al., 2023; Hansen & Bartoszek, 2012; Ives et al., 2007; Silvestro et al., 2015). Thus, we chose to use Brownian Motion (BM) as the underlying evolutionary model in all our analyses, as intraspecific variance can be estimated as a nuisance parameter directly from species' data in the fitting process, then added as a scaling factor to the diagonal of the phylogenetic variance-covariance matrix (Clavel et al., 2019; Housworth et al., 2004; Ives et al., 2007). In contrast, intraspecific variance cannot be incorporated in a lambda (λ) model (Freckleton et al., 2002; Revell, 2010) because the parameter λ and the intraspecific variance are not separately identifiable parameters (Ho & Ané, 2014).

We first estimated the maximum likelihood estimate (MLE) of the evolutionary correlation matrix (Revell & Collar, 2009) between performance variables while using the BM model (function "phyl.vcv()" from *phytools*; version 2.1-1, Revell, 2024) for all arboreal species and for species within Hylidae. To calculate the uncertainty for these correlations, we conducted parametric bootstrapping. We first simulated BM 1,000 times on the phylogeny with all arboreal species or with just hylid species. We used the function "sim.corrs()" from *phytools* to simulate performance variables under the MLE of the phylogenetic correlation matrix. We then estimated the evolutionary correlation matrices for the simulated data sets and calculated 95% CI for each of its elements.

To test whether divergence was indeed higher when lineages evolved for a longer time period (all arboreal species: 114.9 mya, vs. Hylidae: 59.1 mya), we measured the magnitude of divergence as the sum of the variances of phylogenetic independent contrasts (PIC) of the four performance variables, unstandardized by branch lengths, for species within Hylidae and across all arboreal species. Given that PICs are differences between sister lineages, the variance of unstandardized PICs can be interpreted as a measure of divergence along the phylogeny (whereas PICs standardized by divergence time represent rate estimates; Garland, 1992; Harmon et al., 2021). We used the 1,000 simulated datasets under a BM model, as described above, to recalculate the variance of PIC on each sample, and then estimate 95% CI for the magnitude of divergence in performance. We then checked whether it overlapped between Hylidae and all arboreal species.

After verifying that performance variables were correlated at the interspecific level (see Results), we used a multivariate phylogenetic generalized least-squares (PGLS) regression to estimate the form–function relationships between species (Clavel & Morlon, 2020). We used all four performance variables as response variables and SVL, leg length, leg muscle mass, and foot area as the predictors in these regressions. We variance standardized the response variables. We also mean-centered and scaled the predictors to their standard deviations, in order to calculate standardized partial regression coefficients. These coefficients allowed us to compare the relative influence of each morphological variable on performance (Sokal & Rohlf, 1995). We ran the PGLS regressions with the package *mvMORPH* (version 1.1.9, Clavel et al., 2015) using the BM model, again choosing this model so as to estimate and account for intraspecific variance. We performed these analyses at two levels: within the family Hylidae (15 species) and across all species (43 species). These two levels allowed us to test whether form–function relationships within Hylidae were more similar to the ones found in *H. cinerea*, compared with relationships across all arboreal species. For all PGLS models, we estimated parameters using the penalized likelihood method, as it performs better when the number of traits approaches the number of taxa, as in Hylidae, but also performs well when the number of taxa is higher than number of traits (Clavel et al., 2019).

To quantify uncertainty in our estimates of the partial regression coefficients in the PGLS, we simulated the response variables 1,000 times using the MLEs of the fitted model's parameters (BM with error model; function "simulate()" in *mvMORPH*). We then reestimated the regression parameters with the standardized predictors in all 1,000 simulated datasets and calculated 95% confidence intervals for the regression coefficients in the same way as described above. Finally, to estimate how much variance was explained by the predictors in the multivariate PGLS, we regressed the observed response values on the predicted values (based on the fitted model) and extracted the R^2 values, following Chira et al. (2018).

We recognize that the estimation of intraspecific variance as a parameter in the *mvMORPH* "mvgls()" function, as we did here, may not be ideal for comparative analysis. That is, when intraspecific data are available, they can be used to directly estimate intraspecific error (Ives et al., 2007). For example, individual data could in principle be used in the "mvlgs()" function by adding individuals from the same species as zero-branch-length polytomies in the species tree. However, instead of exploring that option, we incorporated intraspecific data by performing form–function multivariate regressions using a recently developed method, the extended-PGLS (E-PGLS; Adams & Collyer, 2024). A strength of E-PGLS is to compare within-species patterns (e.g., allometry) across species while taking phylogenetic independence into account (Adams & Collyer, 2024). That said, we could not harness the full power of E-PGLS with our dataset, because—with the exception of *H. cinerea*—our within-species sampling was low for most species (one to seven individuals). Therefore, given the high sample size needed to accurately estimate variances (Wolter, 2007), the estimation of intraspecific variance for performance variables using E-PGLS may be unreliable in our case. Thus, we compare *mvMORPH* and E-PGLS results with caution. Details are given in Supplementary Material.

As a specific form–function hypothesis, we predicted that leg length would contribute more to both swimming and jumping compared to leg muscle mass (Moen, 2019; Nauwelaerts et al., 2005), given the importance of climbing for arboreal species in general and the negative effect that heavy muscle tissue can have on performance of this behavior. We also expected foot area to contribute to swimming but not necessarily jumping (Richards, 2010; Richards & Clemente, 2013).

Results

Repeatability of and correlations between performance variables in *H. cinerea*

Repeatability was higher for jumping performance (velocity: 0.49, acceleration: 0.36) than for swimming performance (velocity: 0.28, acceleration: 0.27), indicating substantial within-individual variation across high-performance trials for both behaviors (consistent with repeatabilities in other lab-measured behaviors; Bell et al., 2009). When accounting for within-individual variation to estimate performance correlations, we found positive correlations between jumping and swimming for velocity and acceleration, although only the correlation for velocity had a 95% CI that was mostly positive (Table 1, Figures S1–S3). The very wide 95% CI for the correlation for acceleration was related to the high variation of between-individual variance estimates for both swimming and jumping. We found similar results when analyzing only peak performance, in which only the correlation for velocity was significant (Table S1).

Relationships of hindlimb traits with jumping and swimming performance in *H. cinerea*

We found significant form–function relationships for only swimming performance across individuals of *H. cinerea* (Table 2). These results matched our expectation of a higher contribution of leg length to performance, but only for swimming and in the opposite direction. The partial regression coefficient for leg length was significantly negative for swimming velocity and of a higher absolute value than leg muscle mass for swimming acceleration (Table 2). Yet, foot area was not important for swimming performance, in contrast to our predictions. Results were very similar when using only peak individual performance and OLS multivariate regression (Table S2). The morphological predictors collectively explained 10% of the variance in peak swimming velocity and 17% of the variance in peak swimming acceleration.

Table 1. Variances and covariances for the four performance variables were obtained with the multivariate Bayesian regression model.

Variances	Between-ind	Within-ind
Swimming velocity	0.33 (0.14, 0.58)	0.66 (0.51, 0.83)
Jumping velocity	0.73 (0.33, 1.16)	0.48 (0.39, 0.59)
Swimming acceleration	0.21 (0.05, 0.40)	0.80 (0.63, 1.00)
Jumping acceleration	0.55 (0.34, 1.10)	0.56 (0.44, 0.70)
Jumping-swimming relationships	**Covariance**	**Correlation**
Velocity	*0.14* (−0.02, 0.38)	*0.60* (−0.04, 0.97)
Acceleration	0.05 (−0.08, 0.23)	0.29 (−0.66, 0.97)

Note. We used repeated measurements of peak swimming and jumping velocity and acceleration for individuals of *Hyla cinerea* across trials as the response variables. ID was modeled as a random factor nested within performance type (i.e., jumping or swimming), and thus covariances and correlations between jumping and swimming performance are only between individuals. The table shows the partition of variance in between-individual and within-individual variation, and their associated 95% credible intervals (95% CI). The between-individual covariances and correlations between jumping and swimming variables are shown at the end of the table. In italics are estimates of covariance or correlation whose 95% CI included negative values but whose negative bounds were close to zero.

Overall, whereas most *H. cinerea* individuals performed similarly for jumping (Figure 2A and C), they differed more distinctly in swimming performance (Figure 2B and D). The fastest swimmers tended to have more leg muscle mass and shorter leg lengths for their body size compared to slower swimmers (Figure 2B).

Interspecific performance correlations between jumping and swimming performance

We found positive significant correlations between jumping and swimming performance for both peak velocity and peak acceleration, at both levels of interspecific analyses—within the family Hylidae and across all arboreal species (including Hylidae; Table 3). Some correlations were also positive and significant between maximum velocity and acceleration within each behavior, especially when analyzing all arboreal species. Yet in these cases, values were lower than correlations within performance type (e.g., velocity) across behaviors.

Relationships of hindlimb traits with jumping and swimming performance across species

Contrasting with the intraspecific analysis, we found several significant relationships between hindlimb morphology and both jumping and swimming performance across all arboreal species (Table 4). More variation in peak velocity was explained by the hindlimb traits (58% for both jumping and swimming) than variation in peak acceleration (45% for jumping and 29% for swimming; Figure S4).

Table 2. Partial regression coefficients of the four performance variables regressed on SVL and hindlimb traits using the multivariate Bayesian model.

Swimming velocity	Mean (95% CI)	Eff. sample
SVL	**0.66 (0.11, 1.33)**	1,835
Leg length	**−0.99 (−1,72, −0.30)**	1,800
Leg muscle mass	0.23 (−0.13, 0.57)	1,800
Foot area	−0.02 (−0.44, 0.32)	1,800
Jumping velocity		
SVL	0.12 (−0.57, 0.82)	1,800
Leg length	−0.24 (−1.12, 0.55)	1,800
Leg muscle mass	0.22 (−0.24, 0.67)	1,800
Foot area	−0.04 (−0.57, 0.40)	1,800
Swimming acceleration	Mean (95% CI)	Eff. sample
SVL	0.31 (−0.28, 0.84)	1,728
Leg length	**−0.86 (−1.48, −0.15)**	1,800
Leg muscle mass	**0.45 (0.11, 0.79)**	1,800
Foot area	−0.08 (−0.45, 0.26)	1,800
Jumping acceleration		
SVL	−0.01 (−0.66, 0.66)	2,019
Leg length	−0.27 (−1.08, 0.49)	1,979
Leg muscle mass	0.04 (−0.40, 0.44)	1,511
Foot area	0.02 (−0.39, 0.49)	1,920

Note. The model is the same as the one we used to estimate components of variance shown in Table 1, with the addition of SVL and hindlimb traits as fixed predictors for each performance type. The table shows the posterior means for the regression slopes and their associated 95% credibility intervals (95% CI). We also include the effective sample sizes of the posterior distribution for each parameter. Values in bold exclude zero from their associated 95% CI. SVL = snout-to-vent length.

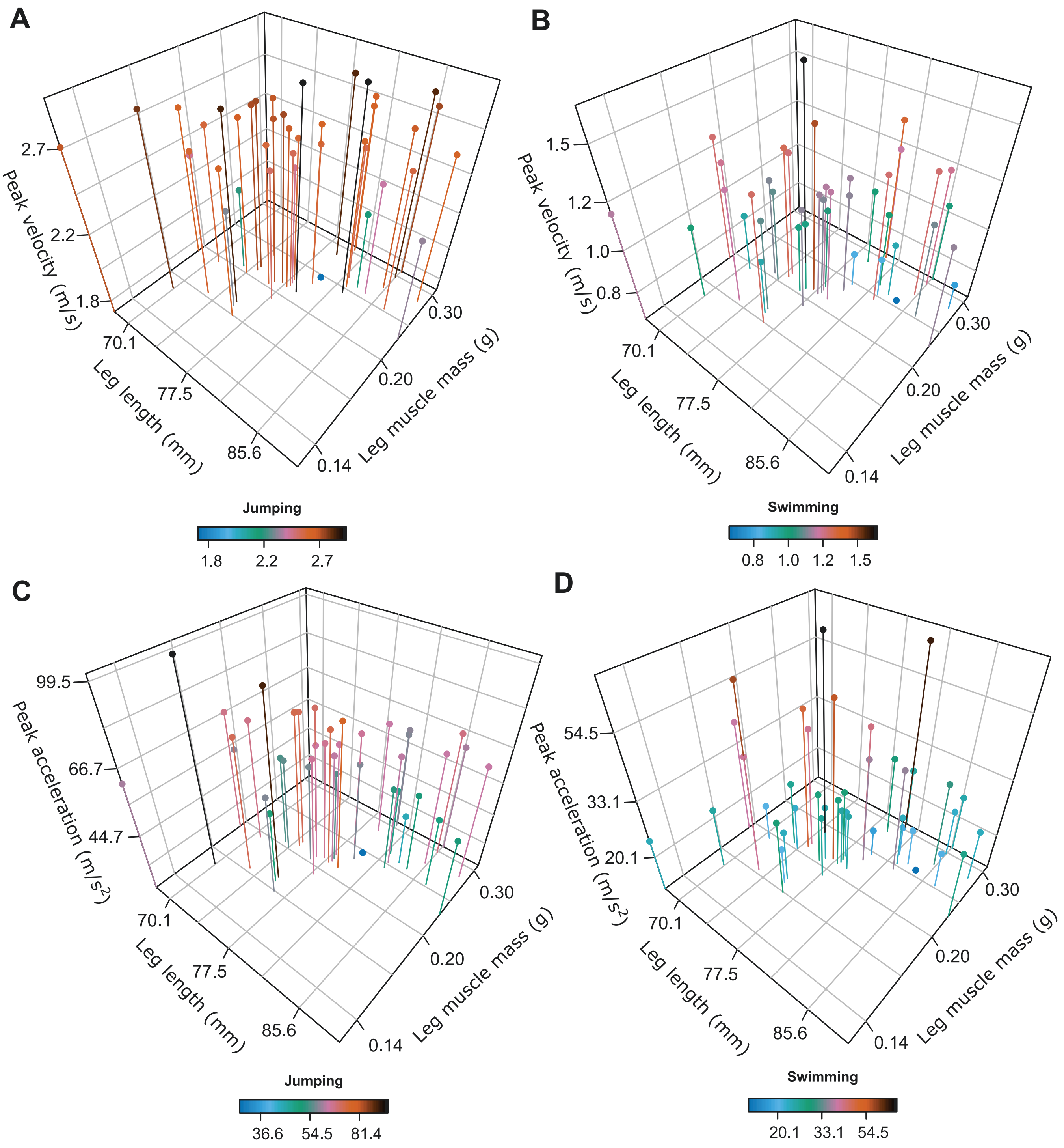

Figure 2. Relationships between locomotor performance and leg traits for *Hyla cinerea*. The 3D plots show the relationships of individual leg length and leg muscle mass with peak velocity (A and B) and peak acceleration (C and D), in jumping (A and C) and swimming (B and D). Note that analyses evaluated the effect of these variables while holding others (snout-to-vent length, foot area) constant. Moreover, the leg-length scale increases from upper left to lower right, whereas the leg muscle-mass scale increases from lower left to upper right. All axes are logged but presented in original units.

In accordance with both our specific predictions, leg length showed larger partial correlation coefficients than leg muscle mass for all four performance variables for all arboreal species. Moreover, foot area showed a positive significant coefficient only for peak swimming velocity, in analyses of all arboreal species (Table 4). Species that jump faster have longer legs for their size, and species that swim faster have longer legs and bigger foot areas (Figure 3). Likewise, species with higher peak jumping and swimming acceleration have longer legs, and also higher muscle mass for swimming acceleration only (Figure 4). However, when we restricted our analyses to the 15 hylid species, we found somewhat different results. In these analyses, leg muscle mass contributed more (than leg length) to swimming acceleration and to velocity in

Table 3. Interspecific correlation matrices of performance variables for all arboreal species or just within Hylidae.

	Jumping velocity	Jumping acceleration	Swimming velocity
All species			
Jumping acceleration	**0.44** (0.07, 0.70)		
Swimming velocity	**0.79** (0.61, 0.90)	0.14 (−0.23, 0.49)	
Swimming acceleration	**0.47** (0.09, 0.71)	**0.68** (0.43, 0.85)	**0.43** (0.06, 0.70)
Hylidae			
Jumping acceleration	0.52 (0.00, 0.82)		
Swimming velocity	**0.80** (0.51, 0.94)	**0.54** (0.07, 0.83)	
Swimming acceleration	0.34 (−0.16, 0.72)	**0.71** (0.32, 0.90)	**0.66** (0.25, 0.87)

Note. Performance correlations were estimated using species' average values of peak performance variables assuming a BM model. Values are maximum-likelihood estimates, with 95% confidence intervals (CI) in parentheses obtained by parametric bootstrapping. We considered estimates statistically significant (in bold) when their 95% CI did not include zero. BM = Brownian Motion.

Table 4. Partial regression coefficients of four performance variables on SVL and hindlimb traits for all arboreal species and for only hylid species.

Peak swimming velocity	All arboreal (*n* = 43)	Hylids (*n* = 15)
SVL	**−1.59** (−2.5, −0.68)	**−2.79** (−4.35, −1.35)
Leg length	**1.28** (0.25, 2.36)	**2.58** (0.81, 4.38)
Leg muscle mass	0.13 (−0.40, 0.66)	**2.21** (1.16, 3.28)
Foot area	**0.81** (0.18, 1.42)	−1.59 (−3.34, 0.17)
Peak jumping velocity		
SVL	**−1.97** (−2.96, −1.12)	**−2.34** (−3.94, −0.93)
Leg length	**2.20** (1.08, 3.28)	**2.86** (0.92, 4.82)
Leg muscle mass	0.51 (−0.04, 1.08)	**1.88** (0.74, 2.95)
Foot area	−0.15 (−0.82, 0.46)	−1.83 (−3.69, 0.01)
Peak swimming acceleration		
SVL	**−2.52** (−3.88, −1.21)	−1.80 (−3.70. 0.05)
Leg length	**1.42** (0.04, 2,90)	1.50 (−0.76, 3.74)
Leg muscle mass	**0.702** (−0.06, 1.45)	**2.05** (0.77, 3.30)
Foot area	0.223 (−0.60, 1.12)	−2.07 (−4.13, 0.13)
Peak jumping acceleration		
SVL	**−2.47** (−3.53, −1.42)	**−2.57** (−4.19, −1.07)
Leg length	**1.48** (0.30, 2.73)	**2.28** (0.34, 4.35)
Leg muscle mass	**0.84** (0.22, 1.49)	**1.81** (−.67, 2.93)
Foot area	−0.31 (−1.10, 0.41)	**−1.98** (−3.76, −0.03)

Note. We used multivariate PGLS to estimate parameters, assuming BM for the model residuals. We also variance-standardized the predictors. Table shows partial regression coefficients and their associated 95% confidence intervals (CI; lower and upper bounds), based on parametric bootstrapping. Estimates in bold were considered significant, as their 95% CI excluded zero. BM = Brownian Motion; PGLS = phylogenetic generalized least-squares; SVL = snout-to-vent length.

both jumping and swimming, and foot area was not relevant for swimming velocity but had a negative effect on jumping acceleration (Table 4). Nonetheless, at both levels of analyses (all arboreal and Hylidae), the directionality of effects—given by the signs of the partial regression coefficients—were mostly the same for the same traits when comparing jumping and swimming performance (Table 4).

When analyzing our data using E-PGLS, we found that only leg length positively influenced performance, for both all arboreal and Hylidae species (Table S4). This result partially agreed with the mvMORPH multivariate PGLS results described above. However, we suggest interpreting with caution the fewer significant effects of morphology on function with the E-PGLS. Previously developed but similar approaches (Adams, 2014; Adams & Collyer, 2018) exhibit lower statistical power than the penalized likelihood framework adopted in the multivariate PGLS in mvMORPH, particularly when among trait correlations are high (Clavel & Morlon, 2020). This reduced power, however, may depend on which inferential framework you use with E-PGLS (e.g., multivariate analysis of variance [MANOVA] statistics that account for trait covariances, which are only possible with many observations and few trait dimensions, may outperform analysis of variance [ANOVA] statistics that do not account for trait covariances). Moreover, our dataset had very few species with large intraspecific sample sizes. Thus, we expect that the intraspecific variances may be not well estimated with E-PGLS in our case and so we emphasize the mvMORPH PGLS results.

Magnitude of divergence in performance and similarity of form–function relationships within *H. cinerea* and across species

The magnitude of performance divergence was highly similar in hylid species (0.33, 95% CI = 0.16–0.53) and all arboreal species (0.30, 95% CI = 0.25–0.47), despite our expectation of higher total divergence across all arboreal species given the older age of their common ancestor. Regardless of potential differences in the amount of divergence, the partial regression coefficients found in both all arboreal species and within Hylidae do not match the pattern found in *H. cinerea*. The only trait that we found strongly related to swimming performance at all three scales was leg length. However, the effects of leg length were opposite within *H. cinerea* (Table 2) and across species (Table 4).

Discussion

Our results indicated a match between performance correlations at intra- and interspecific levels for peak velocity, such that individuals of *H. cinerea* and arboreal species that jumped faster also swam faster (Tables 1 and 3). In contrast, we found a mismatch of form–function relationships across these two levels (Tables 2 and 4). This overall pattern suggests different processes may shape locomotor performance across scales, even within the same microhabitat (arboreal) for which we expected similar selective pressures on form and function. Generally, the mapping of form to function is expected to be similar at different evolutionary levels (e.g., the same biomechanical principles apply at different levels; Emerson & Arnold, 1989). However, our finding of a mismatch across levels may indicate changes in interactions between traits and performance, resulting in changes in the performance and adaptive landscapes over evolutionary time (e.g., Martin, 2016). Below we elaborate on the patterns found at each level in more detail, and we finish by discussing how performance and fitness landscapes may differ within populations and across species.

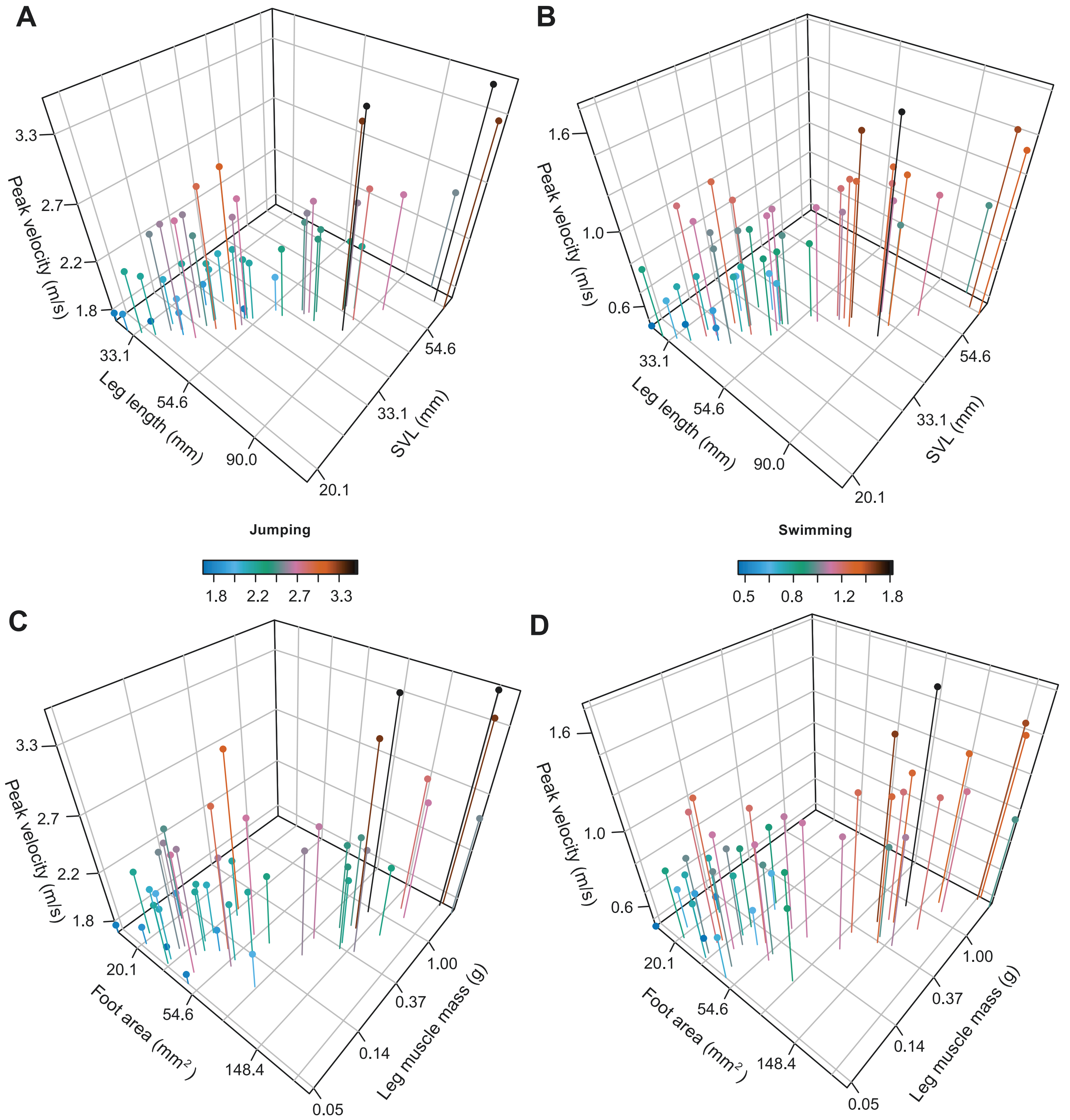

Figure 3. Relationships of locomotor velocity with snout-to-vent length (SVL) and leg traits for all arboreal species. The 3D plots show the relationships of species' mean morphological traits with peak jumping (A and C) and swimming (B and D) velocity. Leg length showed a higher contribution to explain variation in performance variables than leg muscle mass, and foot area was only relevant for swimming velocity (Table 4). Note that plots A and B show that bigger species had higher velocity, which contrasts with the negative coefficients shown in Table 4. Yet, this visual discrepancy only reflects the positive correlation between SVL and leg length, whereas partial regression coefficients estimate the effects of single variables while holding others constant.

Form–function relationships are weak within species and contrast the positive correlation between swimming and jumping velocity

Within species, the positive correlation for swimming and jumping velocity does not seem associated with similar effects of the same morphological traits on both behaviors (Figure 2). This may be partly due to the fact that the correlations themselves were not exceptionally high (Table 1), leaving room for different variables to drive performance in different behaviors. Moreover, the form–function relationships for *H. cinerea* individuals were weak in general, with variation in morphology explaining much less variation in performance than across species.

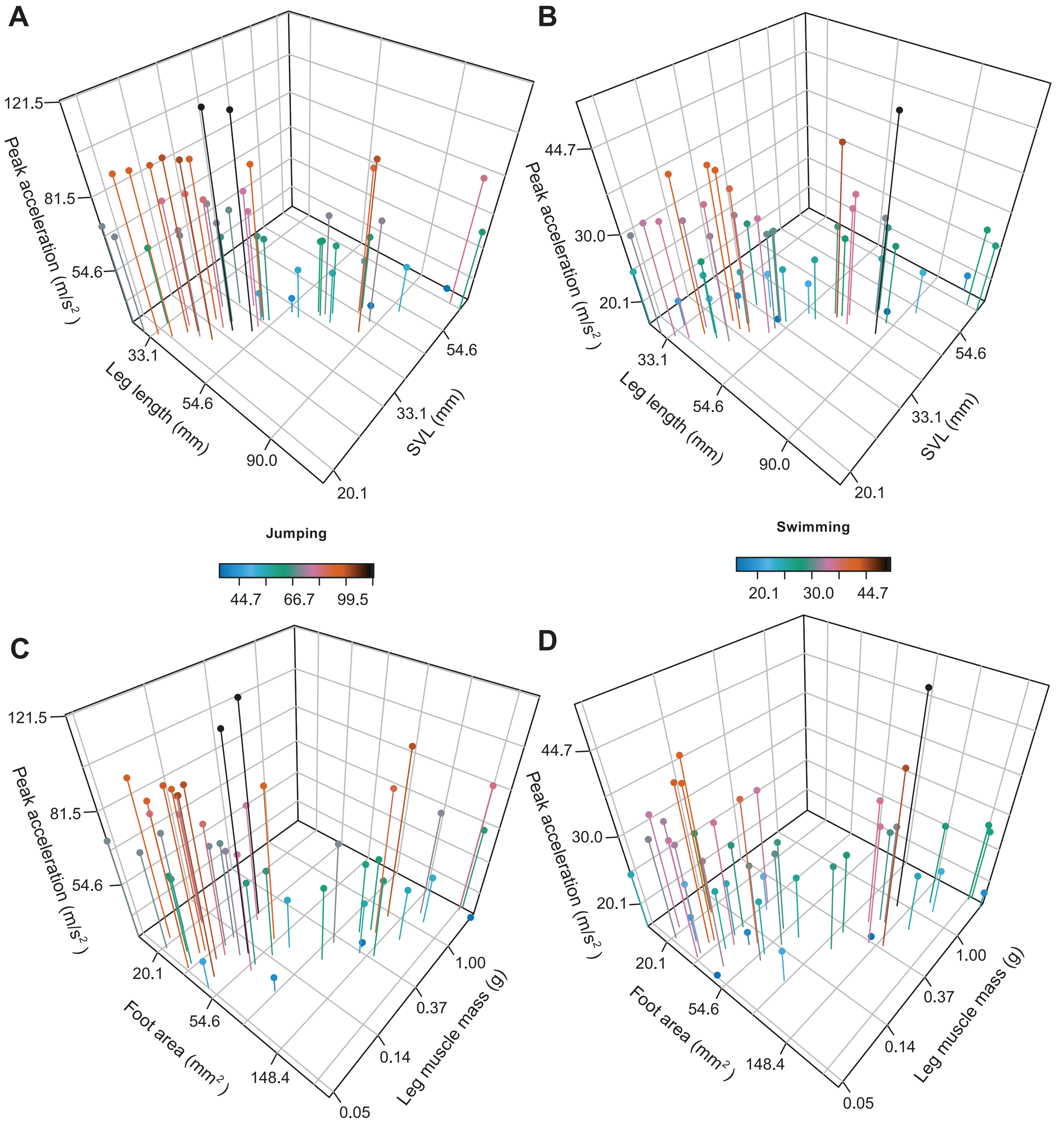

Figure 4. Relationships of locomotor acceleration with snout-to-vent length (SVL) and leg traits for all arboreal species. The 3D plots show the relationships of species' mean morphological traits with peak jumping (A and C) and swimming acceleration (B and D). Again, leg length explained more variation in performance variables than did leg muscle mass. Foot area was not relevant for any behavior. As in Figure 3, note that each panel here only shows the relationship between two morphological variables and performance, whereas the phylogenetic generalized least-squares model considered all four variables at once (Table 4).

In jumping performance, especially, most individuals performed similarly independent of morphological variation (Figure 2), indicating that many body forms within species attain a similar level of performance. We see two key reasons that may explain the invariance of jumping performance to morphology. First, this pattern suggests that the hindlimb traits may be on a performance ridge (Arnold, 2003; also see Whibley et al., 2006, for an example of a fitness ridge), in which variation in morphology can exist without consequences for jumping performance (Moen, 2019). Second, in contrast to a high role in fitness, jumping ability may not strongly contribute to individual fitness, at least in this population of *H. cinerea*.

On the other hand, individual differences in swimming ability may be under some selective pressure, given that we found a significant relationship between leg length and swimming performance. If we interpret performance gradients as part of the total selection on morphology (Arnold, 1983, 2003), this result suggests that swimming ability may explain some of the differences in individual fitness in *H. cinerea*. For instance, selection may be acting to increase swimming velocity by reducing frictional drag produced by longer legs, hence favoring shorter legs (Peters et al., 1996; Richards, 2010).

Yet, our analysis does not exclude the possibility that similar kinematics of both behaviors across individuals drives the positive correlation between swimming and jumping velocity, independent of differences in morphology (e.g., Peters et al., 1996; Kamel et al., 1996). For instance, step-cycle patterns in hopping and swimming are very similar, in that the limbs move in an asymmetrical gait pattern (i.e., forelimbs act together and hindlimbs also act together, but fore- and hindlimb movements are decoupled). Moreover, both behaviors include extended suspension (i.e., an extended period of time in the air for jumping and in the gliding phase for swimming; Peters et al., 1996). Overall, the way that morphology maps onto performance across different functions within species, and the ability of such form–function relationships (as opposed to kinematics) to produce performance correlations, has seldom been explored. However, such studies may provide insights into processes that shape intraspecific patterns (e.g., Holzman et al., 2022; Tan et al., 2024).

Form–function relationships are strong across species and congruent with the positive correlation between swimming and jumping performance

Contrasting with our intraspecific results, the effects of SVL and hindlimb traits were indeed similar on both jumping and swimming performance for all arboreal species and within Hylidae (Table 4). Moreover, variation in morphology explained a substantial amount of variation in performance (29%–58% across analyses and response variables). Combined, these results suggest a mechanical basis for the concerted evolution of both behaviors over evolutionary time. This mechanical basis may have its origin in shared biomechanical principles for different species underlying performance in jumping and swimming. It may have also resulted from similar selective pressures on both behaviors across a broader range of species, leading to stronger form–function relationships and similar effects of traits on performance in different behaviors (Arnold, 2023; Arnold et al., 2001; Felsenstein, 1988; Ghalambor et al., 2003). However, another important factor in the evolution of form–function relationships is the genetic correlations between traits, which may reflect functional and/or developmental constraints (Cheverud, 1984, 1996; Simon et al., 2025a; Simon & Moen, 2023; Walker, 2007). Constraints may be shaped by shared development, such as conserved growth patterns shaping the evolution of hindlimbs in frogs (e.g., Simon et al., 2025a). Selection may also constrain evolutionary trajectories to enhance functional performance if functional interactions between traits are relevant to mean fitness (Cheverud, 1984; Jones et al., 2004, 2007, 2014; Pavlicev et al., 2011). Hence, form–function relationships may play a stronger role in producing performance correlations at wider evolutionary scales than within species.

A positive evolutionary correlation between peak jumping and swimming velocity has been previously shown for a broader range of frog species that differ in microhabitat, with the simultaneous optimization of these behaviors achieved by enhancing either relative leg length or leg muscle mass (Moen, 2019; Moen et al., 2021a). The form–function relationships that we found indeed indicate that bigger muscle mass increases both swimming and jumping performance (especially acceleration), yet leg length showed a stronger influence on performance in these behaviors, especially when analyzing all arboreal species (Table 4). Given that more (heavy) muscle tissue would increase body mass, likely a disadvantage for species that climb, Moen (2019) suggested that increasing leg length (rather than muscle mass) could enhance jumping performance without disrupting climbing performance in arboreal species. By expanding the number of arboreal species in our analysis to 43 species, we showed here that this prediction holds across a broad diversity of arboreal species.

However, while generally consistent, the effects of morphology on performance differed somewhat for species in Hylidae. In particular, hylids showed stronger effects of leg muscle mass on swimming and jumping (Table 4). This result indicates that mechanical sensitivity can vary across different levels of evolutionary divergence, at least in terms of time, if not phenotypic diversity. Indeed, we expected more performance divergence to have accumulated for all arboreal species, which evolved for a longer time than hylids, but we found the same magnitude of performance divergence in both groups. This could be due to differences in evolutionary dynamics. If the main process producing divergence across nonhylid arboreal species has been an Ornstein–Uhlenbeck (OU) process, a strong pull toward the optimum can lead to less divergence across those species than across hylids if the divergence in the latter group was mostly driven by BM (Hansen, 1997). To test this possibility, we compared models of performance evolution, including a model that shifts from OU to BM with the emergence of Hylidae. However, we found strong support for a multivariate BM model driving performance evolution across all taxa (see Table S5). Regardless, divergence in mechanical sensitivity can be an important factor in determining functional diversity, given that traits with stronger effects on performance tend to evolve faster (Anderson & Patek, 2015; Holzman et al., 2012; Muñoz et al., 2017, 2018). However, differences across clades in mechanical sensitivity do not necessarily result in divergence in performance or in correlations among types of performance, as we have shown here.

Why do form–function relationships within species not match those across species?

A key finding of this study is that form–function relationships do not match between *H. cinerea* and across species within Hylidae or across all arboreal species. This suggests that the evolutionary processes acting on the mapping of morphology to performance within species differ from those acting across species. For instance, intraspecific competition for resources or mates, which depends on the frequencies of different individual phenotypes, is likely very important for shaping form–function relationships within populations. In contrast, functional constraints and trade-offs associated with different ecological niches may be more relevant to shaping differences across species in form–function relationships (Martin, 2016). Accordingly, the interspecific form–function relationships may have differed from intraspecific relationships because interspecific ecological variation is much higher than within populations of a single species. While we focused on arboreal species to reduce ecological variation, these species still vary in the substrates they inhabit, varying from tall grasses to shrubs to tree canopies (see Table S3). In other words, the coarseness of a single microhabitat term like "arboreal" may hide variation in selective pressures across species.

Therefore, such ecological variation may underlie variation in the relevance of some behaviors for fitness, such as swimming and/or jumping, relative to others, like climbing. Some arboreal species may not perform well in swimming but may show high performance in climbing (e.g., canopy specialists that breed outside of water; Herrel et al., 2013). In contrast, other arboreal species may swim well, especially if they breed in water, but do not climb very well. These differences in the relative importance of distinct behaviors for fitness across species may indicate different strengths of functional constraints (i.e., how much traits interact with each other to execute a function) and trade-offs (i.e., how much optimizing one function versus another influences fitness), which may drive variation in form–function relationships (Bergmann & McElroy, 2014; Garland et al., 2022; Ghalambor et al., 2003; Holzman et al., 2011; Wainwright, 2007; Walker, 2007). However, other interspecific factors beyond functional optimization may have also contributed to variation in form and function, such as phylogenetic constraints or other unmeasured factors (Hansen & Bartoszek, 2012; Polly et al., 2016; Simon & Moen, 2023). In particular, the evolution of trait correlations in frog hindlimbs seems driven by developmental constraints related to allometric growth that act as evolutionary lines of least resistance, channeling most divergence across species to size variation while also influencing the evolution of jumping performance (Simon et al., 2025a).

One potentially interesting consequence of changes in the strength of functional constraints and trade-offs over evolutionary time is that the variation in form–function relationships across species may result in traits that affect performance in one of the behaviors more strongly than in others (i.e., higher mechanical sensitivity). For instance, given that foot area only affects swimming velocity and not jumping velocity, swimming performance could be optimized by selection favoring larger foot areas, more so in species that breed in water, without having any effect on jumping velocity. While the relationship between mechanical sensitivity and rates of evolution has been explored to some degree (Anderson & Patek, 2015; Holzman et al., 2012; Muñoz et al., 2017, 2018), understanding why such differential sensitivity arises in the first place is less clear. We suggest that differences in the relative contributions of different functions to fitness across environments, resulting in changes in the relative strengths of functional constraints and trade-offs (Simon & Moen, 2023), may be an important driver of differential mechanical sensitivity at the macroevolutionary scale.

An important caveat of our study is that our intraspecific analyses considered individuals from only a single population. Such a sampling design makes interpretation of our results across scales more difficult. Ideally, one would study form–function relationships in multiple populations, given that the balance of selective forces on performance may change in different environmental conditions (Ghalambor et al., 2003) and therefore could reflect differences in environments across species. For example, Taverne et al. (2021) found a match of form–function relationships across 16 populations of 2 species of *Podarcis* lizards. In this case, the ecological differences in diet within species were also mirrored across species. Yet, the differences in diet were related to the differential availability of food on islands on which the lizards occur (Taverne et al., 2021). Given that the ecology of *H. cinerea* seems similar across its distributional range (Dodd, 2023), this scenario may be unlikely for our study system. Future work that analyzes multiple populations of *H. cinerea* would be able to address this issue.

Despite this caveat, most intraspecific studies on form–function relationships in frogs do not show strong effects of morphology on performance (but see Araspin et al., 2023), especially size and jumping (e.g., James et al., 2007; Wilson et al., 2000), which is also the case for hindlimb length and various jumping variables in anole lizards (Toro et al., 2003). An explanation for these weak form–function relationships found within populations is that performance may be under stabilizing selection, instead of directional selection. The latter seems more relevant for the evolution of average phenotypes for form and function at the macroevolutionary scale (e.g., Moen, 2019; Simon et al., 2025a). In the case of stabilizing selection, the relevant measure of such nonlinear selection would be performance surfaces and quadratic performance gradients using nonlinear regressions of form on function (Arnold, 2003). Yet, estimation of empirical performance surfaces is rarely done (but see Simon et al., 2019 for an example). Moreover, the sample sizes needed to properly estimate multiple quadratic gradients may be quite large (Simon et al., 2022), precluding an analysis of multivariate stabilizing selection on function across several species.

Conclusion

We conclude that a match of form–function relationships across evolutionary levels likely depends on the similarity of the contributions of each specific behavior to fitness within and between species, even if they belong to the same broad microhabitat category (i.e., arboreal). We found that the same traits can show different effects on jumping and swimming performance at different scales, differences that may have evolved because of changes in the strengths of functional constraints and trade-offs across a broader diversity of arboreal frogs. This change in the balance of selective forces over evolutionary time indicates that the dynamics of performance landscapes within populations may be quite different from the dynamics of a macroevolutionary performance landscape.

Supplementary material

Supplementary material is available online at *Evolution*.

Data availability

The data and code from this manuscript were deposited in Dryad Digital Repository (Simon et al., 2025b), https://doi.org/10.5061/dryad.sf7m0cghx; and Zenodo, https://doi.org/10.5281/zenodo.14933462.

Author contributions

M.N.S. and D.S.M. conceptualized the project. D.S.M. acquired funding. All authors collected data. M.N.S. led data analyses, coding, and writing of the manuscript, with input and revisions from D.S.M. All authors approved the final draft.

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Conflict of interest

The authors declare no conflict of interest.

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