Foraging mode constrains the evolution of cephalic horns in lizards and snakes

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Abstract

A phylogenetically diverse minority of snake and lizard species exhibit rostral and ocular appendages that substantially modify the shape of their heads. These cephalic horns have evolved multiple times in diverse squamate lineages, enabling comparative tests of hypotheses on the benefits and costs of these distinctive traits. Here, we demonstrate correlated evolution between the occurrence of horns and foraging mode. We argue that although horns may be beneficial for various functions (e.g., camouflage, defence) in animals that move infrequently, they make active foragers more conspicuous to prey and predators, and hence are maladaptive. We therefore expected horns to be more common in species that ambush prey (entailing low movement rates) rather than in actively searching (frequently moving) species. Consistent with that hypothesis, our phylogenetic comparative analysis of published data on 1939 species reveals that cephalic horns occur almost exclusively in sit-and-wait predators. This finding underlines how foraging mode constrains

the morphology of squamates and provides a compelling starting point for similar studies in other animal groups.

1. BACKGROUND

The heads of many animals support eye-catching appendages. Such species range from hose-nosed weevils to rhinoceroses, and from angler fish to narwhals. The functions of these protruding cephalic structures are well understood in some groups (e.g., dung beetles and ungulates [1]), but less so in others, including squamate reptiles. The heads of numerous species of lizards and snakes are adorned with crests, spines, spikes, or other projections (which we refer to as ‘horns’ - Figure 1). These spectacular appendages may play a role in aspects such as foraging [2,3], enhancement of camouflage (by disrupting the outline of the head) [4–6], protection [7–11], and intraspecific interactions including combat and courtship [12–15]. Phylogenetic associations between horns and species’ morphology, ecology, and habitat have been used to infer fitness advantages of horns (e.g., [10,16–19]). In contrast, the potential costs of possessing such structures have rarely been mentioned.

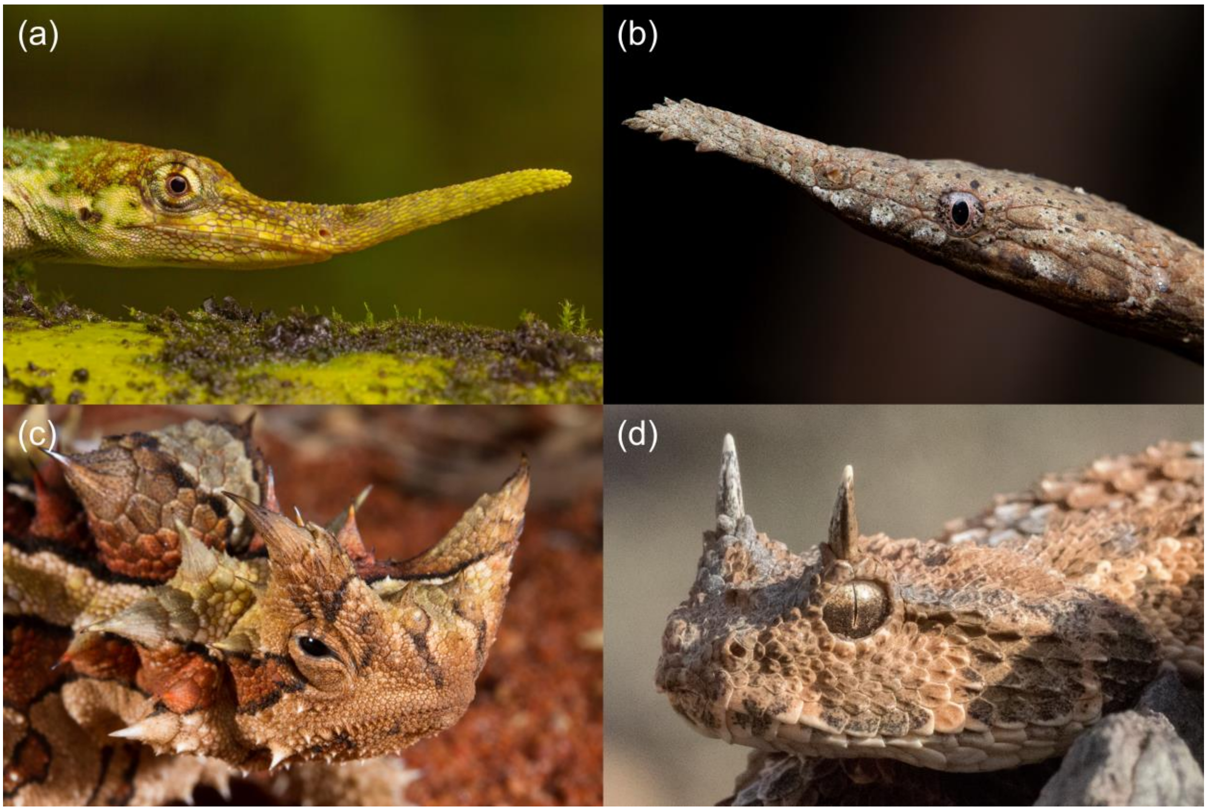

Figure 1. Examples of the diversity of cephalic horns in squamates. Rostral appendages in *Anolis proboscis* (a) and *Langaha madagascariensis* (b); squamosal-parietal and supra-ocular horns in *Moloch horridus* (c) and supra-ocular horns in *Cerastes cerastes* (d). Photo credits: Javier Ábalos Álvarez (a); Frank Deschandol (b); Stephen Zozaya (c); Laura Ruysseveldt (d).

Morphological traits entail both benefits and costs, and the evolution of any trait is driven by the balance between those two sides of the equation. For example, body armour in cordylid lizards provides protection (e.g., in *Ouroborus cataphractus* [20]) but restricts locomotion and flexibility, and thus is most evident in sedentary heavy-bodied species [21]. Costs for cephalic horns might include hindering locomotion and rendering an individual more visible when it moves. In general, camouflage works best when an animal is immobile [22,23]. We posit that protruding structures on the head may render a moving reptile more easily discernible from the background, hence more obvious to both predators and prey, or even hinder movements [24]. This hypothesis predicts that the benefit-to-cost ratio for cephalic horns is higher in sedentary individuals than in more active ones.

Many squamate species can be classified as either sit-and-wait foragers or actively foraging species [25,26]. Foraging style in squamates is associated with a suite of behavioural, physiological, morphological and life history characteristics, supporting the existence of a 'foraging syndrome' [27,28]. If horns are more conspicuous when animals are moving, we expect that these structures should occur more often in sit-and-wait predators than in widely foraging species. Here we test this hypothesis through phylogenetically informed comparative analyses.

2. MATERIALS AND METHODS

(a) DATA COLLECTION

We retrieved data on foraging mode from an updated version of the dataset of Meiri [29] and other published studies (see electronic supplementary material, Table S1 for full list of references), for a total of 1939 squamate species classified either as active or sit-and-wait foragers. Species with mixed foraging modes, and those lacking data on foraging mode, were excluded. For each of these 1939 species, we then collected data on the presence and absence of horns, visually assessed from images on ReptileDatabase [30] and 'research grade' observations from iNaturalist [31]. When images of a species were not available from those sources, we consulted recent publications on the taxon or original descriptions (see electronic supplementary material, Table S1 for full list of references).

We defined as 'horns' any protruding structure present in the rostral, ocular or occipital area of the head (Figure 1). Some of these structures fall into the category of 'true horns', being bony protrusions covered by a keratin sheath (e.g., in some chameleons [32]), whereas others are protuberant bony cranial processes and/or soft projections composed of connective tissue covered by one or multiple keratinous scales. Rostral horns were usually composed of either enlarged nasal (sub-, post-, supra-, inter-), rostral and/or fronto-nasal scales (e.g., in *Anolis proboscis*, *Langaha madagascariensis*, *Cyclura cornuta*). Ocular horns were either protruding ocular (supra-, post-) or supraciliary scales (e.g., in *Moloch horridus*, *Cerastes cerastes*, *Correlophus ciliatus*), whereas occipital horns included all overgrowths of parietal (e.g., crests, processes) and squamosal (e.g., tufts, spines, horns, casques) scales (e.g., in *Basiliscus basiliscus*, *Phrynosoma cornutum*, *Anolis chamaeleonides*). Species with any of those structures were considered horned. Species exhibiting appendages only in the adult stage (e.g., *Ceratophora stoddartii*), or in only one sex (e.g., *Anolis proboscis*), or species showing horn polymorphism (e.g., *Cerastes cerastes*), were also classified as horned. If horns were not evident from either images or descriptions, the species was classified as hornless. Species with elongated snouts (e.g., *Oxybelis fulgidus*) and/or specialised rostral scales (e.g., 'hog-nose', 'shovel-nose', 'leaf-nosed', and 'quill-snouted' snakes) were also classified as hornless because they lack protruding structures. We mapped our data on a time-calibrated phylogeny for squamates [33] for phylogenetic analyses.

(b) ANALYSES

Prior to phylogenetically informed data analysis, we explored associations between cephalic horns and foraging mode using chi-square (χ^2) statistics. After pruning the phylogenetic tree to include only the 1939 species covered in this study, we tested for phylogenetic signal in both variables by calculating Fritz and Purvis' D [34] (10 000 permutations; 'phylo.d' function; 'caper' package [35]). We then ran phylogenetic generalized linear models (PGLM logistic regression; ‘phyloglm’ function; 2000 bootstraps; ‘phylolm’ package [36]) to quantify the predictive power of foraging mode on the presence of cephalic horns (binomial variable: horned = 1; hornless = 0). We used Pagel’s [37] PGLS method (‘fitPagel’ function; ‘phytools’ package [38]) to test for a phylogenetic correlation between horns and foraging mode. We conducted such tests under both ‘equal rates’ (ER) and ‘all rates different’ (ARD) evolutionary models, exploring different dependency relationships between the two variables. Next, we performed ancestral state reconstructions via stochastic character mapping (1000 simulations; ‘make.simmap’ function [38]) to estimate the number of transitions from hornless to horned in squamate evolutionary history. We ran reconstructions under both ER and ARD scenarios and retained the most parsimonious model (i.e., lowest number of transitions).

To test the robustness of our results with respect to phylogenetic uncertainty, we repeated the PGLM test on a set of 1000 trees, randomly sampled from the 10 000 trees used to generate our adopted phylogeny [39] via the ‘tree_phyglm’ function of the ‘sensiPhy’ package [40].

3. RESULTS

Of the 1939 squamate species in this study, 53% were reported to be active foragers (n = 1031) and 47% to be sit-and-wait foragers (n = 908). Nine percent (n = 175) of all species were horned and 91% were hornless (n = 1764) (electronic supplementary material, Table S2a). The vast majority of horned squamates were sit-and-wait foragers (94%; n = 164; vs active foragers 6%, n = 11; $\chi^2 = 167.77$, d.f. = 1, $p < 0.001$) (Figure 2b; electronic supplementary material, Table S2b). Phylogenetically informed analyses corroborated the relationship between foraging mode and cephalic horns (β ± SE: 0.810 ± 0.3, pseudo-R^2 = 0.5, $z = 2.7$, $p < 0.01$) (electronic supplementary material, Table S3a). Also, all Pagel’s tests supported correlated evolution between horns and sit-and-wait foraging ($p < 0.001$) (electronic supplementary material, Table S4a).

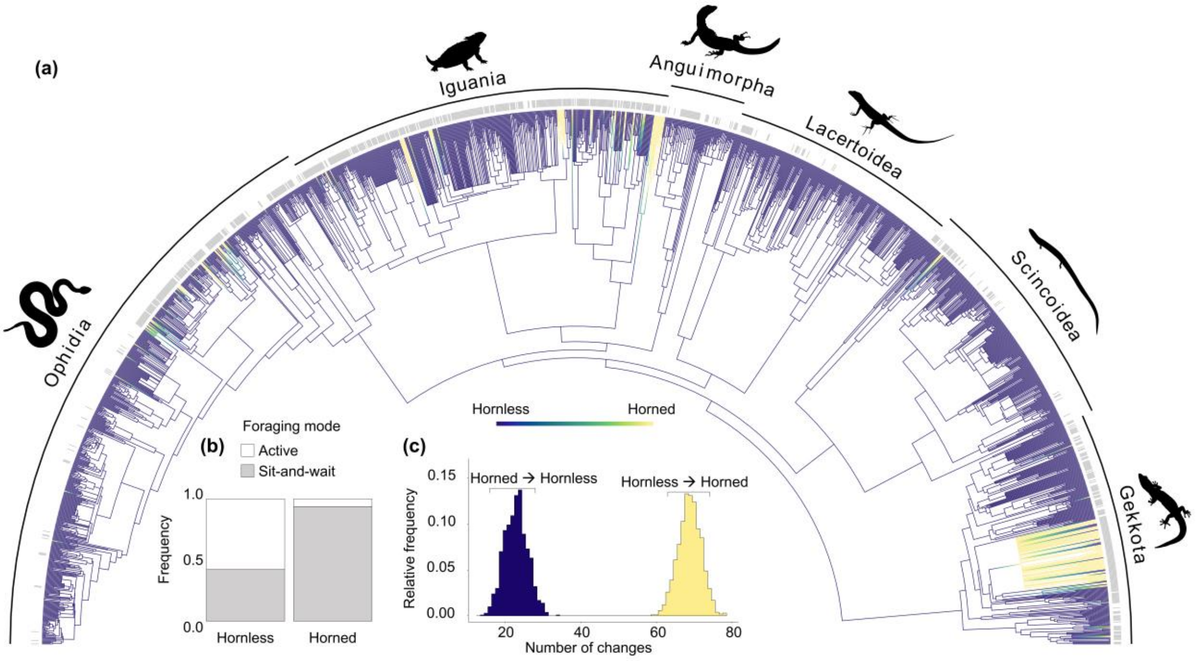

Figure 2. Horn expression across the adopted squamate phylogeny (a), with proportion of foraging mode (b) and frequency of trait gains and losses (c). Squamate phylogeny (1939 species) indicating the posterior probability of cephalic horns, obtained via stochasticity mapping along branches (ER model; 1000 replicates), with sit-and-wait foragers indicated at the branch tips of the tree (a). Frequencies of horn losses (from horned to hornless state) and gains (from hornless to horned state) across the 1000 replicates are also shown (c), together with the proportion of active and sit-and-wait foragers amongst hornless and horned squamates considered in this study (b). Silhouettes images from PhyloPic (https://www.phylopic.org/).

Fritz and Purvis' phylogenetic signal test revealed that horn presence exhibited moderately strong phylogenetic clumping ($D < 0$, $p_0 = 0.65$, $p_1 = 0$), as expected under a Brownian motion model of trait evolution ($D = 0$) (electronic supplementary material, Table S5). Stochastic character mapping over 1000 reconstructions (model = ER) revealed an average of 92 transitions (Figure 2a), of which 69 were independent gains (range = 63-74) and 23 were losses (range = 17-29) of horns across squamate phylogeny (Figure 2c; electronic supplementary material, Table S6a).

Furthermore, the evolutionary models considering interdependent evolution between the two variables scored best (lower AIC), suggesting that foraging mode had a role in horn evolution, but also that cephalic appendages (when present) influenced the species' foraging habits (electronic supplementary material, Table S4b). Results from the sensitivity analysis (β ± SE: 0.855 ± 0.3, $z = 2.9$, $p < 0.01$ - electronic supplementary material, Table S3b) furtherly supported our initial PGLM results (electronic supplementary material, Table S3a), suggesting that they are not influenced by phylogenetic uncertainty.

4. DISCUSSION

Consistent with our predictions, cephalic horns occur mostly in sit-and-wait predators. This result is unlikely to be due to chance, as correlated evolutionary changes between horns and sit-and-wait foraging have occurred several times in squamate phylogeny (Figure 2). Furthermore, our analyses show not only that shifts between states in both horns and foraging mode are common in squamates (electronic supplementary material, Table S6-7), but also that these shifts have happened together - or in tandem, in many cases (electronic supplementary material, Figure S1). This pattern suggests that our significant results are not driven by phylogenetic inertia, where a few clades happen to retain both traits [41].

Previous research has identified multiple plausible functions (benefits) of horns. For example, cephalic ornaments in many lizards are more developed in adult males than in females, and are used in territorial displays, courtship and/or male-male combat bouts (e.g., [8,14]). Where present in both sexes, horns may also serve in species recognition (e.g., in chameleons [12]). Other plausible functions of cephalic horns include foraging: for example, rostral projections of the tentacled snake (*Erpeton tentaculatum*) are mechanosensory structures that aid this sit-and-wait predator to capture fish [3]. Plausibly, sharp rigid spines on the head also may discourage a predator from seizing the animal (e.g., in *Phrynosoma* spp. [10] and *Moloch horridus* [11]). Lastly, cephalic horns may enhance the effectiveness of camouflage for a more sedentary reptile by disrupting the outline of the head [6]. Except for the latter hypothesis, all these functions should apply equally to active-foragers as to sit-and-wait predators, and thus cannot explain the strong association between cephalic horns and foraging mode revealed by our analyses.

Turning to the costs of cephalic horns, we suggest that complex protruding structures on an animal's head render it more detectable against the background while moving. Thus, a trait that enhances camouflage when the animal is immobile may have the reverse effect when the animal moves rapidly [22,42]. Theoretical and empirical studies on camouflage consistently demonstrate that detection of a complex outline is dependent on movement [43,44], but more direct experimental tests would be valuable. Ideally, such studies would incorporate rates of movement. Some chameleons, for example, move slowly but consistently through the habitat despite their overall reliance on sit-and-wait foraging [45]. At such slow rates of movement, cephalic horns may still help in camouflage.

Some of the most interesting cases of cephalic horns involve horned species that are active foragers rather than sit-and-wait predators: that is, exceptions to the general rule. If cephalic horns are a disadvantage to a fast-moving animal (by rendering it more conspicuous), why do some active foragers have cephalic horns? The answer may lie in features either of the horns, or of the movement patterns of the species involved. For example, males of the sea snake *Emydocephalus annulatus* develop pronounced rostral spines only during the mating season and use them to prod females during courtship [13,46]. In that case, the small (and temporary) forward-projecting spine would have little impact on the snake's visibility to predators, especially given the low movement rates of this species and the scarcity of predators in shallow-water habitats [47]. Small forward-projecting rostral spines are also seen in some of the other 'exceptions to the rule', such as the arboreal snakes *Ahaetulla nasuta* and *Philodryas baroni*. For these active foragers, however, horns may be more beneficial (e.g., for camouflage) than detrimental.

The functional relationships between cephalic ornamentation and foraging mode seen in our broadscale comparisons could be explored in more detail within clades that exhibit variation in these traits. An interspecific link between body shape (often associated with foraging mode) and investment into defensive and offensive structures (e.g., spines and horns) has been documented in several lizard lineages, whereby stockily built species have larger structures [21,48]. In phrynosomatid lizards, horn size appears to depend on predation pressure [10], and species with larger cephalic horns are slower and more specialised sit-and-wait foragers than are congeners with smaller horns [48]. Correlations between habitat type and horn morphology in vipers [17], and ornamentation conspicuousness (including horns) in agamid lizards [6], further support the idea that variation in habitat and, consequently in exposure to predators, may affect a species' investment into cephalic horns.

Intraspecific variation in horn elaboration also provides exciting research opportunities. For example, a single population of vipers can contain individuals with horns and others without, sometimes in the same litter (e.g., *Cerastes cerastes* [49]). It would be fascinating to see if the correlation between foraging mode and cephalic horns occurs within, as well as among, populations. Studying finer-scale variation in foraging behaviour (e.g., movement rates [26,50]) and degrees of horn development, rather than treating both as binary variables, may also prove insightful.

Cephalic structures often differ between the sexes (e.g., in *Langaha* spp. [51] and *Ceratophora* spp. [16]) and/or are developed in one sex only (e.g., *Anolis proboscis* [15,52]). In agamid lizards, the evolution of sexually dimorphic cephalic and body ornamentations occurred either in one sex independently or in both sexes contemporarily, with subsequent transition to male-biased dimorphism [53]. We hypothesise that in such cases, sex differences in horn size may be associated with sex differences in movement patterns (and perhaps in foraging mode), as commonly occur in squamates (e.g., *Acrochordus arafurae* [54,55]).

Our results reinforce suggestions that cephalic horns in lizards and snakes have evolved for a range of functions, and have arisen independently multiple times. This leaves many possibilities open for future studies on the significance and function of such enigmatic structures. Importantly, our analyses suggest that the evolution of horns in squamate reptiles may have been influenced more heavily by constraints (i.e., failure of camouflage when the animal moves frequently) than by advantages.

While we tested only squamates, our hypothesis may apply to additional taxa. Cephalic appendages are found in many other species, from arthropods to vertebrates including fish, amphibians, and mammals [1]. In all those groups, there are examples of foraging modes that range from ambush to active searching [56–60]. We predict that the association between foraging mode and cephalic horns will apply to such groups as it does to lizards and snakes. Analyses of selective forces for trait elaboration must consider costs as well as benefits when interpreting diversity in organismal morphology.

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Data Accessibility. Data and codes are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.fqz612jzm [61].

The data are also provided as table S1 in electronic supplementary material [62].

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