

Living in the danger zone: Exposure to predators and the evolution of spines and body armor in mammals

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Mammals have independently evolved a wide variety of morphological adaptations for use in avoiding death by predation, including spines, quills, dermal plates, and noxious sprays. Although these traits appear to protect their bearer from predatory attack, it is less obvious why some species evolved them and others have not. We investigated the ecological correlates favoring the evolution of specialized defenses in mammals, focusing on conspicuousness to predators due to body size and openness of habitat. We scored species for the degree to which they are protected by spines, quills, dermal plating, and sprays and used phylogenetic comparative analyses to study the morphological and ecological factors that may favor their evolution. We show that medium-sized insectivorous mammals (~800 g to 9 kg) that live in open habitats are more likely to possess one of these defensive traits to reduce predation. Smaller species (<200 g) and those in closed habitats can typically rely on crypsis to avoid predators, and larger species (>10 kg) are less susceptible to predation by most small- to medium-sized predators. We discuss how diet, metabolic rate, and defensive strategy evolve in concert to allow species to exploit this ecomorphological “danger zone” niche.

KEY WORDS: Antipredator, defense, insectivory, quills, spines.

To forage and search for mates, animals are often forced to move into exposed areas of their habitat, in which they might employ a wide variety of antipredator behaviors to minimize the risk of detection and capture (Lima and Dill 1990). Some species, however, must spend a great deal of time in such exposed areas, far from refugia, and may be under stronger natural selection to evolve more permanent “on-board” morphological defenses, such as defensive armor or weaponry for use in close combat, in case they are confronted or attacked by a predator far from safety (Caro 2005; Emlen 2008). Being larger in size and living in more open habitats not only makes detection by visual predators more likely, but also makes escape to more distant refugia less likely when chased by swift predators. Sticklebacks living in marine environments with predators bear spines on their back and armored plates on their lateral surfaces, but these features are reduced in freshwater in which predators are rarer (Reimchen 1992; Barrett et al. 2008). In Lake Washington, the water became more transparent after pollution was reduced, making the fish more conspicuous to predatory trout; in response, spiny defenses evolved to be much more ro-

bust (Kitano et al. 2008). Many studies have demonstrated that prey living in open, exposed environments (e.g., pelagic zones) with variation in abundance of predators that rely on vision to detect prey demonstrate plasticity in the development of protective morphologies (O'Brien et al. 1979; Stenson 1987; Smith and Jennings 2000). Avian predators exert positive directional selection favoring longer horns on lizards (Young et al. 2004), and the cordylid lizard *Ouroborus cataphractus*, for example, has more robust dermal armor than close relatives, due to its unique habit of visiting termite colonies far from their nearest retreat site, leaving it more exposed to terrestrial predation (Broeckhoven et al. 2015). In terrestrial mammals, Stankowich and Caro (2009) found that nearly all species of Bovidae in which females carried horns were either (1) highly exposed in their environments (as measured by shoulder height \times openness of habitat) and used their horns as antipredator weapons or (b) guarded exclusive territories and fought other females with their horns. Although we assume that these defensive morphologies have great current utility in reducing predation risk, nearly all animal species are under some sort



of risk of predation, and the question of why some species evolve specialized antipredator traits and others do not is less clear. In this study, we investigate how increased exposure and vulnerability influences the evolution of body armor (spines, quills, dermal plates) and noxious chemical defenses in mammals.

Morphological armor and weaponry in some shape or form has evolved independently several times to varying degrees in mammals (Table 1, Fig. 1; Stankowich 2012). Echindas (Tachyglossidae), tenrecs (Tenrecinae), hedgehogs (Erinaceidae), and some rodents (e.g., Echimyidae) have short permanent spines over some or all of their body (Vincent and Owers 1986). Old and New World porcupines (Hystricidae, Erethizontidae) have short-to-long quills that may become detached and lodged in the skin of predators. Armadillos (Dasypodidae) and pangolins (Manidae) have dermal plates made of keratin covering their bodies, forming a very strong shield against the bites of predators. Noxious spray defenses have evolved independently several times within Carnivora, are usually advertised with bold aposematic color patterns (Stankowich et al. 2011), and are favored in nocturnal species that are at greater risk from mammals, which results from intermediate body sizes and living in open habitats (Stankowich et al. 2014). The antipredator utility of these traits seems clear, but the ecological conditions that favor their evolution in some taxa but not others are not, and the degree of protection provided by different types of defense likely varies significantly and is mostly unknown.

Previous authors have focused on how constraints on body size and metabolism influence the evolution of body armor. Although small mammals may simply be unable to grow and develop expensive body armor that is robust enough to be effective due to the high metabolic demands of small bodies, Lovegrove (2000, 2001) suggested that as mammals evolve larger body masses, from small (200 g) to large (>4 kg), they gradually lose their ability to conceal themselves due to small size and yet are still too small to defend themselves in combat with larger predators. He argued these intermediate-sized mammals are, therefore, left with the option of either evolving morphologies to attain running speeds greater than allometric predictions (requiring high basal metabolic rates [BMRs]) or rely on body armor for protection (requiring minimal BMRs); this latter effect with minimal BMRs is particularly strong in areas with unpredictable resource availability because energy conservation is favored. Lovegrove's results showed that armored mammals have lower BMRs. Feeding behavior can also have a significant influence on the need for antipredator defenses. McNab (1984) showed that myrmecophagous mammals (diet of primarily ants and termites) have lower BMRs than mammals with other feeding styles. Because lower BMRs limit locomotor ability and escape speed, these myrmecophagous species tend to have body armor. There are, however, many armored species that are not myrmecophagous, but are, instead primarily insectivorous

(e.g., tenrecs, hedgehogs). We suggest that, because terrestrial species that are primarily insectivorous may spend a large proportion of their time and energy rooting in the soil with their heads down, thereby reducing their ability to use their eyes and nose to be vigilant for or detect odor cues of approaching predators and forcing them to rely on other sensory modalities to detect predators, mammals that are primarily insectivorous similarly may be at relatively greater risk of not detecting attacking predators and would benefit from body armor if confronted at a close range. Although these authors were focused on mechanistic correlations between body armor and metabolism, we still lack a general understanding of how this link between physiology and morphology interacts with ecology. Here, we focus on the sources of selection that favor the evolution of extreme antipredator morphologies and attempt to provide a conceptual model for how enhanced predation risk affects the evolution of defenses.

In this study, we focus on how variation in predation risk influences the evolution and strength of mammalian defenses. Just as there should be a lower body mass threshold that promotes the evolution of body armor, there should also be an upper body mass threshold, above which prey are too large for all but the largest predators to consume, or at which body armor becomes too energetically costly. Only 52 of 246 (21%) species of Carnivoran predators are known to kill prey larger than 5 kg, and only 36 of 246 (15%) take prey larger than 10 kg (Stankowich, Fay, Kresky, unpubl. data). These values are 13 of 309 (4%) and 5 of 309 (2%), respectively, for Falconiform and Accipitriform birds of prey and 2 of 196 (1%) and 1 of 196 (0.5%), respectively, for owls (Stankowich, Fay, Kresky, unpubl. data). This suggests that prey larger than 5–10 kg are likely only going to be vulnerable to a few, if any, different predator species in any one location in their range, limiting selection favoring the maintenance of body armor.

We compiled data on defensive ability, body mass, habitat openness, and feeding behavior and across Mammalia. We predicted that species that are intermediate in body size (~200–10,000 g) and living in more open environments are more conspicuous to predators, are exposed in their environment, and will be more likely to have stronger morphological defenses. We also predicted that being primarily insectivorous will further promote the evolution of body armor in exposed species.

Methods

We sought to quantify the degree to which individual mammal species have some type of body armor, including permanent spines, detachable quills, and armored plates. We first identified the terrestrial mammalian groups that contained species that have evolved significant morphologies that seemed clearly adapted for defense (and not some other purpose such as sexual

Table 1. Examples of defensive scores from different mammalian taxa.

Order	Family	Species	Common name	Defense score			
				1	2	3	4
Afrosoricida	Tenrecidae	<i>Tenrec ecaudatus</i>	Common tenrec	6	8	8	5
Afrosoricida	Tenrecidae	<i>Hemicentetes semispinosus</i>	Lowland streaked tenrec	21	24	18	19
Carnivora	Mephitidae	<i>Mephitis mephitis</i>	Striped skunk	48	60	60	39
Carnivora	Viverridae	<i>Genetta genetta</i>	Common genet	32	40	40	26
Carnivora	Ailuridae	<i>Ailurus fulgens</i>	Red panda	16	20	20	13
Cingulata	Dasypodidae	<i>Dasypus novemcinctus</i>	Nine-banded armadillo	48	60	48	15
Eulipotyphla	Erinaceidae	<i>Erinaceus europaeus</i>	Western hedgehog	21	24	18	19
Eulipotyphla	Erinaceidae	<i>Hemiechinus auritus</i>	Long-eared hedgehog	12	12	8	12
Monotremata	Tachyglossidae	<i>Zaglossus bruijnii</i>	Western long-beaked echidna	48	60	48	39
Pholidota	Manidae	<i>Manis javanica</i>	Sunda pangolin	48	60	48	27
Rodentia	Echimyidae	<i>Echimyus saturnus</i>	Dark spiny tree-rat	10	12	12	9
Rodentia	Echimyidae	<i>Proechimys guyannensis</i>	Cayenne spiny rat	4	4	4	4
Rodentia	Erethizontidae	<i>Coendou prehensilis</i>	Brazilian porcupine	42	48	36	38
Rodentia	Erethizontidae	<i>Erethizon dorsatum</i>	North American porcupine	36	48	48	27
Rodentia	Hystriidae	<i>Hystrix indica</i>	Indian crested porcupine	48	60	60	39
Rodentia	Hystriidae	<i>Trichys fasciculata</i>	Long-tailed porcupine	10	12	12	9

Equations and descriptions for how each defensive score was calculated are described in the Methods. Defense score 1 ranges from 0 to 48; Defense scores 2 and 3 range from 0 to 60; Defense score 4 ranges from 0 to 39.

combat [e.g., horns, antlers], locomotion [e.g., hooves, claws]). We identified groups bearing (a) permanent robust spines: Tachyglossidae, Tenrecidae, Erinaceidae, Echimyidae; (b) detachable quills: Hystriidae, Erethizontidae; (c) epidermal plates or scales: Dasypodidae, Manidae; and (d) noxious secretions: Carnivora. All other mammalian taxa were judged to not have a significant morphological defensive armor or weapon and given defensive scores of 0 (see below). Note that other rodent genera have distinct spiny fur (e.g., *Acomys*), but we chose to set a conservative threshold for what constituted an efficacious defensive spine at 1 mm in thickness; further, spines with a thickness below this level were not reliably detectable in photographs. For each species in groups (a–c), we used one to three high-quality photographs from books (e.g., Nowak 1999) and internet resources (e.g., Arkive [www.arkive.org], American Society of Mammalogists Image Library [http://www.mammalsociety.org/image-library]) to score five different armor variables and use them to compute objective defense scores, rather than subjectively put species on a scale of 0–5 or 0–10. We scored *Body coverage* as the amount of the body covered by spines, quills, or armor plates: 0 = no coverage (no armor); 1 = dorsum only; 2 = dorsum and flanks; 3 = dorsum, flanks, and ventrum. We also scored whether the animal was protected on its *Head* (0 = no, 1 = yes) and *Tail* (0 = no, 1 = yes). For those species with spines or quills, we also scored the approximate *Length* (1: <2 cm; 2: 2–5 cm; 3: >5 cm) and *Thickness* (1: soft or coarse fur only <1 mm thick; 2: ~1 mm thick; 3: 1–2 mm thick; 4: >2 mm thick) of the longest, most robust

spines/quills on the body. Using descriptions in Nowak (1999), we scored whether each genus of protected animals was able to *Roll* into a ball to further protect itself during predatory attacks (0/1); rolling into a ball typically conceals all vulnerable body parts. Using these data, we generated equations to quantify the degree to which a species was protected with body armor; these equations generally multiply the extent of armor coverage (Body coverage [0–3], Head [0/1], Tail [0/1], Roll [0/1]) on the body by the robustness of that armor (Hair Length [1–3] and Thickness [1–4]); to test how robust our findings were to variation in how we calculated the defensive score, we came up with four different equations and ran the analyses on each. For species with spines and quills:

$$\text{Defense score 1} = (\text{Body coverage} + \frac{1}{2}\text{Head} + \frac{1}{2}\text{Tail} + \text{Roll}) \times \text{Length} \times \text{Thickness}$$

$$\text{Defense score 2} = (\text{Body coverage} + \text{Head} + \text{Tail} + \text{Roll}) \times \text{Length} \times \text{Thickness}$$

$$\text{Defense score 3} = (\text{Body coverage} + \text{Head} + \text{Tail}) \times \text{Length} \times \text{Thickness}$$

$$\text{Defense score 4} = (\text{Body coverage} + \frac{1}{8}\text{Head} + \frac{1}{8}\text{Tail} + \text{Roll}) \times \text{Length} \times \text{Thickness}$$

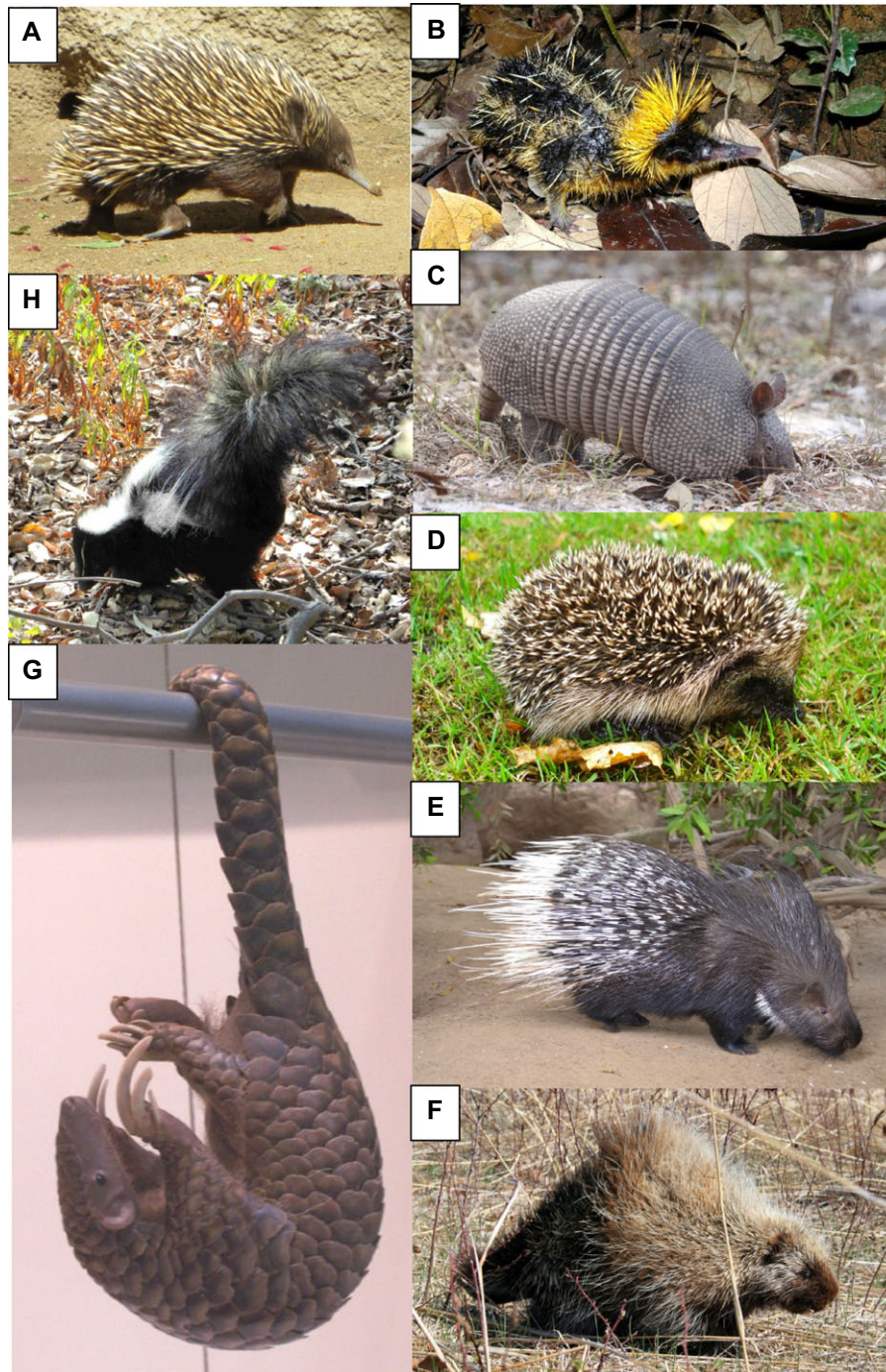


Figure 1. Representative examples of defensive morphologies described in this study (Flickr attribution photo credit). (A) Short-beaked echidna (*Tachyglossus aculeatus*, T. Stankowich); (B) lowland streaked tenrec (*Hemicentetes semispinosus*, F. Vassen); (C) nine-banded armadillo (*Dasypus novemcinctus*, C. Simmons); (D) European hedgehog (*Erinaceus europaeus*, M. Talbot); (E) Indian crested porcupine (*Hystrix indica*, T. Stankowich); (F) North American porcupine (*Erethizon dorsatum*, USFWS Midwest); (G) Chinese pangolin (*Manis pentadactyla*, M. Pa'i Ki'i); (H) striped skunk (*Mephitis mephitis*, T. Stankowich).

For example, the Brazilian porcupine (*Coendou prehensilis*) has a Defense score $1 = [2 + \frac{1}{2}(0) + \frac{1}{2}(1) + 1] \times 3 \times 4 = 42$ (Table 1) out of a maximum of 48. For species with epidermal or dermal plates or scales, there were no scores for Length or

Thickness of hair. Armadillo and pangolin armor are very strong and can withstand the bites of large carnivore predators (Chen et al. 2011) unlike porcupine quills, which must be erect to be effective against a predator. For the sake of comparison and putting armor

and spines/quills on the same defensive scale, and because Length \times Thickness has a maximum value of 12 in species with spines and quills, we replaced these factors with a multiplier:

$$\text{Defense score 1} = (\text{Body coverage} + \frac{1}{2}\text{Head} + \frac{1}{2}\text{Tail} + \text{Roll}) \times 12$$

$$\text{Defense score 2} = (\text{Body coverage} + \text{Head} + \text{Tail} + \text{Roll}) \times 12$$

$$\text{Defense score 3} = (\text{Body coverage} + \text{Head} + \text{Tail}) \times 12$$

$$\text{Defense score 4} = (\text{Body coverage} + \frac{1}{8}\text{Head} + \frac{1}{8}\text{Tail} + \text{Roll}) \times 12.$$

Defense score 1 had a maximum value of 48, scores 2 and 3 had maximum values of 60, and score 4 had a maximum of 39 and all equations have a minimum score of 0 (all nondefended animals). To score the noxiousness of Carnivorans (group d above), we incorporated published scores (Stankowich et al. 2011, 2014) of the ability of Carnivorans (members of order Carnivora) to spray noxious anal gland secretions in defense toward predators (*Spray behavior*) into the dataset: “0 = no evidence of emitting anal gland secretions during predatory encounters; 1 = emits foul scent from anal glands or oozes secretions from the anal glands; 2 = ejects anal gland secretions in a nondirected weak stream or spray; and 3 = ejects anal gland secretions in a directed, aimed stream or spray at the potential predator.” To integrate these scores onto the scales of our three defensive scores, we simply multiplied them by 16, 20, 20, and 13 for Defensive scores 1, 2, 3, and 4, respectively; this technique gives highly effective sprayers such as striped skunks (*Mephitis mephitis*) and zorillas (*Ictonyx striatus*) the maximum defensive score, equal to the best defended armadillos and porcupines. Although many other mammals emit a foul smell when they are harassed by predators, we identified the striped possum (*Dactylopsila trivirgata*) as having exceptionally potent noxious secretions that are secreted through its skin and gave it scores of 16, 20, and 20 for the three defensive scores, respectively, similar to Carnivorans that just ooze secretions from anal glands. All other mammal species lacking spines, quills, dermal plates, or noxious secretions received a *Defense score* of 0. Example scores from a variety of defended species are shown in Table 1. We only used these objectively calculated defense scores because we feared subjectively ranked defense scores by a third party would artificially inflate scores from larger or more well-known taxa (e.g., armadillos) and underestimate scores from smaller or more obscure taxa that might be very well defended for their size (e.g., tenrecs). Nevertheless, the results from these objective scores are only as reliable as the equations used to calculate them and should be treated with some degree of caution.

To test hypotheses about the factors that influence antipredator evolution across all terrestrial mammals, we were limited to factors for which data were widely available across diverse orders. We collected average *Body mass* (g) for each species primarily from the Masses of Mammals Database (Smith et al. 2003). For remaining species with missing masses in orders in which morphological defenses are found, we attempted to collect body mass from other published sources (e.g., Nowak 1999; Wilson and Mittermeier 2009; Kingdon et al. 2013). Body mass was \log_{10} -transformed to achieve a normal distribution (Body mass 1).

We downloaded species-level habitat data from the IUCN Redlist database (IUCN 2011) and the presence or absence of each species was scored (0/1) for each of the 18 habitat types (below). Following Stankowich et al. (2011, 2014), each species was scored as present or absent in each habitat type (0/1), each habitat type was given a score between 0 and 1 corresponding to the relative ability to visually detect an animal in the habitat (0 = completely concealed/dense, 1 = completely barren), and the average score of the habitats each species was present in was calculated (*Openness*) using the following scores: Temperate Forest (0.2), Tropical Forest (0.1), Savanna (0.7), Temperate Shrubland (0.6), Tropical Shrubland (0.5), Tundra (0.9), Temperate Grassland (0.8), Tropical Grassland (0.8), Wetlands (0.3), Rocky (0.8), Desert (0.95), Marine (intertidal, coastal, supratidal) (0.8), Artificial Grassland (0.8), Urban (0.8), Artificial Marine (0.8), and Caves/Subterranean (0.05). For example, a species that lived in Savanna, Temperate Grassland, and Temperate Shrubland would receive an *Openness* score of $(0.7 + 0.8 + 0.6)/3 = 0.7$. Previous studies that have used this scoring method (Stankowich et al. 2011, 2014) have shown their results are robust to slight variations in these individual habitat scores. Species diets were collected from the MammalDIET database version 1.0 (Kissling et al. 2014); in this study, the authors gathered primary diet data on mammal species and for those species that lacked dietary information, they inferred (*extrapolated*) diets for these species from similarly related species (3329/5364 species = 62%). Internal and external validation showed that these extrapolations were reliable for the species primary food items and the most common diet categories had high potential for correct extrapolation. To get as complete a dataset as possible, we treated their primary and extrapolated data as equally valid. From these data we scored species as “primarily” *Insectivorous* (1) if Kissling et al. (2014) scored them as an “Insectivore” and all other food types (mammals, birds, reptiles, fish, and plants) were scored as either not eaten, secondarily eaten, or only occasionally eaten. Any species not satisfying these criteria were considered not primarily insectivorous and received a score of 0. The database has many omnivorous species that list several of these food types as primarily eaten, so our goal was to characterize species that focus mainly on insects but occasionally may take some other food type. The final complete dataset

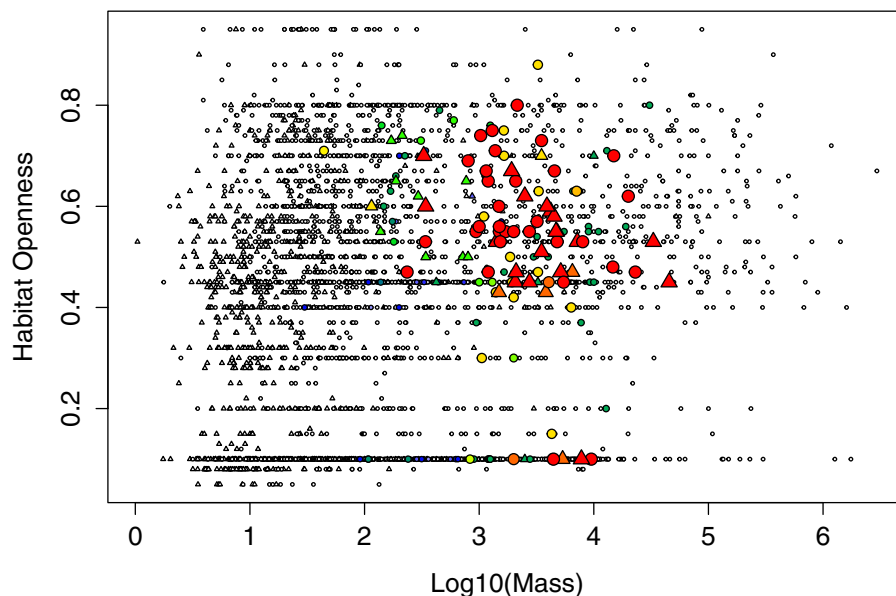


Figure 2. Scatterplot showing relationship among body mass, openness of habitat, and morphological Defense score 1. Small open markers denote undefended species. Larger colored markers denote defended species; increasing size and “warmth” of color of the marker indicates greater defense score. Triangle markers represent species that are primarily insectivorous; circle markers represent noninsectivores.

contains 3502 terrestrial mammal species and is available as on-line supplementary material.

ANALYSES

We hypothesized that as lineages with low body mass evolve to be larger past some critical point (e.g., 200 g), there should be a correlated increase in strength of morphological defenses (i.e., positive relationship between body mass and defense). We also hypothesized that as intermediate-sized mammals evolve to be even larger than some critical mass where far fewer predators are able to kill them, we should see a correlated decrease in strength of morphological defenses (i.e., a negative relationship between body mass and defense). Rather than use polynomial or global regression models that require a single predictive formula to be valid over the entire data space, we used regression trees to subdivide the data to examine how the predictors influence the defense score in different subgroups. For example, habitat openness may be positively correlated with defense score but only for species in a certain range of body masses. These tests do not control for phylogeny, but instead are a way to visualize and describe the different ways the predictors influence the response. We conducted Regression Trees Analysis using the “tree” package (Ripley 2014) in *R* (R Core Team 2012). To avoid overfitting with too many branches, the tree was pruned to the smallest size compatible with minimum 10-fold cross-validated error using the *prune.tree* and *cv.tree* functions in the tree package.

Because we hypothesized that the direction of selection changes depending on body state, we chose to transform body

mass so that as all species evolved toward intermediate size (whether from very small or very large), the change in body size would be unidirectional and testable by traditional phylogenetic comparative analyses. Therefore, we identified the approximate midpoint of the entire mammal body mass distribution on a logarithmic scale as $\log_{10}(\text{Body mass}) = 3.5$ (Fig. 2). For all species with mass greater than this value, we subtracted the difference between their $\log_{10}(\text{Body mass})$ and this midpoint from the midpoint itself so that as the mass increased above 3.5, the transformed body mass declined toward zero. So for Body mass 2, if $\log_{10}(\text{Body mass}) \leq 3.5$, then $\text{Body mass 2} = \log_{10}(\text{Body mass}) - 3.5$; if $\log_{10}(\text{Body mass}) > 3.5$, $\text{Body mass 2} = 3.5 - (\log_{10}[\text{Body mass}] - 3.5)$. Using this transformed predictor, our hypothesis predicts a positive correlation between changes in body mass and changes in defensive score, independent of the actual mass of the lineages.

To test our hypotheses about defenses, we ran four regression trees (uncorrected for phylogeny) and four phylogenetically corrected analyses as pairs. We examined the effect of body mass, habitat openness, and insectivory on defensive scores 1–4; we used Body mass 1 for the regression tree and Body mass 2 for the phylogenetic analysis. We used the first tree from the set of 100 complete species-level mammalian phylogenies generated by Faurby and Svenning (2015) to account for phylogenetic effects. To analyze defense scores, we conducted Phylogenetic Generalized Least Squares (PGLS) analyses using the “caper” package (Orme et al. 2012) in *R* (R Core Team), where lambda is computed using maximum-likelihood methods. In the PGLS models,

we included the interaction term between Openness and Body mass 2 because we predicted that defended animals would be both intermediate in size and live in open habitats.

Results

Species with some sort of morphological defense (spines, armor, noxious odor) ranged in body mass from 30 g to 45 kg, but most fell within the range 800 g to 9 kg (Fig. 2). The regression trees for the three defense scores varied in number of terminal nodes, but all agreed identically on the first two main splits (Fig. 3). Defended species were most strongly clustered into mammals with \log_{10} (Body mass)—that is, Body mass 1—greater than ~ 2.9 (i.e., ~ 800 g) and that are primarily insectivorous. Beyond these splits, the different defense scores varied in how much they were split further by Habitat openness and Body mass. Defense score 1 fit the second most complex tree (nine nodes, Fig. 3A), with the most heavily defended species having \log_{10} (Body mass) 3.2995–3.528 (2.0–3.4 kg) and living in more open habitats (Openness > 0.415), or having \log_{10} (Body mass) 3.528–3.946 (3.4–8.8 kg). Defense score 2 had similar results (Fig. 3B), again with the most defended species having \log_{10} (Body mass) 3.2435–3.928 (1.8–8.5 kg) and living in open habitats (Openness > 0.44). The tree for Defense score 3 (Fig. 3C) did not bifurcate further beyond the initial body mass and primary insectivory splits. Finally, the Defense score 4 fit the most complex tree (10 nodes, Fig. 2d), with the most heavily defended species falling into two distinct groups: (1) noninsectivorous with \log_{10} (Body mass) 2.887–3.320 (0.8–1.6 kg) and living in more open habitats (Openness > 0.555), and (2) insectivorous with \log_{10} (Body mass) 3.096–3.928 (1.2–8.5 kg) and living in more open habitats (Openness > 0.444).

PGLS analyses of the four defense scores using Body mass 2 (see Methods for explanation) all agreed, showing a significant interaction effect of Body mass \times Habitat openness and a main effect of diet. Increases in body mass in small lineages and decreases in body mass in large lineages toward intermediate masses (i.e., increase in Body mass 2) paired with increases in openness led to correlated increases in defensive ability (Interaction effect Openness \times Body mass 2: Defense score 1: $\lambda = 0.985$, $t = 2.0836$, $P = 0.0373$; Defense score 2: $\lambda = 0.985$, $t = 2.0963$, $P = 0.0361$; Defense score 3: $\lambda = 0.983$, $t = 2.1858$, $P = 0.0289$; Defense score 4: $\lambda = 0.984$, $t = 2.0514$, $P = 0.0403$). Increasing defensive ability was also correlated with transitions to a primarily insectivorous diet (Defense score 1: $t = 2.6602$, $P = 0.0078$; Defense score 2: $t = 2.5641$, $P = 0.0104$; Defense score 3: $t = 2.3865$, $P = 0.0171$; Defense score 4: $t = 2.5913$, $P = 0.0096$). The main effects of Habitat openness and Body mass 2 were not significantly correlated with defense score in

any model ($0.1054 > P > 0.1937$) using the phylogenetically corrected analyses.

Discussion

We found that intermediate-sized primarily insectivorous species living in more open habitats are more likely to have some sort of specialized morphological defensive strategy. We found that as lineages of small mammals evolve a larger (more intermediate) body size they are likely to evolve some type of body armor. We also found evidence of further elaboration of the defensive morphology being favored by living in exposed habitats in which prey are more visible to predators in most clades. Together, our results suggest that species that are more exposed in their environments due to larger size and open habitats are selected to evolve body armor. Finally, adopting a primarily insectivorous diet also favors the evolution of body armor, possibly due to the reduced ability to rely on vision and olfaction in insectivores that root around for prey in the earth; having body armor provides protection if an animal is surprised by an undetected predator at close range.

As Lovegrove (2001) originally speculated, as small rodent-sized mammals evolve larger body sizes, it presumably becomes more and more difficult to achieve crypsis; intermediate-sized animals are therefore too large to hide but too small to defend themselves in combat with an avian or mammalian predator, unless they are carnivorous predators themselves (e.g., small Carnivorans). Alternatively, spines and armor may not be an effective defense on smaller mammals if they cannot evolve to be robust or strong enough to withstand carnivore biteforce. Tenrecs are small and spined but still susceptible to occasional predation by savvy mammalian predators (Eisenberg and Gould 1970). Greater exposure to predators due to size and living in more open habitats also favors the evolution of other special defenses (e.g., defensive horns in female Bovids: Stankowich and Caro 2009). Our results showed that species with high defense scores also had high Openness scores, but closer inspection indicates that taxa differed in the proportion of their defended species that live in open (>0.5) habitats. The significant interaction effect with body mass was likely driven by tenrecs (5/5 defended species live in open habitats), Carnivorans (45/68), armadillos (13/19), and hedgehogs (12/12). On the other hand, defended rodents were more associated with closed habitats and more arboreal activity—Echimyid spiny rats (19/22 defended species live in closed [<0.5] habitats), New World porcupines (7/8), Old World porcupines (6/11).

Overall, there appears to be a danger zone for mammals that are intermediate in size (~ 800 g to 9 kg) and living in open habitats (shrublands, grasslands, deserts, savannahs, tundra; Fig. 2). Species near the boundaries of this zone have weaker defenses. Fifty-five of the 232 species weighing 800 g to 9 kg and having openness scores greater than or equal to 0.5 have body armor.

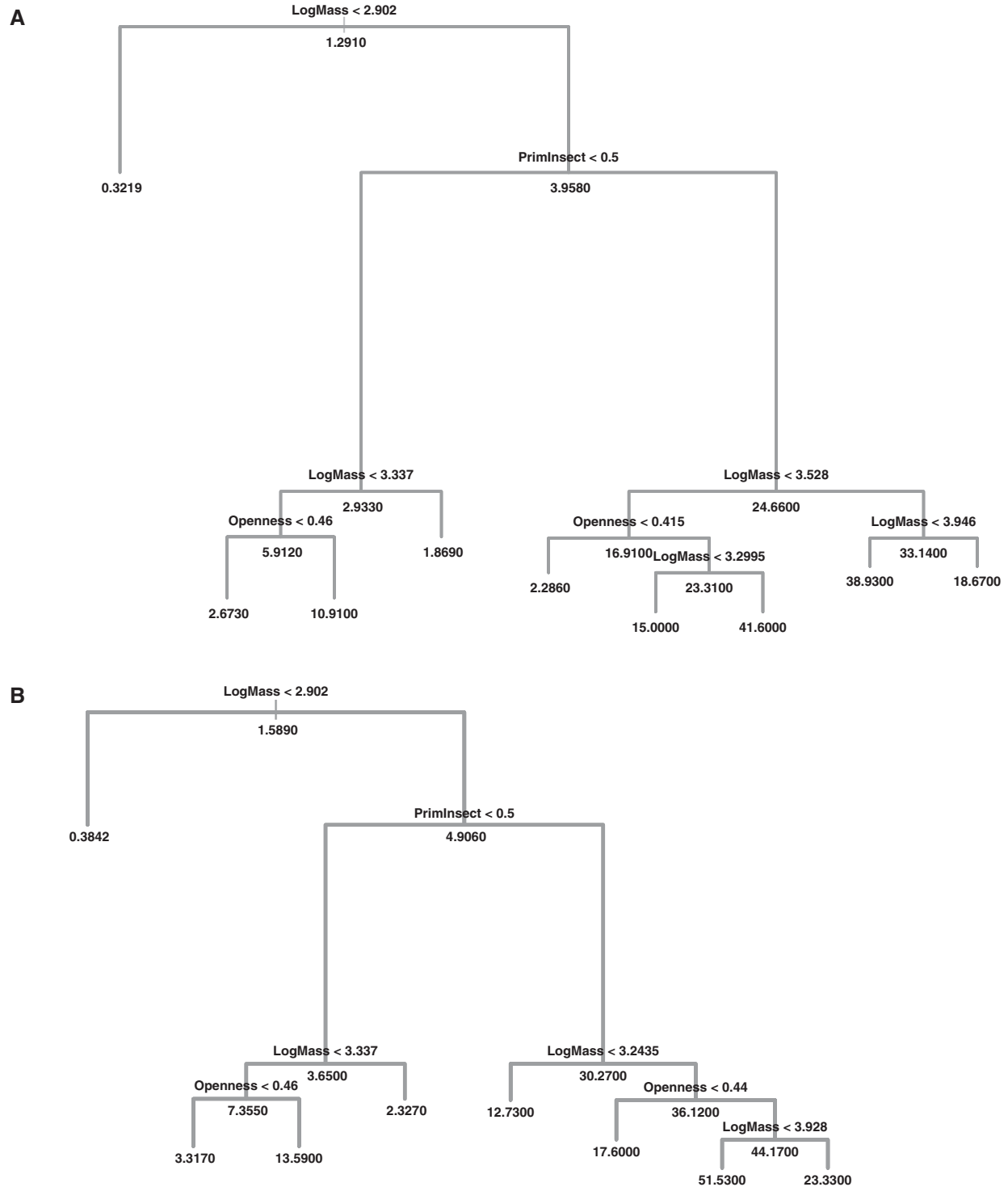


Figure 3. (Continued).

Of the remaining 177 species that lack body armor, 62 are saltatorial and have a specialized means of rapid escape, and 43 are Carnivorans that are either predators themselves or likely have adaptations to defend themselves against larger carnivores. The residual species ($N = 53/232 = 23\%$) may have other strategies for avoiding high exposure to predation risk, including reliance on

protection in tunnels or water, loose or thick skin, large claws and teeth, vigilance benefits of large group size, or climbing into whatever trees are present. So, 77% of the species in the danger zone have some sort of significant defensive strategy. Species weighing less than ~ 200 g can more easily achieve crypsis through small size or use burrows to escape predators; species weighing greater

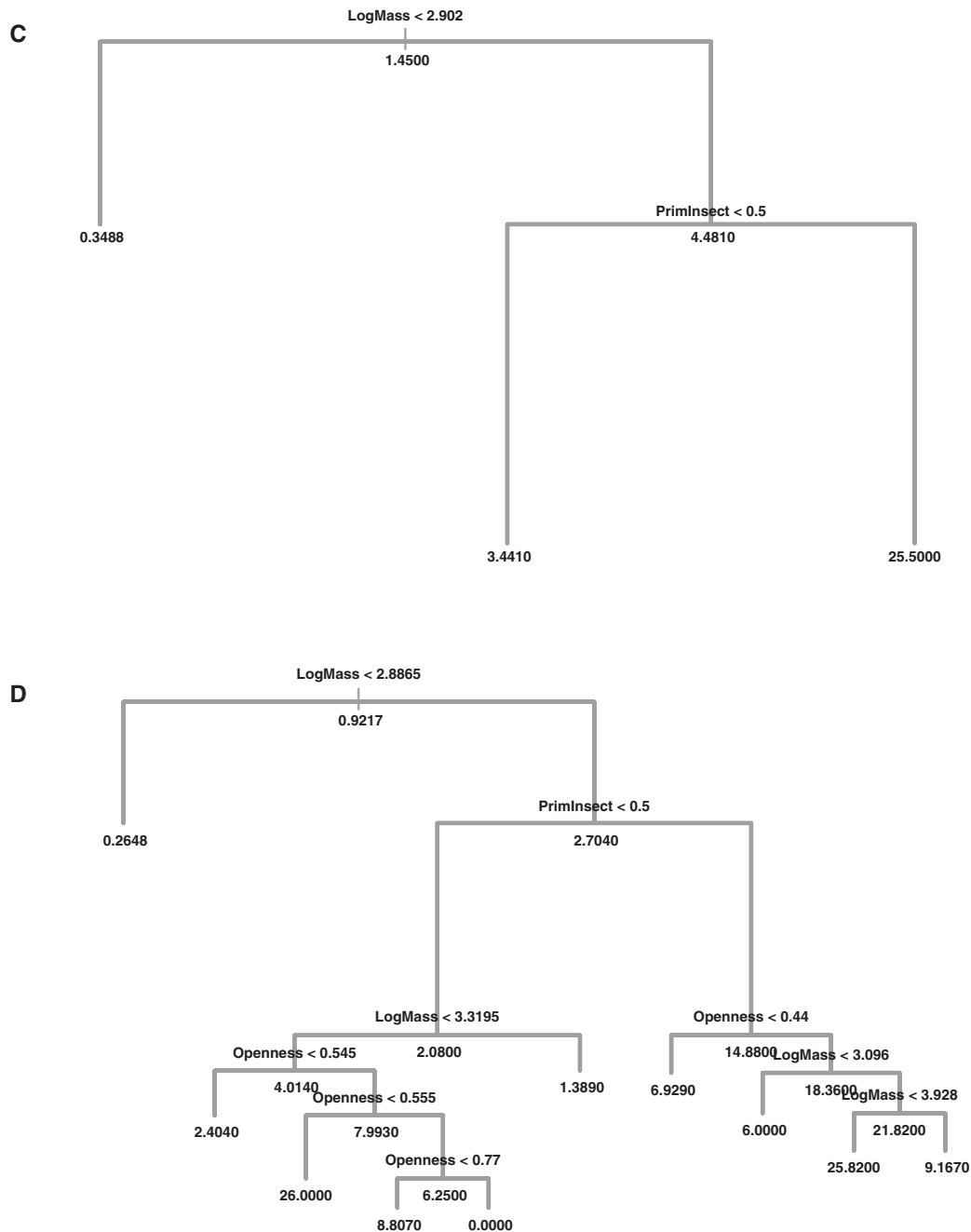


Figure 3. Regression trees of the effects of body mass, openness, and insectivory on (A) Defense score 1, (B) Defense score 2, (C) Defense score 3, and (D) Defense score 4. The separation rule is displayed above each node and the average defense score of the node is displayed below the node. Branch lengths are proportional to the decrease in impurity at each step. LogMass = Body mass 1, Openness = Habitat openness, PrimInsect = Primarily insectivorous (0/1).

than ~10 kg have reduced predation risk, have a greater ability to defend themselves or outrun their predators, or are unable to maintain the energetic costs of maintaining and carrying increasingly heavier morphological weapons; species living in closed habitats can presumably still avoid detection even at large body sizes and have less need for antipredator weapons (Stankowich and Caro 2009). The danger zone appears to be an ecomorpho-

logical niche that requires the species that exploit it to have more elaborate, specialized forms of antipredator defense, be they morphological (e.g., armor, spines, sprays) or behavioral (e.g., rapid escape speed, aggression).

Previous studies have focused on the proximate correlates of mammalian body armor, demonstrating that armored species and insectivorous species have lower BMRs than other groups. It is not

clear, however, whether low BMRs due to insectivory necessitate body armor or whether the evolution of defensive armor allowed species to exploit an insectivorous lifestyle and reduce BMR. Our results shed light on the ultimate correlates of body armor, suggesting that body armor allows protection from predation in species that are particularly at risk: those that are intermediate in size and suffer from reduced vigilance due to a feeding style that requires foragers to keep their heads down at the ground. McNab (1984) suggested that myrmecophagous mammals might have more limited foraging opportunities due to unpredictable prey scattered in the habitat and because the toxic or unpalatable nature of ants and termites limit the quantity a forager could consume at any one time. This reduces energy intake, which reduces BMR and ability to move and escape quickly, which requires foragers to have a protective armor in case they are confronted with a more agile predator. It is striking that the “most insectivorous” intermediate-sized open-habitat mammals (the myrmecophagous pangolins and armadillos) that possibly suffer the worst effects of foraging on vigilance bear the most consistently extreme body armor, which does not require behavioral aggression to thwart predatory attack. Therefore, hypotheses regarding the evolution of body armor due to diet, BMR, and predation risk are complementary. The sources and direction of selection on robustness of body armor, however, are complex both inter- and intraspecifically (Broeckhoven et al. 2015). The data presented here allow us to integrate proximate and ultimate explanations of body armor evolution.

Although the vast majority of defended species fit in the danger zone, there are some outliers that deserve a closer look. As mentioned above, several armored species of intermediate size live *only* in very closed habitats (e.g., tropical forests). These species include a few armadillos (Dasypodidae), several spiny rats (Echimyidae) and New World porcupines (Erethizontidae), one echidna (Tachyglossidae), and one Old World porcupine (Hystriidae); n.b., other species may live in a mixture of closed and open habitats, resulting in higher average Openness scores. Selection may favor the retention of these defenses in closed habitats if they happen to be under particularly strong predation risk from specialized predators that are able to hunt effectively in closed environments. Alternatively, these species may represent outliers within each group that moved back into closed environments after evolution of the defense in their family (i.e., phylogenetic constraint). Most of this group is made up of arboreal South American rodent species, and the fact that harpy eagles (*Harpya harpyja*), which have armored talons, are significant predators of South American arboreal porcupines (The Peregrine Fund 2013) suggests the former: the presence of harpy eagles or similar predators may have necessitated the porcupines’ transition back into the canopy for further protection because their quills were insufficient. Further supporting this hypothesis, these porcupine species vary considerably in coloration and the degree to which dark hair

conceals their quills (Voss et al. 2013), making a reliance on crypsis in the closed canopy a strong detection avoidance strategy.

As the present analysis is a broad overview of defended species, special attention deserves to be paid to explain the form and function of defenses in certain groups. For example, it remains unclear whether spines and dermal plates have different adaptive functions or whether they are equivalent solutions to the same problem and their differences are nonadaptive. Some evidence suggests that the spines of hedgehogs provide a protective cushion if knocked to the ground from an elevated position (Vincent and Owers 1986). It is doubtful that this could be the primary function due to natural selection, but more likely a secondary benefit. Additionally, families exhibiting significant variation in defensive elaboration (e.g., Echimyidae, Erethizontidae, Hystriidae, Tenrecidae, Erinaceidae), and, along the same lines, species showing intraspecific variation in defensive ability, deserve future investigation as they have the potential to illuminate how small temporal or spatial variations in predation risk or other environmental factors favor stronger and stronger defenses. Finally, the current study does not include the very large extinct armored species (e.g., glyptodonts), which would sit far outside of the danger zone proposed here; the predators of those eras were, however, also significantly larger than extant predators, likely necessitating the expansion of the danger zone to include much larger body masses.

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DATA ARCHIVING

Upon publication, the final dataset will be archived as Online Supplementary Material available on the journal website.

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