Correlated evolution of microhabitat, morphology, and behavior in West Indian *Anolis* lizards: a test of the habitat matrix model

A.S. Harrison [a,*], **L.J. Revell** [b] **and J.B. Losos** [a]

[a] Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA 01238, USA

[b] University of Massachusetts — Boston, Boston, MA 02125, USA
[*] Corresponding author's e-mail address: xyz.harrison@gmail.com

Abstract

The habitat matrix model (HMM) explains convergence among arboreal animals as a result of the correlated evolution of morphology, locomotor mode, and habitat use. Although the HMM has generated important insights into the ecology of arboreal species, these tests have left a gap in the habitat-behavior-morphology story by focusing primarily on locomotor performance in lab and field experiments and thus failing to include data on locomotor behavior of undisturbed animals in the wild. We combined data on undisturbed locomotion, habitat use, and morphology for 31 species of arboreal lizard in the genus *Anolis* and used these data to test nine specific predictions arising from the HMM. We find strong support for nearly all aspects of this model. The addition of data on locomotion by undisturbed wild animals offers a more direct and compelling case for the HMM than most previous tests.

1. Introduction

Convergent evolution of species living in similar environments is strong evidence of evolutionary adaptation (Harvey & Pagel, 1991; Conway Morris, 2003; Losos, 2011). Arboreal species often evolve convergent locomotor morphologies, presumably because the structure of their habitat poses distinct challenges compared to locomotion on the ground. The habitat matrix

model (HMM) posits that the three-dimensional matrix of branches that comprise arboreal habitats place functional constraints on how organisms can move, leading to predictable differences among species in habitat use, locomotor behavior, and morphology (Moermond, 1979a, b; Pounds, 1988). A critical, but underappreciated, aspect of this model is that the predicted relationship between habitat and morphology depends on the locomotor mode (e.g., walking, jumping) that an animal utilizes. For example, the relationship between the width of a branch and the optimal length of an animal's limbs depends on how frequently it walks, runs, or jumps under normal conditions (Moermond, 1979a, b).

The HMM makes several specific predictions about the relationships between habitat, morphology and behavior (summarized in Table 1) based on functional arguments concerning the demands of specific locomotor modes and the conditions under which each mode is optimal (Moermond, 1979a, b; Pounds, 1988). The first type of prediction relates habitat to locomotor mode. For example, species using perches that are low to the ground and closely spaced will tend to jump among perches (Prediction 1), because jumping between perches provides greater mobility than running or walking along a single perch. The second type of prediction relates locomotor mode to morphology. For instance, species that jump frequently are predicted to have longer tails and shorter forelimbs to control pitch during jumping, combined with longer hindlimbs to propel their leaps (Prediction 2). The sum of the predicted relationship between habitat + behavior and behavior + morphology is a third type of prediction relating habitat to morphology. For example, combining the two predictions described above leads to a third prediction that species using low, dense perches will have longer tails and hindlimbs, and shorter forelimbs (Prediction 3), as a consequence of their frequent jumping.

The predictions of the HMM have proved to be a useful framework for prior studies of arboreal locomotion in a variety of taxa (e.g., primates: Crompton, 1984; birds: Moreno & Carrascal, 1993; possums: Schmitt & Lemelin, 2002; squirrels: Essner, 2007; and lizards: Vanhooydonck et al., 2000; Herrel et al., 2001; Kohlsdorf et al., 2001; Bickel & Losos, 2002; Goodman et al., 2008). By and large, however, these studies have not included data on locomotor behavior in nature. Rather, previous studies have primarily investigated the predictions of the HMM from two angles. First, the third type of prediction (habitat + morphology) has been supported by

Table 1.
Predictions of the habitat matrix model.

Prediction	Class of prediction	Result
Species that jump frequently		
1 Species using dense, low perches will jump more frequently than they walk or run	Habitat + behavior	Low perch height correlated with high jumping frequency in H + B canonical correlation 2 ($R = 0.41$, $p = 0.04$)
2 Species that jump relatively frequently will have longer tails and hindlimbs, and shorter forelimbs	Behavior + morphology	Frequent jumping correlated with short forelimbs and long tails in B + M canonical correlation 2 ($R = 0.64$, $p = 0.01$)
3 Species using low, dense perches will have longer tails and hindlimbs, and shorter forelimbs	Habitat + morphology	Low perch height not significantly correlated with short forelimbs and long tails in H + M canonical correlation 2, but predicted trend is present ($R = 0.47$, $p = 0.08$)
Species that walk frequently		
4 Species using narrow perches will walk more frequently than they run or jump	Habitat + behavior	Narrow perch diameter correlated with high walking frequency in H + B canonical correlation 1 ($R = 0.67$, $p = 0.001$)
5 Species that walk relatively frequently will have shorter limbs and tails and more lamellae	Behavior + morphology	High walking frequency correlated with short limbs and tail and more lamellae in B + M canonical correlation 1 ($R = 0.79$, $p < 0.001$)
6 Species using narrow perches will have shorter limbs and tails and more lamellae	Habitat + morphology	Narrow perch use correlated with short limbs and tails and more lamellae in H + M canonical correlation 1 ($R = 0.84$, $p < 0.001$)
Species that run frequently		
7 Species using broad perches will run more frequently than they walk or jump	Habitat + behavior	Broad perch use correlated with frequent running in B + H canonical correlation 1 ($R = 0.67$, $p = 0.001$)
8 Species that run relatively frequently will have long hindlimbs and forelimbs	Behavior + morphology	Frequent running correlated with long forelimbs in B + M canonical correlation 2 ($R = 0.64$, $p = 0.01$)
9 Species using broad perches will have long forelimbs and hindlimbs	Habitat + morphology	Broad perch use is significantly correlated with long limbs in H + B canonical correlation 1 ($R = 0.84$, $p < 0.001$)

a wide variety of correlational studies (e.g., Herrel et al., 2001; Bickel & Losos, 2002; Essner, 2007; Goodman et al., 2008). For instance, previous work on lizards has shown that habitat use is correlated with many aspects of the phenotype such as body size, limb dimensions, tail length, and movement rate, among others (Williams, 1972, 1983; Losos, 1990b, c, 2009; Losos et al., 1998; Beuttell & Losos, 1999; Butler et al., 2000; Butler & Losos, 2002; Harmon et al., 2005; Vanhooydonck et al., 2006).

A second group of studies has used biomechanics to test the functional relationships between morphology, perch type, and locomotor performance (Losos & Irschick, 1996; Irschick & Jayne, 1999; Mattingly & Jayne, 2004; Vanhooydonk et al., 2006; Goodman et al., 2008). For example, studies that have tested running performance in the lab have shown that limb length and running speed are correlated, but the advantage of long limbs is more pronounced on broad perches (Irschick & Losos, 1999). On narrow perches, long-limbed lizards are still somewhat faster, but are more likely to slip or stumble, leading to a loss of speed (Losos & Sinervo, 1989; Irschick & Losos, 1999). Furthermore, the maximal speeds of species measured in the lab were found to be good predictors of maximal speeds during simulated predator attacks in the wild (Irschick & Losos, 1998). Jumping ability is also correlated with limb length. Specifically, species with longer hindlimbs are capable of jumping farther (Losos, 1990d; Toro et al., 2006), although it appears that jumps of maximum length are rarely performed in the wild (Irschick & Losos, 1998).

While previous studies such as these provide indirect support for the HMM, the model has seldom been tested directly by incorporating data on the frequency of locomotor modes of undisturbed animals (but see Pounds, 1988; Losos, 1990a for exceptions). The predictions of the HMM depend on the link between locomotor mode and habitat and locomotor mode and morphology. In particular, six of the nine predictions of the model concern locomotor mode outright, while locomotor mode is implicit in the other three. In this sense, major portions of the HMM have been neglected by previous work.

In this study, we set out to test nine predictions of the HMM using the arboreal lizard genus *Anolis*, for which the model was originally developed (Moermond, 1979a, b; Pounds, 1988; Losos, 1990a). We combined newly available and previously published field data on locomotor behavior and microhabitat use with morphological measurements for 31 species of *Anolis*

from the Greater Antilles to look for correlations between sets of variables using a phylogenetically corrected canonical correlation analysis. We find the predictions of the HMM to be largely upheld, especially when locomotor behavior is incorporated.

2. Methods

We collected data on the morphology, habitat use, and locomotor mode of adult males from 31 species of *Anolis* lizard from the Greater Antilles (Table 2). We then used canonical correlation analysis (CCA) to look for the strongest correlations between sets of variables. Because species cannot be treated as independent data points, we performed our analyses with phylogenetic correction (pCCA, described in detail below). In total, we performed three canonical correlations: habitat variables vs. behavioral variables, behavioral variables vs. morphological variables, and habitat variables vs. morphological variables. We then examined the correlations that best relate these datasets to determine if they supported the predictions of the HMM.

2.1. Behavior, morphology and microhabitat use

We collected field data during summer months in 1987–1989 and in 1997. Undisturbed lizards were located for observation by slowly walking through the habitat. We observed lizards for up to 20 min (some lizards disappeared from view before the end of the observation session) and included only individuals watched for at least 5 min and which moved at least five times to exclude animals potentially disturbed by our presence. For each individual, we recorded the total number of movements, as well as the proportion of total movements that were classified as running, jumping, and walking. These numbers are summarized in Table 2. We then calculated species' means. For non-Cuban species we also measured perch height and diameter for all perches used during the observation. For the Cuban species adequate comparable perch data were not available, thus only the dimensions of the perch where the lizard was first spotted were used. Both the morphological and microhabitat variables measured in this study have been used extensively in prior ecological and evolutionary studies (e.g., Losos, 1990b; Johnson et al., 2008). Data for Jamaican and Puerto Rican species were previously published in Losos (1990a).

Prior to analyses, we transformed all variables to conform to the statistical expectations of the analysis. Running frequency was excluded (because

Table 2.
Species included in the analysis and their dominant locomotor frequencies.

Island	Species	Preferred locomotor mode		
		Walking	Running	Jumping
Cuba	*Anolis allogus*		46%	43%
	A. alutaceus	35%		56%
	A. angusticeps	66%		
	Chamaeleolis chamaeleonides	89%		
	A. homolechis	45%	44%	
	A. loysiana	52%	41%	
	A. luteogularis	72%		
	A. mestrei	45%		
	A. porcatus	59%		
	A. sagrei	49%	27%	
	A. vermiculatus	55%		
Hispaniola	*A. aliniger*	86%		
	A. brevirostris	96%		
	A. chlorocyanus	70%		
	A. christophei		83%	
	A. cybotes		57%	
	A. distichus		57%	
	A. insolitus	81%		
	A. olssoni		40%	38%
Jamaica	*A. garmani*	45%	45%	
	A. grahmi	31%	49%	
	A. lineatopus		57%	27%
	A. opalinus		70%	
	A. valencienni	72%		
Puerto Rico	*A. cristatellus*		58%	
	A. evermanni	53%	31%	
	A. gundlachi	34%	43%	
	A. krugi	50%		
	A. poncencis	44%	38%	
	A. pulchellus	61%		
	A. stratulus	35%	55%	

of non-independence among proportions summing to 1). Canonical variates that loaded negatively on both jumping and walking were inferred to reflect a high frequency of running for interpretation of the results. Jumping and walking frequency were arcsine square-root transformed (that is, we com-

puted the inverse sine of the square-root; a common transformation for relative frequency data). Because many morphological traits are highly correlated with size, we removed the effect of size (using snout-vent length (SVL) as a proxy for size) from all morphological variables by phylogenetically regressing each variable on SVL and then computing the residuals using the phyl_resid function in R (Revell, 2009). In brief, this function calculates the expected covariance among species assuming a particular phylogeny and model of the evolutionary process (in this case Brownian motion), and accounts for this covariance structure explicitly in a matrix regression. The slope and intercept derived from this procedure are used to calculate the residual value for each species. The details of this calculation can be found in Revell (2009).

2.2. *Evolutionary correlations among characters*

To investigate the relationship between morphology, microhabitat and locomotor behavior, we used canonical correlation analysis. Canonical correlation analysis is a statistical method in which two sets of orthogonal derived variables are calculated from two sets of original variables such that the correlations between corresponding derived variables are maximized. This method allows us to identify linear functions of each set of variables that have maximum correlation with other such sets (Miles & Ricklefs, 1984). The number of correlations generated by this method will be determined by the number of variables in the smaller variable set.

Canonical variables can be interpreted by calculating the correlations between each set of canonical scores and all original traits (Miles & Ricklefs, 1984). These canonical loadings (also called structure coefficients) are included because they can help make the canonical variables more readily interpretable in the original space. Within-set correlations describe the contribution of each trait to its canonical variable, whereas between-set correlations reveal the relation of each trait to the canonical variable in the other set (Miles & Ricklefs, 1984).

Like most standard statistical methods, an important assumption of canonical correlation analysis is that our data represent independent draws from a single underlying multivariate normal distribution. When observations are from species related by a phylogeny, this assumption is typically invalid because differing amounts of shared history among the species in the sample create non-zero expected covariances between the observations for differ-

ent species under most models for the evolutionary process (Felsenstein, 1985; Martins & Hansen, 1997). In the most common evolutionary process model for continuously distributed characters, Brownian motion, the statistical dependence amongst the observations at the tips of the tree is exactly proportional to the shared common history from the root to the common ancestor of the tips (Ives & Garland, 2000; Rohlf, 2001; Revell & Harmon, 2008; Revell, 2008). Under an assumption of Brownian motion, the statistical dependence of the observations from the tips can thusly be removed from the data matrices by explicitly accounting for the covariance matrix derived from the phylogenetic structure and evolutionary model, as in the phylogenetic regression described above (Rohlf, 2001; Revell & Harrison, 2008). The specific linear transformations used are provided in Revell & Harrison (2008) with specific reference to canonical correlation analysis.

This assumption of Brownian motion as evolutionary process can be relaxed somewhat by adding an additional parameter to our model for the covariances between species: λ, initially proposed by Pagel (1999). λ is a multiplier of the covariances between species, and we can identify the joint maximum likelihood estimate of λ that best fits the observations at the tips of the tree. Under this model, the expected covariance between any pair of species relative to their variances is not directly proportional to their common history (as in the typical Brownian motion model), but is a linear function of that history. The value of λ is estimated using maximum likelihood for all traits simultaneously following Freckleton et al. (2002). Since Brownian motion is a special case of the λ model (specifically, one in which $\lambda = 1.0$), we can fit both multivariate Brownian motion and multivariate λ and then pick the best fitting model using standard approaches, such as the likelihood-ratio test.

The behavioral variables that we included in the canonical correlation analysis include log-transformed total movement rate, and arcsine square-root transformed jumping and walking frequencies. Microhabitat variables included were perch height and diameter. Finally, the morphological variables included were SVL, relative lamella number, and the relative length of the forelimb, hindlimb, and tail. For this study, we obtained our point estimate of the phylogeny by subsampling the maximum likelihood tree of Nicholson et al. (2005) to include only the 31 species of this study.

We performed all canonical analyses using the maximum likelihood estimates (MLEs) for λ as well as by setting λ to 1.0, which corresponds to

a strict assumption of Brownian motion. While the results for both models were qualitatively similar, we only report the results for the MLE (λ) analysis because this model has Brownian motion as a special case and thus makes fewer assumptions about the nature of the evolutionary process by permitting covariances between species that deviate from those expected under Brownian evolution. We performed all analyses using the ape and phytools packages in R (Paradis et al., 2004; Revell, 2012; R Core Team, 2013).

3. Results

In all three comparisons (behavior vs. morphology, behavior vs. habitat and habitat vs. morphology) the first canonical correlation was significant (Table 3). For the comparisons of behavior vs. morphology and habitat vs. morphology, the second canonical correlation was also significant (Table 3). The correlations between the original characters and the canonical variates (i.e., the structure coefficients) are given in Table 4 (behavior vs. morphology), Table 5 (behavior vs. habitat), and Table 6 (habitat vs. morphology).

The results of the canonical correlation analyses strongly support seven of the predictions of the habitat matrix model (Tables 4–6). The remaining two

Table 3.

Summary of the phylogenetic canonical correlation analyses for the relationships between: (1) behavior and five morphological variables (morphological variables except SVL were size corrected using separate linear regressions on the phylogenetically transformed data); (2) behavior and two ecological (microhabitat) variables; and (3) morphology and the two microhabitat variables.

	Maximum likelihood λ	Canonical variables	Canonical correlation	Statistical tests		
				χ^2	df	p
Analysis 1: behavior and habitat	0.44	1	0.67	21.24	8	0.001
		2	0.41	4.97	3	0.04
Analysis 2: behavior and morphology	0.26	1	0.79	44.35	20	<0.001
		2	0.64	18.81	12	0.01
		3	0.43	5.18	6	0.08
Analysis 3: habitat and morphology	1.00	1	0.84	38.07	10	<0.001
		2	0.47	6.64	4	0.08

Table 4.
Correlations between behavioral and microhabitat variables, and the canonical variables from the phylogenetic canonical analysis of the microhabitat and behavioral variables.

Original variables	Canonical variables			
	Behavior		Habitat	
	CV$_1$	CV$_2$	CV$_1$	CV$_2$
Behavior variables				
Move rate	−0.04	−0.31	−0.02	−0.21
Walks	−0.98	−0.16	−0.65	−0.13
Jumps	−0.11	0.99	−0.05	0.46
Microhabitat variables				
Perch height	−0.32	−0.41	−0.42	−0.89
Perch diameter	0.52	−0.27	0.83	−0.60

predicted relationships were not supported by our data, although the trend was in the predicted direction.

Prediction 1: species using low perches will jump more frequently. The second canonical correlation between behavior and habitat supports this prediction ($R = 0.41$, $p = 0.04$; Table 3, Figure 1b). Behavior canonical

Table 5.
Correlations (sometimes also called 'structure coefficients') between morphological and behavioral variables, and the canonical variables from the phylogenetic canonical analysis of the behavioral and morphological variables.

Original variables	Canonical variables					
	Morphological			Behavioral		
	CV$_1$	CV$_2$	CV$_3$	CV$_1$	CV$_2$	CV$_3$
Morphological variables						
SVL	0.31	−0.33	0.27	0.26	−0.20	0.21
Lamellae	0.54	0.22	−0.66	0.46	−0.17	−0.25
Forelimb	−0.53	0.60	0.33	−0.44	0.39	0.18
Hindlimb	−0.75	0.03	−0.12	−0.59	0.01	0.02
Tail	−0.43	−0.37	−0.47	−0.29	−0.26	−0.16
Behavioral variables						
Move rate	0.48	0.39	−0.25	0.58	0.60	−0.54
Walk	0.70	−0.36	−0.01	0.86	−0.49	0.20
Jump	−0.30	−0.45	−0.24	−0.34	−0.71	−0.60

Table 6.

Correlations between morphological and microhabitat variables, and the canonical variables from the phylogenetic canonical analysis of the microhabitat and morphological variables.

Original variables	Canonical variables			
	Morphological		Habitat	
	CV_1	CV_2	CV_1	CV_2
Morphological variables				
SVL	0.21	−0.43	−0.04	−0.44
Lamellae	0.30	0.10	−0.03	−0.31
Forelimb	−0.81	−0.57	−0.70	−0.20
Hindlimb	−0.53	0.08	−0.41	−0.11
Tail	−0.15	0.69	−0.04	0.33
Microhabitat variables				
Perch height	0.21	−0.49	−0.08	−0.99
Perch diameter	−0.64	−0.44	−0.99	−0.33

variate 2 (CV_2) is correlated with jumping frequency and habitat CV_2 is negatively correlated with perch height (Table 4).

Prediction 2: species that jump frequently will have forelimbs that are short and longer tails and hindlimbs. The second canonical correlation between behavior and morphology supports this prediction ($R = 0.64$, $p = 0.01$; Table 3, Figure 2b). In this correlation, morphology CV_2 is correlated with forelimb length and negatively correlated with tail length, whereas behavior CV_2 is negatively correlated with jumping frequency and total movement rate (Table 5).

Prediction 3: species using low perches will have longer tails and hindlimbs and shorter forelimbs. Although the predicted trend is present in the second canonical correlation between habitat and morphology, this canonical correlation is non-significant thus this prediction is not statistically supported by our analyses ($R = 0.47$, $p = 0.08$; Table 3, Figure 3b).

Prediction 4: species that use narrow perches will walk more. The first canonical correlation between behavior and habitat supports this prediction ($R = 0.67$, $p = 0.001$; Table 3, Figure 1a). Behavior CV_1 is negatively correlated with walking rate, while habitat CV_1 is correlated with perch diameter (Table 4).

Prediction 5: species that walk frequently will have shorter limbs and more lamellae. The first canonical correlation in the comparison of behavior
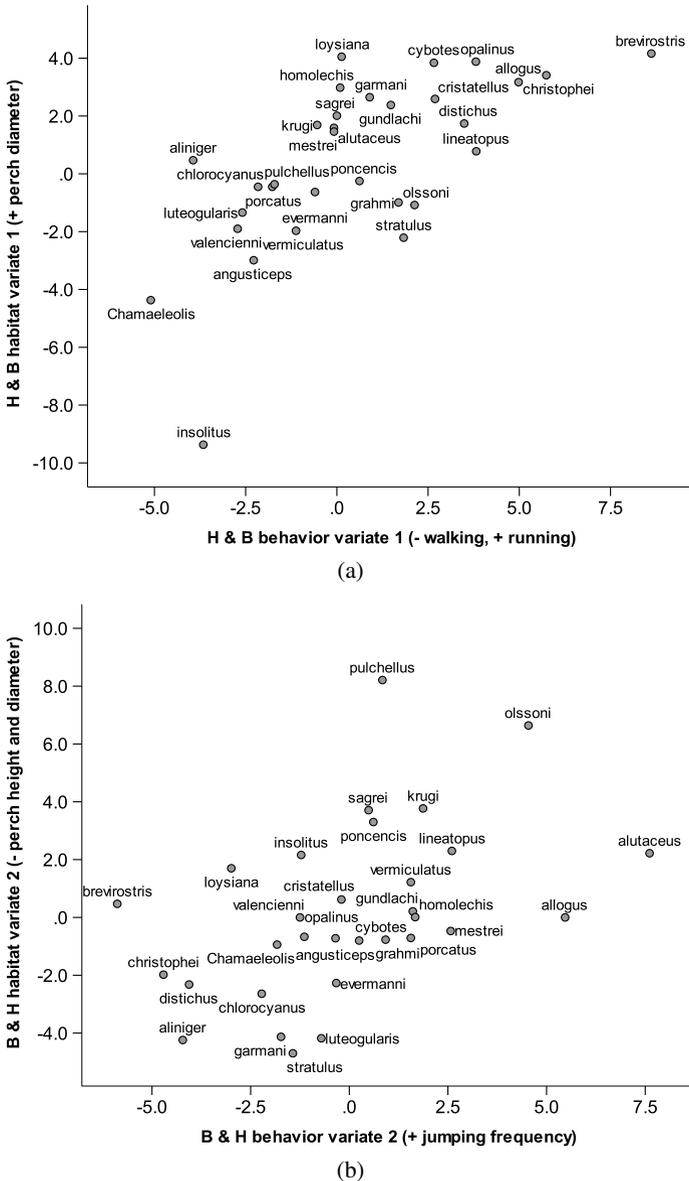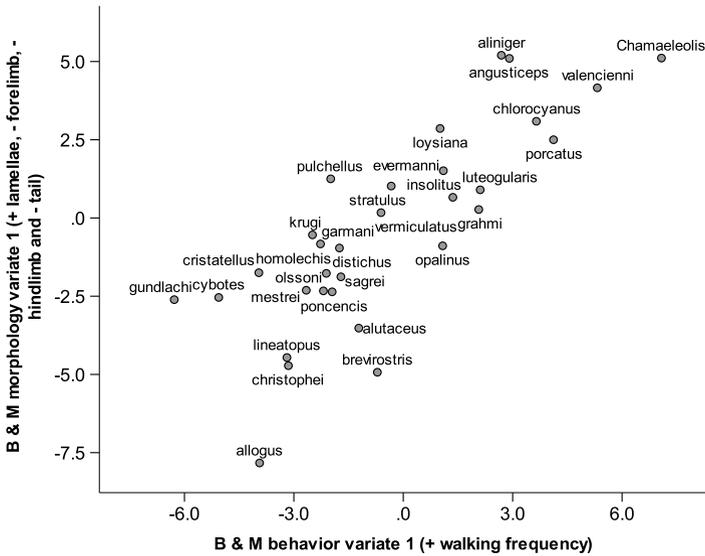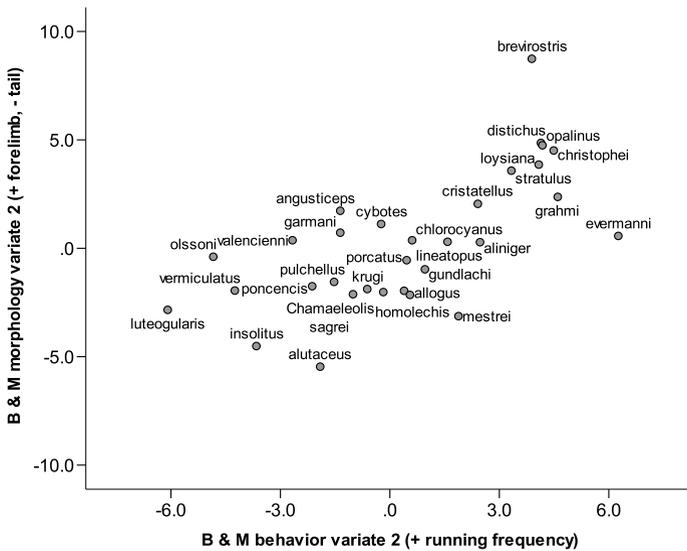
Figure 1. (a) In the first canonical correlation between habitat and behavior, species found on narrow perches tend to walk, as outlined in Prediction 4, while species found on broad perches tend to run (Prediction 7). (b) In the second canonical correlation between habitat and behavior, species living on dense, low perches, have a tendency to jump (Prediction 1).

Figure 2. (a) In the first canonical correlation between behavior and morphology, species that walk frequently have shorter forelimbs and hindlimbs, consistent with Prediction 5 of the HMM. Walking species also have more lamellae. (b) In the second canonical correlation between behavior and morphology, species that jump and move infrequently have shorter forelimbs and longer tails, consistent with Prediction 2.
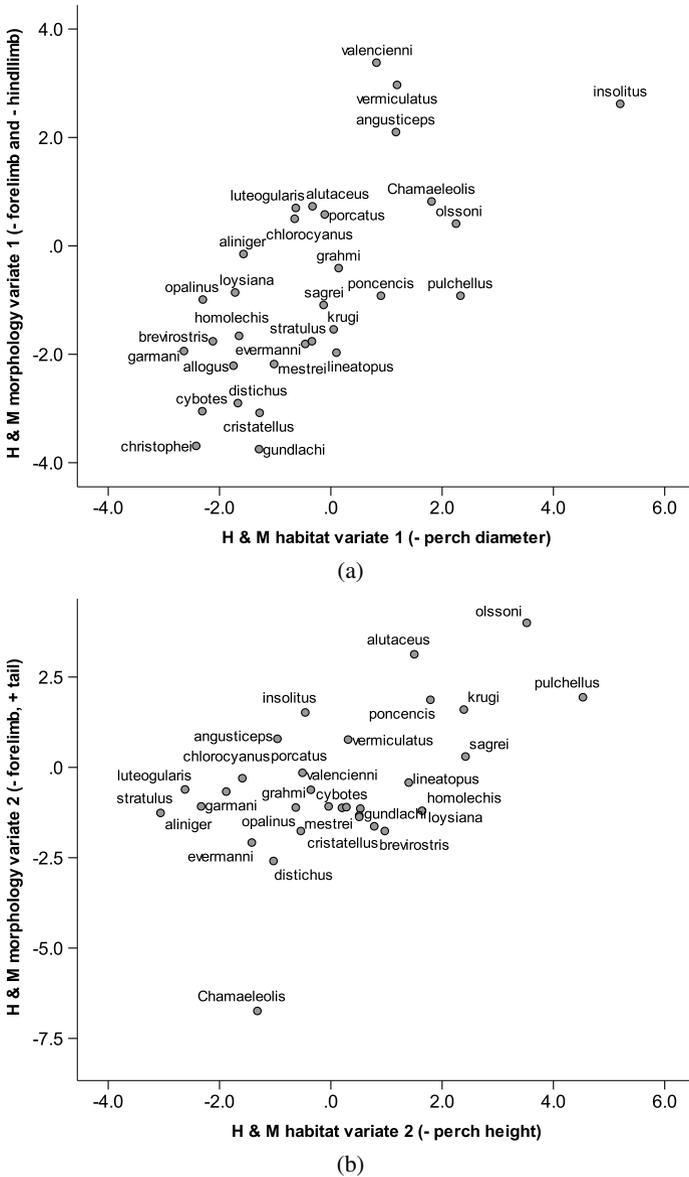
(a)

(b)

Figure 3. (a) In the first canonical correlation between habitat and morphology, species that use narrow perches have shorter limbs (Prediction 6). (b) In the second canonical correlation between habitat and morphology, species that use dense, low perches tend to have longer hindlimbs and tails (Prediction 3), although this relationship is not significant in our dataset. This is true whether the unusual *Anolis chamaeleolis* is included or excluded from the analysis.

and morphology supports this prediction ($R = 0.79$, $p < 0.001$; Table 3, Figure 2a). Specifically, the first canonical variate for behavior (CV_1) is correlated with frequent walking and a high overall movement rate, while CV_1 for morphology is correlated with shorter limbs and more lamellae (Table 5).

Prediction 6: species that use narrow perches will have shorter limbs. This prediction is supported by the first canonical correlation between habitat and morphology ($R = 0.84$, $p < 0.001$; Table 3, Figure 3a). Habitat CV_1 is negatively correlated with perch diameter, whereas morphology CV_1 is negatively correlated with limb length and positively correlated with SVL and lamellae number (Table 6).

Prediction 7: species that use broad perches will walk and jump less frequently and run more frequently. The first canonical correlation between behavior and habitat shows this relationship. CV_1 is correlated with running frequency, while habitat CV_1 is correlated with perch diameter ($R = 0.67$, $p = 0.001$; Table 3, Figure 1a).

Prediction 8: frequently running species will have long hindlimbs and forelimbs. This prediction is supported by the second canonical correlation between morphology and behavior ($R = 0.64$, $p = 0.01$). The second canonical variate for behavior is correlated with running, while the second canonical variate for morphology is correlated with longer forelimbs.

Prediction 9: species using broad perches will have longer forelimbs and hindlimbs. This prediction is suggested by the first canonical correlation between habitat and morphology ($R = 0.84$, $p < 0.001$; Figure 3a). The canonical variate correlated with perch diameter is habitat CV_1, and morphology CV_1 is positively correlated with both fore- and hindlimb length (Table 6).

4. Discussion

Caribbean anoles have become a textbook example of convergent evolution, largely because of the similarities in the locomotor morphology of distantly related species that occupy similar arboreal habitats (Futuyma, 1997; Losos, 2009). The habitat matrix model provides a mechanistic framework for predicting the evolution of these convergent locomotor phenotypes by linking morphology, function, behavior and habitat use (Moermond, 1979a, b; Pounds, 1988; Losos, 1990a). Initially proposed by Moermond (1979a, b)

and elaborated upon by Pounds (1988), the model makes nine testable predictions about the interrelationships of these variables. Our examination of these ideas, using by far the largest comparative behavioral data set yet amassed to examine these questions, confirms seven of the nine predictions of the HMM for anoles using field data on the frequency of different locomotor modes of 31 species. Correlations for the remaining two predictions were in the direction expected, though non-significant.

4.1. Species that jump

We find good support for a correlation between jumping frequently, long tails and short forelimbs, and the use of low perches (which are typically dense; Pounds, 1988). Specifically, there is a strong relationship between low perch use and increased jumping frequency (Prediction 1; Figure 1b) and between jumping and elongated tails plus shortened forelimbs (Prediction 2; Figure 2b); an indirect connection between perch height and limb and tail length is suggested by the data but was not found to be statistically significant (Prediction 3; Figure 3b).

Although our results indicate that perch height and diameter are related to jumping frequency and morphology, we did not find strong support for all of the predicted morphological variables. Tail and forelimb length were strongly related to locomotor mode and habitat, as expected, but hindlimb length was not strongly correlated with jumping. Tail length and forelimb length are both related to controlling pitch during jumping (Gillis et al., 2009; Legreneur et al., 2012), whereas hindlimb length is predicted to increase the overall length of the leap (Losos, 1990b). In previous correlational and functional studies, hindlimb length was found to be a strong predictor of jumping ability (Losos, 1990d; Toro et al., 2004). We are unaware, however, of any previous studies demonstrating a relationship between hindlimb length and jumping frequency. Although it seems reasonable to expect that species that jump frequently may also be capable of longer jumps, this is not necessarily true. It may be the case, at least for a portion of the species included in this study, that the average jump taken in nature is quite short. For example, anoles that live in grasses and shrubs jump frequently but the average gap between perches is small (Pounds, 1988; Losos, 1990c). In this case evolution may not favor especially long hindlimbs, because the ability to jump long distances is not necessary. Indeed, previous work has shown that the maximum jump distances recorded in the lab are almost never observed in

nature (Irschick & Losos, 1998). While we were not able to include data on jump length or perch spacing in this study, the correlation between jump length and jump frequency, and the differences in morphology that evolve as a consequence of each, would be an interesting avenue for future research.

4.2. Species that walk

We find strong support for the connection between frequency of walking, perch diameter, and limb length. Specifically, our data show a relationship between the use of narrow perches and frequent walking (Prediction 4; Figure 1a), frequent walking and the evolution of shorter limbs and increased toepad lamellae (Prediction 5; Figure 2a) and narrow perches and shorter limbs (Prediction 6; Figure 3a). Previous studies have revealed a tradeoff between short legs providing greater 'surefootedness' on narrow surfaces versus longer limbs providing enhanced sprinting and jumping capabilities on broader surfaces (Losos & Sinervo, 1989; Losos & Irschick, 1996; Irschick & Losos, 1998; Spezzano & Jayne, 2004). Likewise, previous correlational studies have found that species found on narrow perches tend to have shorter limbs (Mayer, 1989; Losos, 1990a, b). Taken together, our results and previous work support the prediction that slower but more surefooted walking locomotion is favored over running or jumping on narrow perches.

4.3. Species that run

In species that use broad perches, the HMM predicts running will be favored, as will longer limbs. Our data show running species tend to use broad perches (Prediction 7, Figure 1a). We also found that species that frequently use broad perches have longer limbs (Prediction 8, Figure 3a). Finally, although, the predicted relationship between running and longer limbs (Prediction 9) is suggested by these data, this trend was not statistically significant. The relative weakness of the relationship may reflect the relaxed constraints on locomotion on broad surfaces. Species using narrow perches may be constrained to walking, while species on broader perches can either walk, run, or jump depending on other aspects of habitat such as perch density (Pounds, 1988). The addition of more species to this analysis may help to clarify if the lack of support that we found for the predicted relationship in this case is more likely to be a consequence of the true lack of a relationship or other factors.

4.4. Concluding thoughts

Moermond's framework for understanding the evolution of arboreal loco-
motion (Moermond, 1979a, b) has proven useful to biologists working with
arboreal tetrapods ranging from birds to primates (see Introduction), yet it
could potentially be usefully applied to a much broader group. Many species
are faced with the challenge of moving through a three-dimensional matrix
of vegetation, including some that would not be traditionally defined as ar-
boreal (Moffett, 2000). The idea of the 'canopy' in biology has been applied
somewhat exclusively to the upper reaches of trees, yet the structure of a for-
est canopy poses challenges to locomotion that are similar to those imposed
by many other habitats (Moffett, 2001). For example, for an insect or small
mammal, a prairie is composed of a matrix of grasses that may or may not
bear weight. For animals that live in the leaf litter, movement through the
habitat may be dominated by dead branches. In aquatic habitats, the archi-
tecture of macroalgae are strongly reminiscent of forests. The habitat matrix
model may be a useful way to study the locomotion of insects in grasslands,
small mammals in desert scrub, amphibians in the leaf litter, crustaceans
in kelp, as well as animal locomotion in a range of other situations. While
the biomechanical constraints that shape locomotion in arthropods or other
animals that function very differently from lizards may mean that the rela-
tionships among morphology, locomotion, and habitat are shifted in these
groups, the HMM would provide a useful starting point for future studies of
locomotion through a matrix of vegetation.

However, to give the HMM the broadest possible applicability, it may be
necessary to extend or refine the predictions of the model to make them more
general. Further, although the HMM is based on biomechanical principles, it
could be useful to elucidate the biomechanical mechanisms underlying each
prediction of the model in more detail. Finally, only empirical data from
diverse taxa will be able to establish whether the HMM is broadly useful as
an approach for the study of locomotor evolution or if it is best used in the
narrow slice of taxa for which it has proven useful in the past.

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