Movement correlates of lizards’ dorsal pigmentation patterns

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Summary

1. Understanding the ecological function of an animal’s pigmentation pattern is an intriguing research challenge. We used quantitative information on lizard foraging behaviour to search for movement correlates of patterns across taxa.

2. We hypothesized that noticeable longitudinal stripes that enhance escape by motion dazzle are advantageous for mobile foragers that are highly detectable against the stationary background. Cryptic pigmentation patterns are beneficial for less-mobile foragers that rely on camouflage to reduce predation.

3. Using an extensive literature survey and phylogenetically controlled analyses, we found that striped lizards were substantially more mobile than lizards with cryptic patterns. The percentage of time spent moving was the major behavioural index responsible for this difference.

4. We provide empirical support for the hypothesized association between lizard dorsal pigmentation patterns and foraging behaviour. Our simple yet comprehensive explanation may be relevant to many other taxa that present variation in body pigmentation patterns.

Key-words: antipredator behaviour, camouflage, cryptic coloration, disruptive patterns, foraging behaviour, longitudinal stripes, motion dazzle, movement detection, pigmentation patterns, predation

Introduction

Animal body pigmentation patterns are remarkably diverse and include longitudinal stripes, reticulation, spots, cross bars and blotches. In spite of numerous attempts to explain this diversity (e.g. Cott 1940; Jackson, Iii & Campbell 1976; Caro 2009), the ecological function of pigmentation patterns remains an intriguing research challenge (Kelley & Kelley 2014). We took advantage of the recent upsurge in published information about lizard foraging behaviour to search for movement correlates of pigmentation patterns across taxa.

It has been suggested that dorsal pigmentation patterns interact with movement behaviour to reduce animal vulnerability to predation (Jackson, Iii & Campbell 1976; Stevens et al. 2011). Cryptic body patterns (sensu Stevens & Merilaita 2009) that blend with the natural background (e.g. reticulation, spots, blotches, uniform) may benefit stationary prey by reducing the probability of detection by predators. Yet, these patterns are no longer advantageous when the prey moves (Cott 1940; Thayer 1909). Motion-sensitive visual circuits of a stationary predator can instantly detect movement against a stationary background, regardless of the prey’s dorsal pattern (Stevens et al. 2011; Hall et al. 2013). Conversely, longitudinal stripes that can be considered conspicuous in many environments may be beneficial when the prey moves (e.g. Jackson, Iii & Campbell 1976; Brodie 1992; Allen et al. 2013). This is because longitudinal stripes may deceive the predator’s motion perception creating a motion dazzle that hampers its ability to intercept a moving prey (Jackson, Iii & Campbell 1976; Brodie 1992; Allen et al. 2013; Kelley & Kelley 2014; Rojas, Devillechabrolle & Endler 2014; Hämäläinen et al. 2015; but see Hughes, Magor-Elliott & Stevens 2015; von Helversen, Schoöler & Czienskowski 2013).

Consequently, low mobility species are predicted to have cryptic patterns that decrease their probability of being detected, and highly detectable mobile species should have longitudinal striped pattern to increase their chances of
escaping inevitable predator attacks. We further predicted that an intermediately active prey should benefit from mixed patterns that include longitudinal stripes and motifs of cryptic patterns. Mixed patterns might be less detectable than stripes when stationary and more efficient in generating motion dazzle than cryptic patterns when the prey moves.

Several studies have found association between pigmentation patterns and movement behaviour (Lizards: Carrereto & Vasconcelos 2006; Hawlena et al. 2006; Hawlena 2009; Snakes: Brodie 1992; Frogs: Rojas, DeVillechabrolle & Endler 2014; but see Creer 2005; Ortega, López & Martín 2014); yet only few studies have used a comparative approach to search for this association across species. Jackson, Iii & Campbell (1976) found an association between defence behaviour and dorsal patterns, using qualitative scoring of snake escape behaviour that was based on expert opinions. Allen et al. (2013) essentially used a similar qualitative approach but applied modern statistical techniques to account for phylogenetic non-independence. They too found an association between aspects of defence and foraging behaviours and the snake’s pigmentation patterns.

Using broad behavioural categories that are based on expert opinions is unavoidable when rigorous quantitative data do not exist; yet this approach impairs detailed hypothesis testing. For example, it requires splitting continuous variables (e.g. time spent moving or sprint speed) into subjective groups and prevents exploration of complex behavioural interdependencies using coarse behavioural approximations. Fortunately, since the classic study of Jackson, Iii & Campbell (1976), detailed quantitative measurements of lizard movement behaviour have become routine (Perry 2007). This wealth of quantitative behavioural data provides an excellent opportunity to advance our understanding of the possible links between mobility and pigmentation patterns.

Lizards spend much of their active time foraging. Thus, movement characteristics of lizard foraging behaviour may determine their detectability to predators. Lizard foraging behaviour is commonly characterized by two continuous indices: the percentage of the foraging time spent moving (PTM) and the number of movements per minute (MPM). Using both indices complementarily produces a quantitative depiction of the forager’s movement patterns (Butler 2005). Lizards with high PTM and low MPM move continuously in search for food (‘widely foragers’), lizards with low PTM and low MPM are sit-and-wait foragers and lizards with moderate PTM and relatively high MPM move frequently between ambush sites (‘stop-and-go’) or combine elements of the two distinct foraging strategies. We assume that high PTM and high MPM make lizards more detectable by visual predators (Fig. 1).

Other movement correlates of lizard foraging behaviour for which quantitative data is readily available are foraging speed and maximal sprint speed. Cooper (2007) has suggested that widely foraging lizards continually search for prey using a slower foraging speed to maximize searching efficiency. Ambush foragers, however, must use bursts of high speed to intercept moving prey. Huey et al. (1984) found that maximal sprint speed is associated with foraging behaviour in a few Kalahari lizards. Later, a more comprehensive study suggested that these relationships are more complicated, probably because maximal sprint speed is also influenced by the lizard’s escape strategy (Miles, Losos & Irschick 2007).

We meticulously collected published information on lizard dorsal patterns, body length, foraging indices, foraging speed and maximal sprint speed. Using phylogenetically controlled analyses, we tested the following predictions (Fig. 1): (i) striped lizards have high PTM, relatively high MPM and slow foraging speed; (ii) lizards with cryptic patterns have low PTM, low MPM and high foraging speed; (iii) lizards with mixed patterns of stripes and cryptic motifs have intermediate PTM, MPM and foraging speed. In addition, we explored the association between pigmentation and maximal sprint speed with no a priori predictions.

**Materials and methods**

**DATA COLLECTION AND CATEGORIZATION**

We conducted an extensive literature survey to collect numerical data regarding lizard movement indices including: PTM, MPM, foraging speed and maximal sprint speed. Foraging speed, also known as ‘moving speed’, is the speed measured while lizards forage in the field (Cooper 2007). Therefore, this index is clearly indicative of lizard foraging behaviour. Unfortunately, only a small number of studies have reported foraging speed in lizards.
Maximal sprint speed (i.e. the highest speed recorded during
escape bursts in the laboratory) is a more common movement
index in lizards; yet its validity as a foraging index requires further
confirmation (Miles, Losos & Irschick 2007). To test whether
maximal sprint speed can be used as a foraging index, we explored
the association between the two speed indices.

We used the average PTM, MPM, foraging speed and maximal
sprint speed as quantitative indices of lizard movement behaviour.
If more than one study examined the same species, we used the
results that were based on a bigger sample size and longer focal
observations. When index averages were not reported in the origi-
nal study, we used the value of a single measurement or the
reported maximal values. We assumed that all measurements
related to adult individuals. Data explicitly related to juveniles
were excluded from our data set.

We assigned a pigmentation pattern and a numerical value of
snout-vent length (SVL) to each species using published descrip-
tions. We collected this information from scientific books, field
guides and scientific papers. When this information was not avail-
able, we described the dorsal pigmentation ourselves based on
multiple pictures from books or papers. We defined the dorsal pig-
mentation pattern as the lizard’s mid-dorsal markings (markings
of the flanks and tail were not recorded). All patterns were divided
into three major categories: stripes, cryptic and mixed (Fig. 2).
The striped category includes only patterns of plain longitudinal
stripes; the cryptic category includes all unstriped patterns such as
uniform, reticulation, patches, spots, dots and cross bars; the
mixed category includes patterns of longitudinal stripes with cryp-
tic motifs in between.

Basing our pattern categorization mostly on existing expert
descriptions is advantageous since it minimizes identification mis-
takes and avoids using non-representative morphs as our refer-
ences. This conservative approach is credible for our specific
purposes because of the coarse classification that we used, in that
we have assigned lizards to pattern categories based on whether or
not they have longitudinal stripes and whether the longitudinal
striped pattern is pure or includes elements of cryptic patterns.

We excluded information from Gekkonidae and Chamaeleoni-
dae species due to their nocturnal activity and ability to change
body patterning, respectively. We also excluded from all analyses
61 species that exhibit polymorphism or sexual dimorphism, and 6
species for which pattern information was not available. After
removing those species, our data included 219 species from 17
families.

During data exploration, we noticed large variations in the
quantification of behavioural indices. Different researchers used
different measurement techniques and various sample sizes, took
measurements at different times of the day or at different seasons
and had various measurement durations. Such inconsistencies
added noise to our analyses (Butler 2005; Perry 2007) and turned
our results to a conservative depiction of the associations between
foraging behaviour and pigmentation patterns.

**Statistical Analysis**

Our general approach was to first explore whether lizards with dif-
ferent pigmentation patterns differ in their overall foraging beha-
uour as described by the combination of all quantitative
variables. Following that, we searched for a functional explana-
tion by testing our predictions using smaller numbers of explana-
tory variables each time. To correct for phylogenetic non-
independence, we repeated the analyses that revealed significant
differences using phylogenetically controlled tests (Felsenstein
1985).

In spite of large efforts to assign the four movement indices to
every species on the list, there were many missing values. Thus, as
the number of variables included in an analysis increased, the
effective sample size substantially decreased. We failed to deter-
mine the exact phylogenetic position of some of the species for
which behavioural information was available. This difficulty led to
even smaller sample sizes in the phylogenetic analyses. Conse-
quently, we conducted each analysis on a different subset of spe-
cies that included the largest sample size possible.

The first step was to establish the validity of maximal sprint
speed as a foraging index by testing its correlation to foraging
speed using Pearson correlation tests. We then performed princi-
pal component analysis (PCA) to test whether lizard pigmen-
tation-pattern categories were discernible based on the movement
variables PTM, MPM and foraging speed, and we tested for sig-
nificant differences between categories using MANOVA. We tested
for differences between pigmentation-pattern categories based on
single movement indices (PTM or MPM) using ANOVA along with
Tukey HSD post hoc tests. We used ANCOVA to correct for the

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**Fig. 2.** Body pigmentation-pattern cate-
gories. (a) stripes; (b) cryptic: uniform,
dots, spots, patches, reticulation and cross-
bars; (c) mixed. The individual patterns
within each category depict a large varia-
tion of patterns.

lizard’s SVL when testing for differences based on foraging speed and maximal sprint speed. Tukey HSD post hoc tests for ANOVA were conducted using the \texttt{r} package \texttt{multcomp} (Harmon et al. 2008).

We used phylogenetically corrected analyses to test whether the significant differences between groups hold after precluding the effect of phylogenetic relatedness among species (Garland Jr. et al. 1993). Phylogenetic ANOVA and MANOVA tests were conducted using the function \texttt{aov.phylo} in the \texttt{Geiger} package in \texttt{r} (Harmon et al. 2008). We added slight modifications to this function to conduct phylogenetic ANCOVA. Phylogenetic Hochberg post hoc tests were conducted using the function \texttt{phylANOVA} in the package \texttt{phytools} in \texttt{r} (Revell 2012). We assumed a Brownian motion model of evolution. All simulations included branch length information.

The scaled phylogenetic tree used in the simulations of the phylogenetic corrected analyses was adopted from Pyron, Burbrik & Wiens (2013). This generally well-supported phylogenetic estimate for squamates (i.e. 70% of nodes have Shimodaira–Hasegawa-like values >85) is based on molecular data and included up to seven nuclear genes and five mitochondrial genes. We altered the tree according to the sample of each analysis so it would contain only the examined species, and the species not included in our data base were removed from the tree.

**Results**

Sprint speeds were about 10-fold faster than foraging speeds (sprint speeds: 2.36 m/s ± 0.17; foraging speeds: 0.24 m/s ± 0.03, Fig. S1). We found no correlation between foraging and sprint speeds (Pearson correlation test: \( r = 0.18, P = 0.29, n = 37 \)). We therefore did not consider it a valid index for foraging behaviour. PCA revealed that lizards with striped and cryptic patterns are discernible based on their overall foraging behaviour (Fig. 3, \( n = 47 \)). Interestingly, lizards with mixed patterns mostly fell inside the two other pattern groups. *Ameiva exsul* was the only outlier, being the sole cryptic-patterned species that fell inside the striped-pattern cluster. The separation between the cryptic and the striped patterns was mostly captured by the first principal component, which accounts for 62.7% of the total variability, and has a major loading contribution from PTM (Table 1).

Table 1. Loading of the first two principal components ± SD (MPM, movement per minutes; PTM, percentage time spent moving; FS, foraging speed; SVL, snout-vent length)

<table>
<thead>
<tr>
<th>PC1</th>
<th>PC2</th>
<th>FS</th>
<th>SVL</th>
</tr>
</thead>
<tbody>
<tr>
<td>MPM</td>
<td>PTM</td>
<td>FS</td>
<td>SVL</td>
</tr>
<tr>
<td>0.48 ± 0.07</td>
<td>-0.77 ± 0.05</td>
<td>-0.43 ± 0.09</td>
<td>0.02 ± 0.07</td>
</tr>
<tr>
<td>-0.17 ± 0.43</td>
<td>-0.33 ± 0.27</td>
<td>-0.83 ± 0.09</td>
<td>-0.44 ± 0.17</td>
</tr>
</tbody>
</table>

and MPM were positively associated with PC1, whereas foraging speed was negatively associated with it. Thus, species with cryptic patterns are less active and use faster foraging speed than species with stripes. While MPM and foraging speed also have significant contributions to this principal component, the contribution of SVL to the separation of the pigmentation patterns is negligible (Table 1).

\texttt{MANOVA} revealed that foraging behaviour varied between species with different dorsal patterns (\( F = 6.8 \ d.f. = 2, P < 0.001, n = 49 \); PTM: \( F = 45.95, P < 0.001 \); MPM: \( F = 13.16, P < 0.001 \); foraging speed: \( F = 2.9, P = 0.06 \)). The result held after controlling for phylogenetic non-independence (\texttt{phylogenetic MANOVA}: \( P < 0.001, n = 47 \); PTM \( P < 0.001 \); MPM \( P = 0.015 \); foraging speed \( P = 0.46 \)).

The lizard foraging mode on its own, that is the measured PTM and MPM values, differed according to the dorsal patterns (Fig. 4) (\( F = 10.90, d.f. = 2, P < 0.001, n = 115 \); PTM: \( F = 27.79, P < 0.001 \); MPM: \( F = 3.73, P = 0.03 \)). When tested separately, both PTM and MPM varied between pigmentation patterns (PTM: \( F = 28.18, d.f. = 2, P < 0.001, n = 123 \); MPM: \( F = 3.21, d.f. = 2, P = 0.04, n = 123 \)). Tukey post hoc comparisons indicated that species with cryptic patterns had lower PTM than species with striped and mixed patterns (\( P < 0.001 \) in both cases), and lower MPM only than striped species (\( P = 0.04 \)). After correcting for the phylogenetic non-independence, MPM was no longer different between lizard dorsal patterns, but the rest of the results remained the same (Table 2).

Snout-vent length-adjusted foraging speed differed according to dorsal patterns (Fig. 5a) (\( F = 3.2, d.f. = 2, P = 0.04 \)).

Fig. 3. PCA using PTM, MPM, foraging speed and SVL as lizard-characterizing features. Yellow (squares) indicates striped patterned species, blue (circles) cryptic-patterned species and green (triangles) mixed-patterned species. The outlying cryptic species is *Ameiva exsul*.

Fig. 4. Comparison of mean foraging mode associated with each dorsal pattern category (Mean ± SE). n-stripes = 13; n-mixed = 21; n-cryptic = 81.
Table 2. Significance levels and sample sizes of phylogenetic ANOVA and MANOVA tests for the association between foraging mode and dorsal pigmentation patterns. Bolded P-values indicate significance and consistencies with the parallel standard ANOVA of MANOVA test.

<table>
<thead>
<tr>
<th>Foraging variable/s</th>
<th>Pattern categories</th>
<th>Test</th>
<th>P value</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>PTM and MPM</td>
<td>All categories</td>
<td>Phylogenetic ANOVA</td>
<td>&lt;0.001</td>
<td>108</td>
</tr>
<tr>
<td>PTM</td>
<td>All categories</td>
<td>Phylogenetic ANOVA</td>
<td>&lt;0.001</td>
<td>113</td>
</tr>
<tr>
<td>Cryptic – Stripes</td>
<td>Phylogenetic ANOVA</td>
<td>&lt;0.001</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cryptic – Mixed</td>
<td>Phylogenetic ANOVA</td>
<td>&lt;0.001</td>
<td></td>
<td></td>
</tr>
<tr>
<td>MPM</td>
<td>All categories</td>
<td>Phylogenetic ANOVA</td>
<td>0.34</td>
<td>115</td>
</tr>
</tbody>
</table>

P = 0.05, n = 50). This result did not hold after correcting for phylogenetic non-independence (phylogenetic ANOVA: P = 0.12, n = 48). SVL-adjusted sprint speed did not differ between pigmentation patterns (Fig. 5b) (F = 0.9, d.f. = 2, P = 0.4, n = 171; phylogenetic ANOVA: P = 0.76, n = 150).

Discussion

Our findings provide the first quantitative support to the hypothesized relationships between pigmentation patterns and movement aspects of lizard foraging behaviour. Using phylogenetic corrected comparative analyses, we have shown that lizards with longitudinal stripes have a very different foraging behaviour than species with cryptic patterns. As predicted, striped lizards were substantially more mobile than lizards with cryptic patterns. This difference was largely driven by variation in the percentage of the foraging time the lizards spent moving. Mixed-patterned lizards were divided between the two behavioural strategies and did not present an intermediate behaviour.

It has been suggested that pigmentation patterns are associated with different behaviours (Snakes: Jackson, Iii et al. 1976; Mammals: Ortolani 1999; Fish: Seehauzen, Mayhew & Van Alphen 1999; Price et al. 2008; Ruell et al. 2013; Cephalopods: Zylinski, Orsio & Shohet 2009; Lizards: Hawlena et al. 2006; Frogs: Rojas, Devillechablolle & Endler 2014). For example, Allen et al. (2013) found an association between various snake patterns and individual aspects of either foraging or antipredator behaviours. Indeed, pigmentation patterns may influence the effectiveness of foraging and defence behaviours in different ways. However, those different outcomes should be considered jointly to account for the overall influence on fitness. Moreover, foraging and defence behaviours are expected to be tightly intertwined due to morphological and physiological trade-offs. Our hypothesis overcomes these apparent difficulties by focusing on the ways in which pigmentation patterns and foraging behaviour interact to affect the probabilities to be detected and to survive predator attacks.

Lizards spend much of their active time foraging. Thus, the integrative expression of their foraging behaviour and pattern should determine their detectability to visual predators. We hypothesized that lizards that spend much of their foraging time moving (i.e. high PTM) are highly detectable regardless of their pattern (Edmunds 1974; Hall et al. 2013). These highly visible lizards may benefit from having conspicuous stripes that may enhance their chances to survive inevitable predator attacks by means of motion dazzle (Jackson 1979; Carretero & Vasconcelos 2006; Kelley & Kelley 2014; Hämäläinen et al. 2015). PTM is traditionally regarded as the main index for distinguishing foraging strategies (i.e. active vs. ambush foragers, Whiting & Cooper 1999; Miles, Losos & Irschick 2007). Indeed, PTM was found to be the major behavioural index that differs between striped and cryptic lizards, with striped lizards having substantially higher PTM than cryptic lizards.

The complementary foraging index, MPM, represents the frequency of discrete movement bouts (Perry et al. 1990). The lizard movement incidence is expected to be positively associated with detectability. We found that lizards with cryptic patterns had lower MPM than lizards with striped patterns, but this effect was not independent of phylogenetic relatedness. MPM, when considered alone, cannot capture the full extent of variation in foraging behaviours. This is because species that rarely move (low PTM) and species that rarely stop (high PTM) are bound to have similar low MPM values (see Fig. 2). Thus, the association between pigmentation patterns and MPM must be interpreted with caution.

Lizards with mixed patterns that include longitudinal stripes and motifs of cryptic patterns were not clustered separately in the PCA, but were divided between the stripes and cryptic clusters. Mixed-pattern lizards had higher PTM than lizards with cryptic patterns, but did not differ in MPM from lizards with striped or cryptic patterns. These results do not seem to reflect a genuine intermediate foraging strategy as we predicted. Instead, mixed-patterned lizards behaved either more like cryptic or striped lizards. We failed to identify phylogenetic,
morphological or environmental variables that might explain this division. Possibly, our purposely crude classification ignored important nuances of mixed patterns that might bear ecological significances. For example, mixed-patterned lizards with pronounced stripes may behave more similarly to striped lizards than mixed-patterned lizards with definite cryptic elements.

We predicted that species with cryptic patterns will have higher foraging speed than striped lizards. We based our predictions on the well-acknowledged notion that ambush foragers use burst attacks and hence have higher foraging speeds to intercept a moving prey (Cooper 2007). Lizards that use short bouts of high-speed movements are expected to be less detectable, favouring cryptic patterning. As expected, foraging speed substantially contributed to discriminate pattern groups in the PCA, whereas higher speeds were associated with cryptic patterns. We also found a weak association between dorsal patterns and foraging speed that met our predictions. However, this association was not independent of phylogenetic relatedness. It is important to note that the foraging speed data set is relatively small and therefore the results should be treated as such.

It has been suggested that ambush foragers have high maximal sprint speed (Huey et al. 1984). This hypothesis is based on the widespread expectation that species that use burst attacks as part of their foraging strategy should have higher sprint capacities. This implies a tight association between foraging speed and maximal sprint speed. Our results have rejected this association. Moreover, we found that the realized foraging speeds were much slower than sprint capacity. These findings suggest that lizards use only a small fraction of their maximal running capacity while foraging, seriously questioning the hypothesized association between foraging behaviour and maximal sprint speed. Indeed, we found no differences in maximal sprint speed between striped, mixed and cryptic patterns.

It is widely acknowledged that stripes can create motion dazzle, but the perceptual effects underlying it are still not well understood (Kelley & Kelley 2014 for potential mechanisms). The common assumption is that stripes create motion dazzle while the prey engages in high-speed escape from its predator. Support for this idea is mostly correlative (e.g. Jackson, Iii & Campbell 1976; Brodie 1992; Allen et al. 2013). Attempts to explore this assumption using computer games in which human predators target ‘escaping’ objects have revealed inconclusive results (Stevens, Yule & Ruxton 2008; Scott-Samuel et al. 2011; Stevens et al. 2011; Hall et al. 2013; von Helversen, Schooler & Czienskowski 2013; Hughes, Troscianko & Stevens 2014; Hughes, Magor-Elliott & Stevens 2015). Another overlooked option is that stripes may hamper the predator’s ability to assess the striped-prey form and speed. Consequently, ambush predators may miscalculate the planned point of interception, allowing the striped prey an extra split second to initiate a successful escape. Our study was not designed to tease apart these options. Yet, the strong association between active foraging behaviour and dorsal stripes should supply the impetus to expand the research into the perceptual effects of stripes in hindering and misleading directional movements.

Our comparative results coincide with focal studies that found association between pigmentation patterns and movement correlates of foraging behaviour. Rojas, Devilchabrolle & Endler (2014) found that aposematic frogs (Dendrobates tinctorius) bearing elongated patterns move on average faster and more directional while foraging than individuals with interrupted patterns. Acanthodactylus beershebensis lizards that undergo ontogenetic changes in pigmentation patterns from stripes to blotches exhibit reduction in both PTM and MPM (Hawlena et al. 2006). We urge researchers to critically test our hypothesis by comparing quantified indices of foraging behaviour between individuals or populations of polymorphic species, between sexes in sexually dimorphic species, or between ontogenetic stages in species that undergo pattern changes.

Our movement-patterns hypothesis aims to explain the functional differences between longitudinal stripes and cryptic patterning. This hypothesis does not intend to explain variation among cryptic patterns. We expect environmental conditions to govern this variation. Unfortunately, in spite of an extensive literature search, we could not find comparative information about environmental variables (e.g. habitat, substrate or land cover) that was detailed enough to allow meaningful testing of this hypothesis.

We emphasize that our hypothesized relationship between foraging behaviour and pigmentation patterning does not rule out the possibility that in certain environments stripes can be cryptic (Van der Winden, Strijbosch & Bogaerts 1995; Sherbrooke 2002). Our data base includes two striped lizards with relatively low PTM (Chamaesaura anguina and Podarcis peloponnesiacus). Future studies should focus on characterizing the striped lizard habitats to untangle the possibly two very different functions of this patterning. Unravelling these confounded functions may reveal the actual strength of the association between stripes and mobility in lizards.

In summary, our study provides a simple yet comprehensive explanation for the association between pigmentation patterns and lizard foraging behaviour. Using quantitative behavioural data coupled with a phylogenetic comparative approach, we have shown that striped lizards were more mobile than lizards with cryptic patterns. We attribute these differences to alternative antipredatory strategies. Highly detectable mobile lizards may benefit from motion-dazzle patterns that enhance escape, while less-mobile lizards may profit from patterns that reduce detectability. This functional link between foraging behaviour and pigmentation pattern might be applicable to many other taxa and serve as a starting hypothesis for more detailed exploration. We hope that future studies will test our movement-patterns hypothesis, ultimately applying meticulous manipulations to tease apart, and test its mechanistic details.
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Data accessibility

Data for this paper can be found as supporting information.

References


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Supporting Information

Additional Supporting Information may be found online in the supporting information tab for this article:

**Table S1.** Lizards’ movement behavior and dorsal pigmentation database.

**Appendix S1.** Database references.

**Fig. S1.** The relationship between average values of maximal sprint speed and foraging speed in different species.