

Grab my tail: evolution of dazzle stripes and colourful tails in lizards

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Abstract

Understanding the functions of animal coloration has been a long-standing question in evolutionary biology. For example, the widespread occurrence of striking longitudinal stripes and colourful tails in lizards begs for an explanation. Experiments have suggested that colourful tails can deflect attacks towards the tail (the ‘deflection’ hypothesis), which is sacrificable in most lizards, thereby increasing the chance of escape. Studies also suggest that in moving lizards, longitudinal body stripes can redirect predators’ strikes towards the tail through the ‘motion dazzle’ effect. Despite these experimental studies, the ecological factors associated with the evolution of such striking colorations remain unexplored. Here, we investigated whether predictions from motion dazzle and attack deflection could explain the widespread occurrence of these striking marks using comparative methods and information on eco-physiological variables (caudal autotomy, diel activity, microhabitat and body temperature) potentially linked to their functioning. We found both longitudinal stripes and colourful tails are associated with diurnal activity and with the ability to lose the tail. Compared to stripeless species, striped species are more likely to be ground-dwelling and have higher body temperature, emphasizing the connection of stripes to mobility and rapid escape strategy. Colourful tails and stripes have evolved multiple times in a correlated fashion, suggesting that their functions may be linked. Overall, our results together with previous experimental studies support the notion that stripes and colourful tails in lizards may have protective functions based on deflective and motion dazzle effects.

Introduction

Animals rely on an impressive diversity of colour patterns to protect themselves against predation. As a first line of defence to avoid being consumed, animals can prevent detection or recognition by predators via a range of camouflage strategies (Cuthill *et al.*, 2005; Rowland *et al.*, 2008; Stevens & Merilaita, 2009; Skelhorn *et al.*, 2010). Although camouflaging colours

are typically drab, marks involving bright colours or strong contrasts are not uncommon in prey. One type of salient antipredator marks is deflective marks that manipulate where attacking predators aim their strikes (Poulton, 1890; Humphreys & Ruxton, 2018). By making the predator strike to a direction or body part that will increase the chance of successful escape (for instance, towards the tail of a prey that can escape towards the anterior direction; e.g. fish (Kjernsmo & Merilaita, 2013); mammals (Powell, 1982); lizards (Cooper & Vitt, 1985); insects (Prudic *et al.*, 2015)), such markings can protect the prey from predation. Another type of striking prey coloration, which have been termed *motion dazzle* patterns, includes stripes, bands and zigzags and are thought to protect moving prey by hampering the attacking predator’s perception

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of speed or trajectory (Stevens *et al.*, 2008; Scott-Samuel *et al.*, 2011; Murali & Kodandaramaiah, 2016; Hughes *et al.*, 2017), an idea initially proposed by Thayer (1909).

Numerous lizard species have striking longitudinal stripes on the body (i.e. head and trunk; Fig. S1), and these stripes have long been presumed to have a protective function against predators (Forsman & Shine, 1995; Hawlena *et al.*, 2006). Murali & Kodandaramaiah (2016) recently demonstrated in a simulated predation experiment that used virtual prey and humans as 'predators' that longitudinal stripes on the anterior part of moving objects decrease the perceived speed of the object, and due to this motion dazzle effect, attacks directed to a striped anterior of a prey will instead often hit the posterior. They proposed a protective strategy – *the redirection effect* – wherein motion dazzle is used by moving prey to divert attacks to a nonvital body part. Since most lizards are known to shed their tail when attacked by a predator (termed caudal autotomy; Bateman & Fleming, 2009), they argued that such redirection generated by the stripes on the torso can result in an increased probability of strikes hitting the expendable tail which can be regenerated.

Apart from stripes, another characteristic coloration in lizards includes red, green or blue tails (together hereafter referred to as colourful tails), which typically contrast with the colours of the rest of the body (Fig. S1). Multiple hypotheses have been proposed to explain the adaptive function of colourful tails, including reduction of intraspecific aggression between individuals of different age groups (Clark & Hall, 1970; Fresnillo *et al.*, 2015a) and sexual signalling (Kwiatkowski & Sullivan, 2002; Belliure *et al.*, 2018). Most lizards possess the ability to autotomize their tails (Bateman & Fleming, 2009). Therefore, the most plausible explanation for the occurrence of colourful tails is that bright tail coloration manipulates predators to direct strikes away from the body and towards the tail, which together with caudal autotomy increases the chance of successful escape (Cooper & Vitt, 1985; Watson *et al.*, 2012; Fresnillo *et al.*, 2015b).

In summary, the functions of the two striking colour patterns in lizards – body stripes and colourful tails – have been investigated from various perspectives and in multiple experimental studies, but there is little information on the macroevolutionary aspects of these colour patterns, and about what ecological factors promote their evolution. Here, we test six explicit macroevolutionary hypotheses in lizards related to the concepts of redirection (caused by motion dazzle) and deflection. Since body stripes (Murali & Kodandaramaiah, 2016, 2018) and colourful tail (Cooper & Vitt, 1985; Humphreys & Ruxton, 2018) have both been proposed to divert attacks to the tail and enable prey escape, we expect both of these colorations to be associated with

caudal autotomy. Therefore, we ask whether (i) the absence of caudal autotomy is associated with the absence of stripes or colourful tail.

Since mobility often breaks camouflage (Ioannou & Krause, 2009; Hall *et al.*, 2013), compared to day-resting prey, day activity may promote the evolution of other protective strategies in prey, such as those based on striking coloration. For instance, in spiders and lepidopterans, the evolution of defences involving striking colorations, that is aposematism or mimicry, is associated with diurnal activity and crypsis (background-matching or masquerade) with nocturnality (Merilaita & Tullberg, 2005; Pekár, 2014). Therefore, we hypothesize that (ii) the evolution of striped patterns and colourful tails is more likely in diurnal rather than in nocturnal lizards.

Recent evidence suggests that colour marks with distinct effects can work together to reduce the predation risk of a prey (Caro *et al.*, 2016; Kjærnsmo *et al.*, 2016). Accordingly, if both stripes and colourful tails in lizards serve the common function of diverting attacks to the tail, selection may favour their co-occurrence. Therefore, we tested whether (iii) the evolution of longitudinal striped body patterning and colourful tails is correlated across the phylogeny. Assuming that stripes have a redirective function, dorsal stripes are more likely to be used as signals to aerial predators such as birds, in contrast to lateral stripes which are more likely to be used against terrestrial predators such as snakes and mammals. These predator guilds may differ in their visual systems, and hence, the same tail colour may not be equally effective for attack deflection for both predator guilds (Kuriyama *et al.*, 2016). Therefore, we also explored whether (iv) the position of stripes on the body (*Lateral* or *Dorsal*; Fig. S1) is associated with specific tail colour (red, blue or green).

Finally, because the motion dazzle effect necessitates mobility, two ecological attributes that may influence the evolution of stripes, but not necessarily colourful tails, are body temperature and habitat. Firstly, it has been shown that motion dazzle patterns induce higher targeting error when the prey moves rapidly (Stevens *et al.*, 2008), and therefore, it is expected that prey that rely on motion dazzle patterns escape faster than those that rely on other kinds of protection. Body temperature is positively associated with sprint speed and rapid escape behaviour in lizards (Hertz *et al.*, 1982; Bauwens *et al.*, 1995). If stripes provide protection through the motion dazzle effect, then we expect (v) species with stripes to have higher body temperature as mobility may be constrained at lower body temperature. Secondly, rapid escape from predators is difficult in scansorial (i.e. arboreal and rock-dwelling) environments because of surface discontinuity (Arnold, 1988), and therefore, we hypothesize that (vi) striped species are more likely to be ground-dwelling than stripeless species.

Methods

Data collection

The data set on lizard body and tail coloration representing 1622 species under 36 lizard families (including amphisbaenians) was compiled using the same protocols as in Murali & Kodandaramaiah (2018). Depending on the availability of the data for each analysis, the data set was pruned as needed. Briefly, colour patterns were scored by three volunteers independently based on 7907 images of both adult and juvenile lizards (if available) from online web sources averaging 4.84 images per species, using a custom interface written in MATLAB R2015a [MathWorks; see supplementary Murali & Kodandaramaiah (2018)]. The volunteers were naïve to the hypothesis tested in this study. Presence or absence of the coloration traits was scored as follows [see Fig. S1 for reference image and Murali & Kodandaramaiah (2018) for further details].

Stripes: Presence required that stripes were clearly visible and occurred throughout, from the tip of the snout to tail base. Stripes, if present, were scored as *Lateral*, *Dorsal* or both (see below).

Lateral stripes: Stripes were scored as *Lateral* if they ran along the sides of the body.

Dorsal stripes: Stripes were scored as *Dorsal* if they were restricted to the dorsal body parts.

Colourful tail: Presence required that the following criteria were met: (i) the tail colour was either red, blue or green, that is one of the tail colours that has been suggested to have a divertive function (Cooper & Vitt, 1985; Castilla *et al.*, 1999; Fresnillo *et al.*, 2015a), and (ii) the tail colour differed from the rest of the body.

Red, Blue or Green Tail: Presence or absence of the three tail colours was coded as a binary trait separately for each colour.

To ensure consistency in classifying colour patterns, we asked 10 more volunteers to classify a subset of 100 species chosen randomly from the main data set. We found strong concordance in colour pattern classification across volunteers for both the complete and the restricted data sets classified by the 10 and 13 volunteers, respectively [Fleiss' Kappa index of reliability (McHugh, 2012; main data set, subset): *Stripes* = (0.958, 0.928); *Lateral stripes* = (0.9191, 0.929); *Dorsal stripes* = (0.925, 0.892); *Colourful tail* = (0.953, 0.861)]. Hence, for further analyses, coloration data for each species were randomly taken from the responses of one of the three volunteers.

To test the association between caudal autotomy and protective coloration, we used information on the presence or absence of tail fracture plates compiled by Arnold (1984). The presence of tail fracture plate indicates areas of pre-formed weakness points in caudal vertebrae where breakage occurs easily (Pratt, 1946;

Etheridge, 1967). Diel activity was coded as either nocturnal (1) (including crepuscular and cathemeral, that is irregularly active during any time of night or day) or diurnal (0) following Meiri (2008). Species-specific mean body temperature, measured when the lizard was active, was compiled from literature sources (Sinervo *et al.*, 2010; Meiri *et al.*, 2013). The ecological data on diel activity and habitat were compiled from Meiri (2008) and other regional field guides. Habitat use was classified either as ground-dwelling (0) or as scansorial (1) which includes arboreal and/or rock-dwelling habitats. To account for effects of phylogenetic relatedness among species, we utilized the species level phylogeny of squamate reptiles from Zheng & Wiens (2016). Although data on both colorations were available for 1622 species, data for eco-physiological variables were only available for a subset of species: caudal autotomy ($n = 805$), diel activity ($n = 646$), habitat ($n = 657$) and body temperature ($n = 520$). All analyses were performed in RStudio v 3.3.3 – 'Another Canoe' (R Core Team 2017) unless stated otherwise.

Ancestral state reconstruction

Firstly, to visualize how traits have evolved over time, we performed ancestral state reconstruction for binary coloration traits using two approaches: (i) Bayesian stochastic character mapping [function *make.simmap* from the *phytools* package (Revell, 2012)], which allows more than a single character change to occur along the branch so that evolutionary time can be uncoupled from character change (Huelsenbeck *et al.*, 2003) and (ii) corHMM-based maximum-likelihood method, which takes into account heterogeneity in trait evolution (Appendix S1; Beaulieu *et al.*, 2013).

Correlation between discrete traits (caudal autotomy, stripes, colourful tail, diel activity and habitat)

We tested for the evolutionary correlation between discrete coloration (stripes and colourful tail) and ecological traits (diel activity, habitat use and caudal autotomy) using the software Bayestraits v2 (available at <http://www.evolution.rdg.ac.uk/BayesTraits.html>), implementing the method proposed by Pagel (1994). We used a reversible jump Markov chain Monte Carlo (RJ MCMC) method to obtain parameter estimates from different evolutionary models (*independent* and *dependent*; Pagel & Meade, 2006). The *independent* model of the evolution assumes that there is no correlation between the two binary traits being analysed, whereas in the *dependent* model, the evolution of the traits occurs in a correlated fashion. Hence, the *dependent* model is based on eight possible transition rates between the four character states of the two binary

variables. In accordance with the recommendation by Pagel & Meade (2006), we chose an exponential hyper prior (0,10) as it uses the data to estimate the details about prior distribution of the parameters. All analyses were performed for 10 million iterations with a burn-in of 1 million to avoid including values before MCMC chain convergence. In all analyses, the acceptance ratio ranged between ~ 30% and 40%.

We analysed the output of the MCMC runs using Tracer v 1.6 (Rambaut *et al.*, 2014) to confirm convergence. All runs were assumed to have converged because the effective sample size of all parameters was > 200. We then calculated the log Bayes factor in Tracer for each pair of models (Rambaut *et al.*, 2014). A high log Bayes factor value indicates support for the *dependent* model of the evolution over the *independent* model, such that values < 2 are considered as little evidence, 2–6 as positive evidence and 6–10 as strong evidence (Pagel, 1994; Kass & Raftery, 1995). Since the above model-based analysis cannot include covariates, and to check for robustness of the results, we also performed phylogenetic logistic regression (PLR) using the function *phyloglm* in package *phylolm* (Ho & Ané, 2014) to account for the effect of body size (Murali & Kodandaramaiah, 2018). Maddison & FitzJohn (2014) have pointed out that Pagel's method (Pagel, 1994) can lead to inferences of significant associations between traits even when the traits are common to whole groups of species, which necessarily do not reflect the traits being the part of the same functional unit. Thus, in order to confirm the results obtained from Pagel's method (1994), we also tested for the correlated evolution between binary traits using the pairwise comparison method proposed by Maddison (2000), implemented as the pairwise module in MESQUITE (version: 3.02) using the *two-pair* method (Maddison & Maddison, 2001; Appendix S3).

Although it would be ideal to test for correlation between the position of striped coloration (*Dorsal* and *Lateral*) and tail colour (red, blue and green) by considering the coloration trait alternatives as multiple character states, no comparative method exists to account for the correlation of more than two character states. Therefore, for testing the association between stripe position and tail colour, we tested for the evolutionary correlation between the traits using Bayestraits v 2. A RJ MCMC was used to obtain the parameter estimates with the same settings as for the analysis testing correlation between discrete traits. We coded all the coloration states as separate binary variables (presence or absence), and we compared the log Bayes factor values computed for each pair of binary traits (e.g. *Lateral stripes* and blue tail – Bayes factor computed from the *dependent* and *independent* models, respectively) against other possible pairwise combinations (e.g. *Lateral stripes* and red tail) to check which of the pairwise combinations fitted the data best.

Phylogenetic path analysis

We further explored the causal relation between the evolution of the three discrete variables – stripes, colourful tail and caudal autotomy – using phylogenetic confirmatory path analyses employing the *d* separation method (von Hardenberg & Gonzalez-Voyer, 2013). This was performed using the R package *phylopath* (van der Bijl, 2017) employing a PLR approach. The models (Fig. S5) were ranked based on the C-statistics information criterion (CICc), and models with $\Delta\text{CICc} \leq 2$ were averaged (Gonzalez-Voyer & Von Hardenberg, 2014; Table S21).

Correlation between stripes and body temperature

We employed phylogenetic generalized least squares (PGLS) regression using the packages *nlme* (Pinheiro *et al.*, 2014) and *geiger* (Harmon *et al.*, 2007) in R for analysing the phylogenetic association between body temperature and striped coloration. The data were fitted using three evolutionary models (Ornstein–Uhlenbeck, Brownian motion and estimated lambda model), and the best-fit model was selected based on Akaike weights. The comparisons favoured the lambda model (Table S6), which was employed to infer the results. Since the occurrence of striped coloration is negatively correlated to body size in lizards (Murali & Kodandaramaiah, 2018), we accounted for body size by including snout to vent length (SVL) as a covariate in the analysis.

Evolutionary transitions of character states

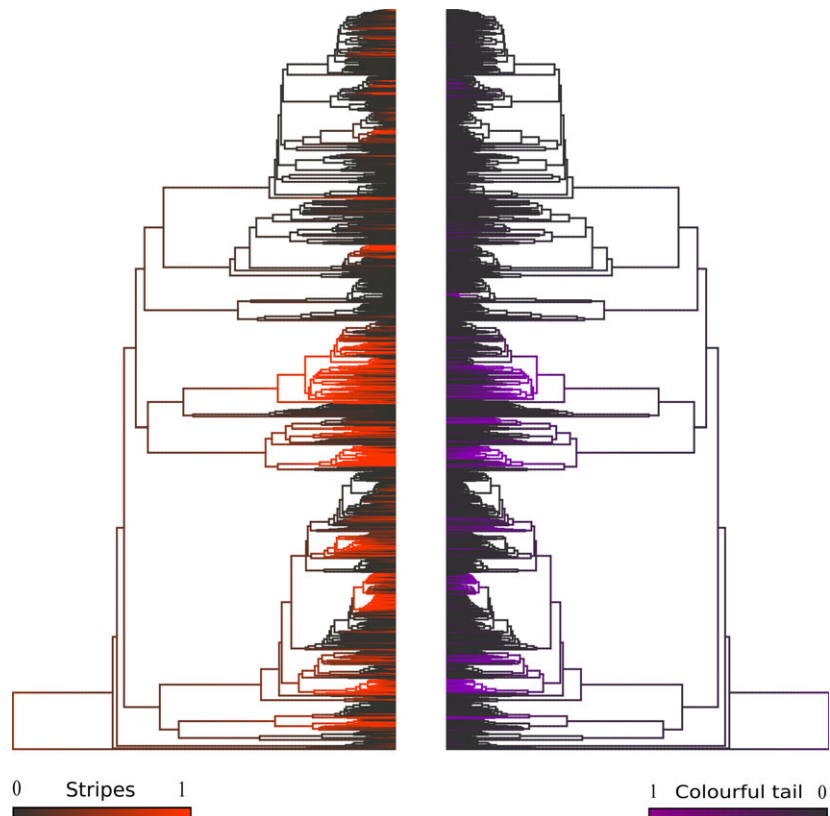
We then explored the direction of correlated discrete trait evolution of striped coloration, caudal autotomy and colourful tail using Bayestraits v 2 (pairwise). This was performed by first restricting all possible transition rates (one by one) that can occur for all pairs of traits independently to zero. Then, we simultaneously restricted all combinations of transition rate parameters that did not differ from zero and compared with the full model (all eight transition rates unconstrained, that is full *dependent* model) using the computed Bayes factor. If the log Bayes factor was < 2, we considered the particular transition rate as not different from zero (Kass & Raftery, 1995; Pagel & Meade, 2006).

Results

Ancestral states of protective colorations

The ancestral state reconstruction using stochastic mapping recovered multiple origins of both striped body (206 times) and colourful tail (108 times) across the phylogeny. The analysis suggested that the probability that the ancestor of lizards had stripes was equal to the

Fig. 1 Ancestral state reconstruction using Bayesian stochastic character mapping of stripes and colourful tail. The colour bar represents the posterior probability of the tip states from 5000 simulations.



probability that it lacked stripes. Similarly, presence and absence of a colourful tail in the ancestor were equally likely (Fig. 1). Likewise, the remaining traits tested (tail colours: red, blue and green; Fig. S2a–c, stripe position: *Dorsal* and *Lateral*) had an equal probability of being present or absent ancestrally (Fig. S2d,e). The corHMM-based ancestral state reconstruction suggested that the rate of evolution of the above protective colorations differs across the clades (Fig. S3).

Correlation between discrete traits (caudal autotomy, stripes, colourful tail, diel activity and habitat)

The Bayestraits analysis provided positive evidence (i.e. *dependent* model was favoured over the *independent* model of the evolution) for the correlated evolution of stripes with all the discrete eco-physiological variables examined (Table 1a). Specifically, striped body coloration was positively associated with diurnal activity pattern, ground-dwelling habitat, colourful tail and caudal autotomy (Figs 2b,c, 3 and 5). The pairwise comparisons also corroborated the above model-based approach (Appendix S3, Table S5a).

Bayestraits analyses indicated that the presence of colourful tail was positively associated with caudal autotomy and diurnal activity (Table 1b, Figs 2d and 4).

Table 1 Evolutionary correlates of discrete eco-physiological traits and protective colorations (a-stripes and b-colourful tail) from Bayestraits analysis.

Trait	Dependent model	Independent model	Log Bayes factor	ΔAIC
(a) Stripes				
Diel activity	−971.9473	−977.7408	2.4498	19.578
Habitat use	−1113.7596	−1123.7067	2.9904	27.894
Colourful tail	−1209.4833	−1233.9303	3.8890	56.894
Caudal autotomy	−812.0225	−846.8656	4.2240	77.686
(b) Colourful tail				
Diel activity	−634.3593	−638.1601	2.0283	15.601
Caudal autotomy	−505.4583	−510.6097	2.3324	18.302

Harmonic mean estimates of the maximum-likelihood values for the dependent and independent models with log Bayes factor values. Bayes factor value of > 2 was considered as positive evidence in support of *dependent* model over the *independent* model of the evolution (Kass & Raftery, 1995). AIC- Akaike's information criterion.

The PLR analysis corroborated the above results after accounting for SVL (Tables S8–S11 and S15–17). However, pairwise comparisons failed to identify a significant association between colourful tail and caudal autotomy (Appendix S3, Table S5b).

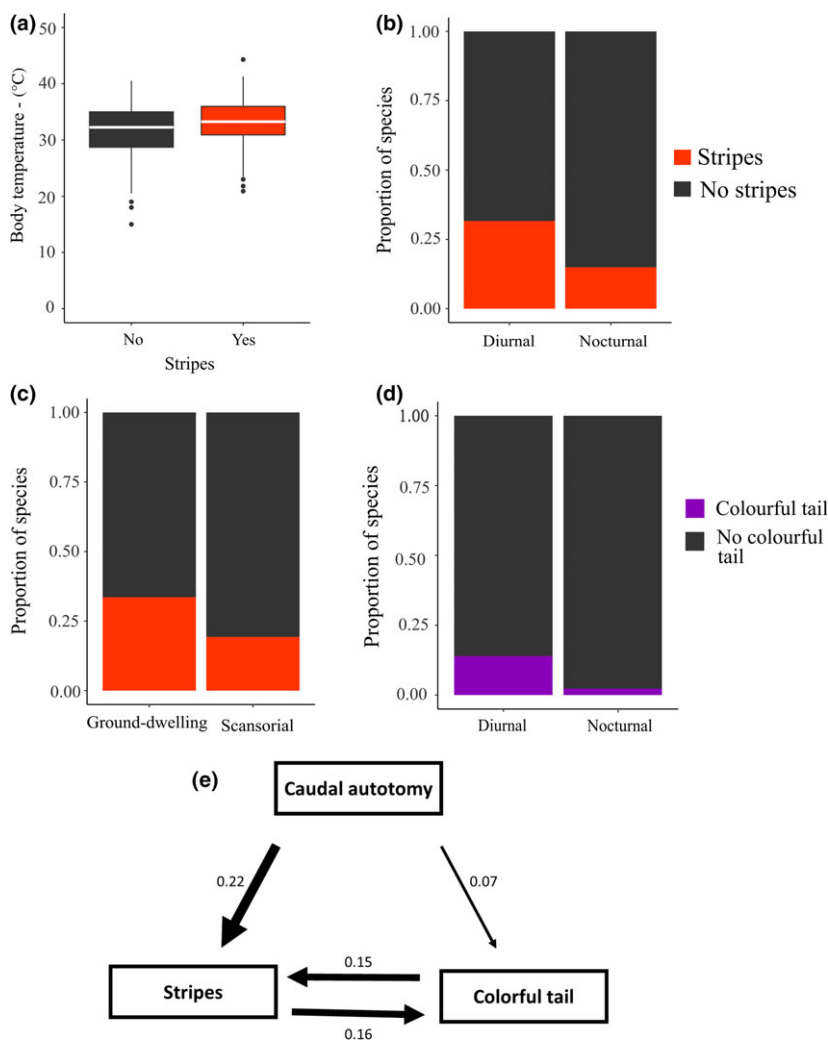


Fig. 2 Plots depicting association between defensive coloration and eco-physiological variables. (a) Boxplots showing median and interquartile range of lizard body temperature; outliers are shown as black circles ($P = 0.0029$). (b) Proportion of striped and nonstriped species which are nocturnal or diurnal (statistics are presented in Table 1). (c) Proportion of striped and nonstriped species which are ground-dwelling or scansorial (statistics are presented in Table 1). (d) Proportion of species with and without colourful tail which are nocturnal or diurnal (statistics are presented in Table 1). (e) Representation of model-averaged best-fitting path models exploring causality among stripes, colourful tail and caudal autotomy (alternative models are as in Fig. S5). Arrow size is proportional to standardized path coefficients, and direction indicates causality.

Except in the analysis involving green tail colour, we found the *dependent* model to be favoured over the *independent* model in analyses testing for correlations between stripe position (*Dorsal* or *Lateral*) and tail coloration (red, blue and green; Table 2). Among the three combinations of *Dorsal* stripes and tail colours, the highest log Bayes factor was for the combination *Dorsal* stripes and red tail (over *Dorsal* stripes and green tail or *Dorsal* stripes and blue tail) indicating that this trait combination is more frequent than the remaining two. The log Bayes factor value of the combination of *Lateral* stripes and blue tail colour was higher than that for the two other combinations (*Lateral* stripes and green tail or *Lateral* stripes and red tail).

Phylogenetic path analysis

The phylogenetic confirmatory path analysis suggests that the evolution of striped coloration and colourful tail is driven by caudal autotomy, rather than the two driving the evolution of caudal autotomy (Fig. 2e). The

analysis also suggests the evolution of stripes and colourful tails is equally influenced by each other (Fig. 2e). However, caudal autotomy more strongly influences the evolution of striped coloration than the evolution of colourful tail (Fig. 2e).

Correlation between stripes and body temperature

We found that striped species had higher body temperature while active than species without stripes (PGLS – Pagel's lambda model: d.f. = 520, $t = 2.99$, $P = 0.0029$; Fig. 2a; Table S7a). This effect was significant even after the model was corrected for body size (PGLS – Pagel's lambda model: d.f. = 506, $t = 2.74$, $P = 0.0063$; Fig. 2a; Table S7b).

Evolutionary transitions of character states

Our analysis exploring evolutionary transitions of striped coloration and caudal autotomy revealed three

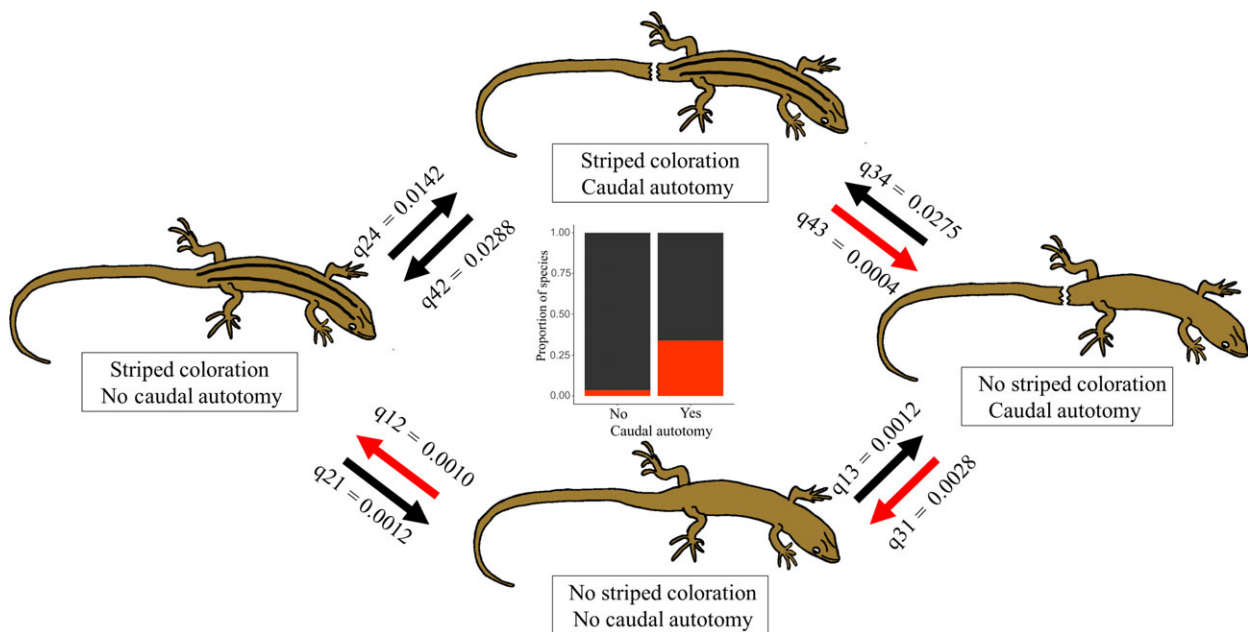


Fig. 3 Predicted evolutionary transitions for the traits longitudinal stripes and caudal autotomy from the Bayestraits analysis. Transitions among states are indicated by the solid black arrow. The red solid arrow indicates transition rate not strongly differing from zero (log Bayes factor < 2 ; Table S18). Inset graph depicts the proportion of striped (orange) and nonstriped (dark-grey) species with and without caudal autotomy. Lizard image with broken tail represents the presence of caudal autotomy.

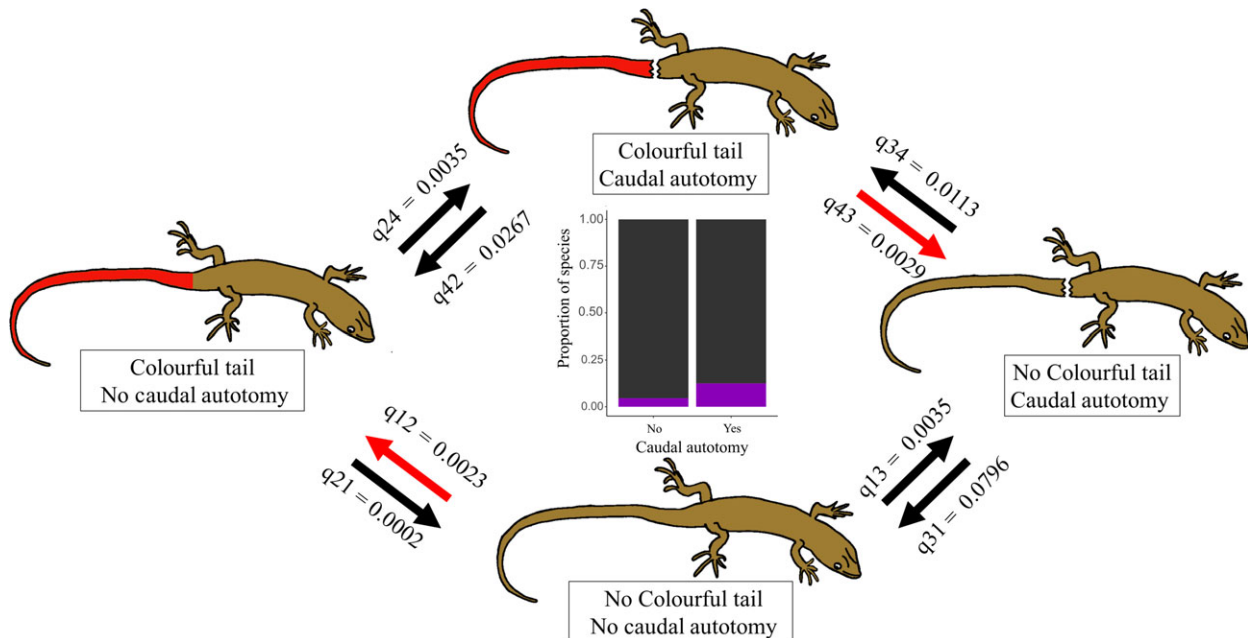


Fig. 4 Predicted evolutionary transitions for the traits colourful tail and caudal autotomy from the Bayestraits analysis. Transitions among states are indicated by the solid black arrow. The red solid arrow indicates transition rate not strongly differing from zero (log Bayes factor < 2 ; Table S19). Inset graph depicts the proportion of species with colourful tail and without the colourful tail which can undergo caudal autotomy. Lizard image with broken tail represents the presence of caudal autotomy. Colourful tail here depicted in red but model was for all three colours (red, blue and green).

Table 2 Evolutionary correlates of stripe position and tail colour from Bayestraits analysis.

Trait combination	Dependent model	Independent model	Log Bayes factor	ΔAIC
(a) Dorsal stripes and tail colorations				
Dorsal-blue	-866.676	-876.153	2.9419	26.954
Dorsal-red	-820.435	-840.595	3.6968	48.32
Dorsal-green	-638.889	-639.474	0.1566	9.17
(b) Lateral stripes and tail colorations				
Lateral-blue	-993.543	-1008.68	3.4106	38.274
Lateral-red	-968.911	-973.133	2.1337	16.444
Lateral-green	-771.451	-772.431	0.6724	9.96

Harmonic mean estimates of the maximum-likelihood values for the dependent and independent models with log Bayes factor values. Bayes factor value of > 2 (in bold) was considered as positive evidence in support of *dependent* model over the *independent* model of the evolution (Kass & Raftery, 1995). AIC- Akaike's information criterion.

transition rates that did not differ from zero (q12, q31 and q43 in Fig. 3, Table S18). The zero-transition rate between stripeless body + caudal autotomy to stripeless body + no caudal autotomy (q31; Fig. 3) suggests that the loss of caudal autotomy is unlikely after it has been gained. The zero-transition rate between striped body + no caudal autotomy and stripeless body + no caudal autotomy (q12; Fig. 3) indicates that gain of stripes might occur only after gain of caudal autotomy.

Likewise, we found the transitions rates from colourful tail + caudal autotomy to no colourful tail + caudal autotomy (q43; Fig. 4; Table S19) and no colourful tail + no caudal autotomy to colourful tail + no caudal autotomy (q12; Fig. 4; Table S19) to be zero. This suggests that gain of colourful tail is usually preceded by gain of caudal autotomy.

However, analyses of transition rates between striped body and colourful tail did not suggest any of the transition rates to be equal to zero (Fig. 5; Table S20). Comparison of transition rates across states indicates greater transition rates (specifically q24 over q42, and q21 over q12 in Fig. 5) towards combined presence or absence of the traits, suggesting that both trait combinations might be stable once evolved.

Discussion

Despite several experimental studies on body stripes and colourful tails in lizards – two widespread types of salient marks, long thought to work against predation – their evolutionary patterns have so far received little attention. Our phylogenetic comparative analyses based on a large and robust data set shed light on the macroevolutionary trends of these colour patterns, and the ecological attributes influencing their evolution.

Importance of caudal autotomy

Caudal autotomy is found in the vast majority of lizards and is thought to function mainly against predation (Bateman & Fleming, 2009). This defence strategy appears to have evolved at least 280 million ago years in reptiles (LeBlanc *et al.*, 2018). However, some lineages have lost this feature, likely due to increased costs associated with tail regeneration and locomotion (Arnold, 1984; Bateman & Fleming, 2009). Unless a lizard can lose its tail, diversion of attacks from the body to the tail is unlikely to be beneficial. Therefore, we expected the evolution of stripes and colourful tails to be correlated with the ability to autotomize tails. This is supported by our analyses where we used the presence of tail fracture plates as a proxy for caudal autotomy. Moreover, the analysis of evolutionary transitions revealed that stripes and colourful tails are more likely to evolve after caudal autotomy has evolved (Figs 3 and 4), rather than caudal autotomy evolving after stripes or colourful tails. Thus, caudal autotomy appears to be a prerequisite for the evolution of these protective colorations (Marazzi *et al.*, 2012). This was further supported by the phylogenetic path analysis (Fig. 2e).

We also found that not all lizards with caudal autotomy possess stripes or colourful tails (Figs 3 and 4). This could be because these colour patterns need not be a necessary condition for caudal autotomy to be effective against predation in lizards (Bateman & Fleming, 2009). For example, diversion of predatory attacks to the tail can also be achieved behaviourally by 'wagging' the tail (Cooper, 2001). Alternatively, caudal autotomy might be essential for these colorations to be effective, because attack diversion to the tail without tail loss is unlikely to result in escape from the predator. This is further supported in our data set, where stripes and colourful tail are present only in 2.3% and 2.8%, respectively, of lizards which cannot autotomize their tail.

Diurnal activity and evolution of striking colorations

Defensive colours might be ineffective against visual predators during nocturnal conditions. Since the effectiveness of cryptic coloration is known to be deteriorated by movement (Ioannou & Krause, 2009; Hall *et al.*, 2013), diurnally active animals may be forced to rely on other protective strategies involving bright colours (Merilaita & Tullberg, 2005; Hawlena *et al.*, 2006; Pekár, 2014). Our results indicate that both stripes and colourful tails are associated with the diurnal activity (Fig. 2b,d), supporting the idea that striking colorations are more likely to evolve in diurnally active animals as a result of constraints imposed on other defensive strategies (e.g. background-matching) by movement (Merilaita & Tullberg, 2005).

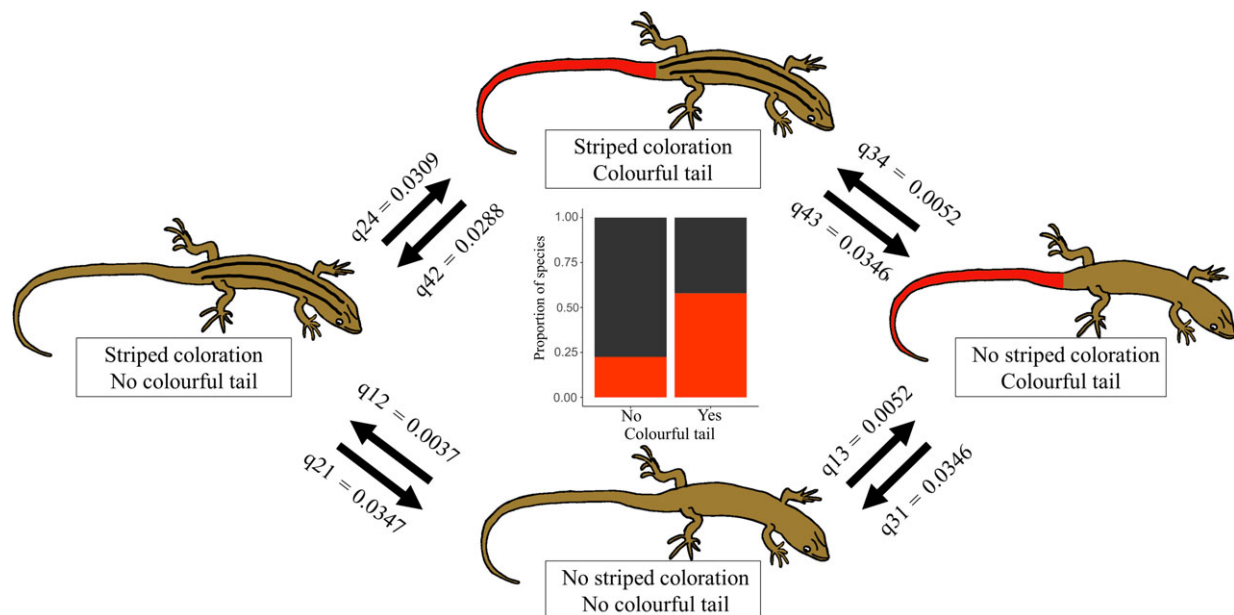


Fig. 5 Predicted evolutionary transitions for the traits longitudinal stripes and colourful tail from the Bayestraits analysis. Transitions among states are indicated by the solid black arrows. All the transition rates were found to be different from zero (log Bayes factor > 2; Table S20). Inset graph depicts the proportion of striped (orange) and nonstriped (dark-grey) species with and without the colourful tail. Colourful tail here depicted in red but model was for all three colours (red, blue and green).

Mobility and stripes

As expected, there was a correlation between stripes and higher body temperature. In ectotherms, mobility is constrained by body temperature (Hertz *et al.*, 1982; Bauwens *et al.*, 1995). The association of higher body temperature with the presence of striped coloration suggests that striped species may rely on rapid escape as a defence, which in turn is essential for stripes to function in motion. This is further supported by the results in a comparative study on snakes (Allen *et al.*, 2013), which indicated an association between longitudinal stripes and rapid escape as a primary defence. Additionally, the association between lower body temperature and stripeless state suggests that the evolution of other protective colorations (e.g. background-matching coloration) may be favoured in animals because of thermal constraints on escape speed (cf. Merilaita & Tullberg, 2005).

The correlation between striped coloration and ground-dwelling nature further highlights the idea the evolution of stripes in lizards might be linked to species with greater mobility (Halperin *et al.*, 2017). Effective movement is hindered in complex arboreal environments which may impose constraints on sprint speed, making stripes ineffective. Furthermore, the surface area of contact in arboreal habitats is lesser than in ground-dwelling habitats, which may further limit sprint speed. For example, Irschick & Losos (1999) have shown that sprint performance in arboreal *Anolis* lizards is positively associated with the surface diameter of the

branches. Therefore, cryptic coloration may be favoured in scansorial lizards. Indeed, some authors have observed that scansorial lizards generally have cryptic coloration, forage slowly and adopt aggressive displays or stealthy escape as the primary defence rather than immediate resort to flight (Arnold, 1988; Irschick & Losos, 1996, 1999). We note that colourful tail is not associated with habitat or body temperature, suggesting that rapid escape may not be equally important for attack deflection by coloured tails (Fig. S4).

Correlation between stripes and coloured tails

Our study provides the first comprehensive support for the correlated evolution of longitudinal body stripes and colourful tails in lizards in a macroevolutionary context, suggesting that there may be a functional association between the traits. The analysis of evolutionary transitions also revealed that the combination of traits remains stable once evolved. Taking into account the experimental evidence (Murali & Kodandaramaiah, 2016), it is likely that stripes and colourful tails act in concert to enhance the adaptive benefit of each other against consistent selection from visually oriented predators (cf. Kjærnsmo *et al.* 2016). Although the exact perceptual mechanism is unknown, it is possible that during motion, a colourful tail might function as a better trackable feature, thereby increasing the probability of attacks directed to the tail (Murali & Kodandaramaiah, 2016), whereas longitudinal stripes by

themselves are difficult to track in motion (Hogan *et al.*, 2016). Interestingly, in many lizard species (e.g. *Acanthodactylus beershebensis*, *Plestiodon* spp), striking tail colour is known to fade upon maturation and this fading coincides with loss of body stripes (Takeo Kuriyama & Hasegawa, 2017; Hawlena *et al.*, 2006). Furthermore, the presence of stripes and coloured tail appears to be related to predation pressure – both traits are absent when predation pressure is low (Brandley *et al.*, 2014). These observations lend further support to the proposed functional association between stripes and coloured tails in lizards.

It is well known that visually striking, sexually selected signals may reduce survival due to increased risk of detection by predators (Endler, 1983; Zuk & Koluru, 1998). Therefore, sexual signals are expected to evolve as compromise between opposing pressures of sexual and natural selection through predation (Endler, 1983; Husak *et al.*, 2006). In some species of lizards, it has been shown that the colourful tail also functions as a sexual signal (Kwiatkowski & Sullivan, 2002; Belliure *et al.*, 2018). Therefore, in those species, an evolutionary correlation between stripes and colourful tails could also arise if stripes had evolved to offset the predation cost associated with enhanced detectability due to colourful tails. Further studies on the role of striped coloration in species that are sexually dimorphic for tail coloration (e.g. Belliure *et al.*, 2018) may help understand if there is a link between striped coloration and the role of colourful tails in sexual signalling.

A more detailed analysis of stripe position and tail coloration revealed that the evolution of *Dorsal* stripes is correlated with red tail and the evolution of *Lateral* stripes with blue tail. We reason that different visual predators may impose selection favouring particular combinations of tail colour and the positioning of stripes in lizards. The majority of striped lizard species are strictly ground-dwelling, and the angle at which the different predators (aerial vs. ground-dwelling) typically view and attack lizards is therefore likely to differ. Furthermore, it has been shown that red tail colour attracts attacks by birds of prey such as raptors (Fresnillo *et al.*, 2015a), and blue tails appear to function against terrestrial predators such as snakes or ground-dwelling birds (Cooper & Vitt, 1985; Brandley *et al.*, 2014; Kuriyama *et al.*, 2016). We therefore posit that different visual predators may impose selection favouring particular combinations of tail colour and the positioning of stripes in lizards. However, these results must be taken with caution as in the current analysis, we cannot account for the potential bias arising due to sampling artefacts.

Robustness and limitations of the results

Murali & Kodandaramaiah (2018) found body size in lizards to be negatively associated with the presence of

stripes. Although body size (SVL) is correlated to some of the ecological traits we examined (Tables S7–S17), we recovered the main findings as in the evolutionary pathway model (i.e. using Bayestraits) after accounting for the effect of body size by employing a regression-based analysis (Tables S7–S17).

Some of the correlations that we found might also be caused by a common selective pressure not related to predation and difficult to account for using the currently available methods (Maddison & FitzJohn, 2014). Further, we also acknowledge the limitation that our analysis indicates a correlation among traits and not causation (Freckleton, 2009). For instance, the phylogenetic associations between diurnal activity and colorations are not necessarily explained only by the deflection and motion dazzle effects. Striking colours may be used in sexual signalling (Kwiatkowski & Sullivan, 2002; Belliure *et al.*, 2018), which also could make them more likely to be found in diurnal species. Unrelated to predation, diurnal species may also have higher body temperature or different habitat preferences compared to nocturnal species, and this may have led to a correlation between striking colorations and body temperature. However, considering that thermoregulation does not predict striking colours or stripes, and that in lizards there is stronger experimental evidence for the antipredator function of tail coloration and longitudinal stripes than for sexual signalling (see Introduction), it appears unlikely that the role of visual predation would be irrelevant.

Other than predation, colourful tails in lizards have been suggested to work in intraspecific communication such as social (Clark & Hall, 1970; Fresnillo *et al.*, 2015a) and sexual signalling (Kwiatkowski & Sullivan, 2002; Belliure *et al.*, 2018). Further, striped coloration is reported to be one of the commonest forms of colour pattern observed in some species of lizards with female-limited pattern polymorphism and is thought to reflect selection due to different life history strategies (Paemelaere *et al.*, 2011; Ortega *et al.*, 2015). Therefore, it is possible that in some lizard species that were classified to have stripes and colourful tails in our study, these traits have functions unrelated to predation. However, since our overall results across the lizard phylogeny suggest that these colour patterns are linked to traits that are related to predation (i.e. caudal autotomy and rapid escape), a link that would not be expected for other functions (e.g. sexual signalling), we argue that predation likely has had a central role in shaping the evolution of these traits. Further, given the strong support for the functioning of stripes and colourful tail against predation in the previous studies (Jackson *et al.*, 1976; Cooper & Vitt, 1985; Castilla *et al.*, 1999; Hawlena *et al.*, 2006; Stevens *et al.*, 2008, 2011; Watson *et al.*, 2012; Brandley *et al.*, 2014; Fresnillo *et al.*, 2015b; Murali & Kodandaramaiah, 2016, 2018), we believe

that our findings should be applicable to the majority of lizard species.

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Authors' contributions

The study was initially conceptualized by GM and developed with inputs from UK and SM. GM collected the data, performed the statistical analysis and generated the figures. GM, SM and UK drafted the manuscript.

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Competing interest

The authors declare that they have no competing interests.

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Supporting information

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

Appendix S1 Ancestral state reconstruction.

Appendix S2 Phylogenetic signal.

Appendix S3 Correlated evolution of traits.

Appendix S4 Eco-physiological correlates of striped coloration.

Appendix S5 Eco-physiological correlates of colourful tail.

Appendix S6 Bayes factors for evolutionary transitions of character states.

Figure S1 (a) Reference image used for coding lizard coloration (Photo by Fritz Geller-Grimm via Wikimedia Commons).

Figure S2 Ancestral state reconstruction using Bayesian stochastic character mapping of (a) Red tail color (b) Blue tail color (c) Green tail color (d) Dorsal stripes (e) Lateral stripes.

Figure S3 Ancestral state reconstruction using hidden rates model left: striped coloration; right: colourful tail.

Figure S4 Plots depicting association between colourful

tail (presence (violet) vs. absence in dark-grey) and eco-physiological variables (a) Boxplots showing median and interquartile range of lizard body temperature; outliers are shown as black circles ($P = 0.2123$) and (b) Proportion of species with and without colourful tail which are ground-dwelling or scansorial ($P = 0.7199$).

Figure S5 Alternative models tested in phylogenetic path analysis.

Table S1 Model selection for the transition matrix used in the ancestral state reconstruction by Bayesian stochastic mapping implemented in *phytools* (Revell, 2012).

Table S2 Model selection for rate category in corHMM for striped coloration.

Table S3 Model selection for rate category in corHMM for colourful tail.

Table S4 Estimated phylogenetic signal for colouration traits utilized in this study.

Table S5 Results of the pairwise correlation analyses between discrete eco-physiological variables and (a) striped body and (b) colourful tail.

Table S6 Model comparisons for the evolutionary model used in the PGLS analysis testing relation between striped coloration and body temperature.

Table S7 Summary of the PGLS model on correlation between defensive colorations and eco-physiological variables.

Table S8 Model summary of phylogenetic logistic regression analysis on association between striped coloration and diel activity.

Table S9 Model summary of phylogenetic logistic regression analysis on the association between striped coloration and habitat.

Table S10 Model summary of phylogenetic logistic regression analysis on the association between striped coloration and colourful tail.

Table S11 Model summary of phylogenetic logistic regression analysis on the association between striped coloration and caudal autotomy.

Table S12 Model comparisons for the evolutionary model used in the PGLS analysis testing relation between colourful tail and body temperature.

Table S13 Summary of the PGLS model on correlation between colourful tail and eco-physiological variables.

Table S14 Evolutionary correlates of discrete eco-physiological traits and colourful tail from Bayestraits analysis.

Table S15 Model summary of phylogenetic logistic regression analysis on association between colourful tail and diel activity.

Table S16 Model summary of phylogenetic logistic regression analysis on the association between colourful tail and habitat.

Table S17 Model summary of phylogenetic logistic regression analysis on the association between colourful tail and caudal autotomy.

Table S18 Evolutionary transitions of character states for striped body coloration and caudal autotomy (Main Text Fig. 3) from Bayestraits analysis.

Table S19 Evolutionary transitions of character states for colourful tail and caudal autotomy (Main Text Fig. 4) from Bayestraits analysis.

Table S20 Evolutionary transitions of character states for striped body coloration and colourful tail (Main Text Fig. 5) from Bayestraits analysis.

Table S21 Comparison across possible models in phylogenetic path analysis.

Data deposited at Dryad: <https://doi.org/10.5061/dryad.156ss6b>

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