

ECOLOGICAL DRIVERS OF ANTIPREDATOR DEFENSES IN CARNIVORES

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Received October 2, 2013

Accepted December 19, 2013

Mammals have evolved several morphological and behavioral adaptations to reduce the risk of predation, but we know little about the ecological factors that favor their evolution. For example, some mammalian carnivores have the ability to spray noxious anal secretions in defense, whereas other species lack such weaponry but may instead rely on collective vigilance characteristic of cohesive social groups. Using extensive natural history data on 181 species in the order Carnivora, we created a new estimate of potential predation risk from mammals and birds of prey and used comparative phylogenetic methods to assess how different sources of predation risk and other ecological variables influence the evolution of either noxious weaponry or sociality in this taxon. We demonstrate that the evolution of enhanced spraying ability is favored by increased predation risk from other mammals and by nocturnality, but the evolution of sociality is favored by increased predation risk from birds of prey and by diurnality, which may allow for enhanced early visual detection. These results suggest that noxious defenses and sociality are alternative antipredator strategies targeting different predator guilds under different lighting conditions.

KEY WORDS: Anal secretions, antipredator, birds of prey, Carnivora, predation risk, sociality.

Mammals have evolved a wide variety of defensive strategies to minimize risk of predation (Caro 2005; Stankowich 2012). Antipredator defenses vary in effectiveness with different types of predators such that a strategy that minimizes mortality from one predator type may be useless or even a liability if used against a different type of predator with a different hunting strategy (Caro 2005). Consequently, closely related taxa that vary in activity, habitat, or geographic range may face different predator guilds and adopt starkly different antipredator strategies. Members of the order Carnivora, that are principally preyed upon by larger mammalian Carnivorans, birds of prey, and owls (Nowak 1999; Wilson and Mittermeier 2009), show great diversity in defensive behaviors, including noxious weaponry, predator mobbing by prey groups, extreme ferocity, and crypsis (Stankowich 2012).

Anal secretions are often used in social communication in Carnivorans (Burger 2005) but in some species they may be

more noxious and ooze out when harassed by predators, creating a foul odor (e.g., *Mustela erminea*, *Viverra* spp., *Meles meles*). Other species eject noxious fluid in a stream (e.g., *Genetta* spp.) and can even direct that stream toward the predator (e.g., Mephitidae, *Ictonyx* spp.; Stankowich et al. 2011; Arbuckle et al. 2013). Noxious anal gland secretions have evolved several times among terrestrial carnivores (Ortolani and Caro 1996; Stankowich et al. 2011; Arbuckle et al. 2013) with a positive correlation between the relative ability to use noxious secretions as an antipredator defense and boldness/salience of coat pattern (Stankowich et al. 2011). Despite this understanding, the recipients of these targeted defenses are poorly known, although it is recognized that birds of prey (especially owls) are a common source of carnivore mortality (Table S1; Wilkinson 1913; Verts 1967; del Hoyo et al. 1994, 1999; König and Weick 2008; Lesmeister et al. 2010) and other wild carnivorous mammals occasionally kill aposematic



sprayers too (Verts 1967; Ortolani and Caro 1996; Nowak 1999; Wilson and Mittermeier 2009; Lesmeister et al. 2010).

Many carnivores live in social groups and may gain antipredator benefits from enhanced vigilance and/or a greater ability to defend themselves against predators (Rood 1986; Krause and Ruxton 2002). Although some large hypercarnivorous species hunt ungulates in coordinated groups (MacNulty et al. 2012), many social carnivores actually hunt or forage alone. Here, group living may reduce predation risk through safety in numbers, enhanced vigilance effects, or the ability to mob predators (Rood 1983; Rasa 1989; Caro 1994). In fact, Rood (1986) argued that predation risk could have been the primary selective pressure promoting and maintaining sociality in small carnivores. Here, using comparative phylogenetic methods and a novel estimate of potential predation risk, we examine the ecological contexts in which both noxious defenses and sociality arise in terrestrial Carnivorans, the Mammalian Order where aposematic noxious defenses are most widespread and well developed (Caro 2009), where cohesive social groups are found in a number of species, and where the bearers of these defenses are active predators themselves but also fall prey to larger mammalian and avian predators.

In this study, we compare sources of predation risk against each other (from Carnivoran mammals and birds of prey) along with other ecological, morphological, and behavioral factors to investigate four hypotheses (a–d) regarding the ecological drivers of antipredator strategies systematically (Table S1). Accordingly, we might expect noxious spray defenses to evolve under (a) increased potential predation risk from other mammals, which have powerful olfactory senses for locating prey and identifying conspecifics (Ewer 1973; Conover 2007), relative to potential predation risk from birds of prey, which tend to be less sensitive to odors and be more visual predators (but see Roper 1999; Caro 2005). We might also expect noxious spray defenses when (b) prey are active at night (Arbuckle et al. 2013) because they may be more likely to be confronted by a predator at close range where noxious defenses would be useful, and where they are less capable of detecting predators using long-range vision (n.b., carnivore olfactory bulb size does not vary with activity cycle (Gittleman 1991), providing little support for a greater reliance on olfaction for predator detection at night). In contrast, diurnal prey may rely on vigilance to detect predators and avoid close-range encounters.

Hypotheses (a) and (b) are not mutually exclusive, and if both are important we would strongly predict noxious weaponry in carnivore prey suffering high nighttime risk from mammals and enjoying low daytime risk from birds of prey (summarized in Table S1).

We would expect sociality to evolve where (c) there is increased potential predation risk from birds of prey because (1) it enhances constant three-dimensional hemispheric vigilance

necessary to spot predatory birds flying overhead, or (2) it facilitates group defense: some intrepid carnivores mob attacking predators including birds of prey or even smaller mammalian predators (e.g., jackals, *Canis mesomelas*), although not large terrestrial mammalian predators (e.g., lions, *Panthera leo*). We might also expect sociality where (d) daytime activity permits prey to take advantage of increased long-range collective vigilance and early warning (e.g., alarm calls) that are possible in stable social groups (n.b., while some carnivores may see well at night, vigilance in mammals is lower at night than during the day (Beauchamp 2007), and low light levels make monitoring of conspecifics and detection of predators difficult).

Hypotheses (c) and (d) are not mutually exclusive, and if both are important we would strongly predict sociality especially in carnivore prey subject to high daytime risk from birds of prey but enjoying low nighttime risk from mammals (summarized in Table S1). In addition, noxious defenses and sociality may also be favored in species that lack the option of escaping to a refuge (e.g., water, trees, burrows); in species that are small or intermediate in size because they may be threatened by larger mammalian predators but are too large to be cryptic or agile; and in species that are carnivorous where intraguild predators may engage in kleptoparasitism (but see Arbuckle et al. 2013).

Methods

Defenses (e.g., spraying, aggression, enhanced vigilance, mobbing) can be very effective at deterring predators and minimizing actual mortality (Caro 2005); therefore, neither attempted nor successful predation constitute a robust measure of the selection pressures acting on prey antipredator responses. Given this fact, we decided to estimate potential risk from predators for each prey species, agnostic to any antipredator adaptations they may have. We created a composite measure of potential predation risk modified from those used in similar analyses of interspecific killing in carnivores (Caro and Stoner 2003; Hunter and Caro 2008). We calculated potential predation risk from mammals (Carnivorans specifically) and birds of prey (Accipitriformes, Falconiformes, and Strigiformes) separately by measuring overlap in geographic range and correcting for body size differences between the predator and prey, dietary preferences of the predator, habitat overlap, and activity time overlap (see below). These estimates ignore all antipredator defenses, enabling us to test the role of potential predation risk in the evolution of antipredator traits.

CARNIVORE DATA

We used previously scored data on noxious spray behavior, activity behavior, lifestyle, body mass in mammalian Carnivora (Stankowich et al. 2011). *Spray Behavior* was assigned an ordinal score from 0 to 3 based on their ability to use noxious anal gland secretions in defense against predators: 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. *Activity* was scored as 1 = nocturnal only, 2 = nocturnal and crepuscular, 3 = cathemeral, 4 = diurnal. We used lifestyle data defined as follows: *Arboreality* (0 = not arboreal, 1 = semiarboreal, 2 = arboreal), *Natatoriality* (i.e., propensity for swimming; 0 = terrestrial, 1 = aquatic), and *Fossoriality* (0 = does not use burrows at all, 1 = uses burrows of other species or natural cavities in rocks, fallen logs, or the earth, or 2 = excavates own burrows). Body masses reported previously (Stankowich et al. 2011) were \log_{10} transformed. *Carnivory* was scored from dietary information drawn mainly from Nowak (1999). Species were scored based on how strongly they relied on mammalian prey in their diet: 0 = eats no mammals, 1 = omnivore but occasionally eats small mammals, 2 = omnivore but regularly eats mammals the size of rabbits or larger (≥ 1 kg), 3 = strictly carnivorous and eats mammals the size of rabbits or larger. We also scored *Group Hunting* behavior as 0 = unlikely to eat mammals or solitary hunter, 1 = forms groups to hunt larger mammalian prey. We used previously scored data on *Sociality* (Ortolani and Caro 1996), where 1 = solitary, 2 = pairs, 3 = variable group, and 4 = social. *Habitat Openness* was calculated from habitat categories downloaded from IUCN (2011), and species were scored as present or absent in several categories. Each category was assigned an “openness” score following (Stankowich and Caro 2009; Stankowich et al. 2011) where 1 indicates completely open and 0 indicates completely closed. The mean openness score was calculated for each species and multiplied by 100. Categories and scores are as follows: Tropical Forest (subtropical, tropical dry, moist, montane, swamp forest) = 0.1, Temperate Forest (temperate, boreal, subarctic, subantarctic) = 0.2, Wetlands = 0.2, Tropical Shrubland (subtropical, tropical dry, moist, high-altitude shrubland, Mediterranean-type shrubby vegetation) = 0.5, Temperate Shrubland (temperate, boreal, subarctic, subantarctic) = 0.6, Savanna (dry, moist) = 0.6, Temperate Grassland (subarctic, subantarctic, temperate) = 0.8, Tropical Grassland (subtropics, tropical dry, seasonally wet, high-altitude grassland) = 0.8, Rocky = 0.8, Marine (intertidal, coastal, supratidal) = 0.8, Artificial Grassland (arable, pasture, plantations, rural gardens, old degraded tropical forest) = 0.8, Urban = 0.8, Artificial Marine = 0.8, Desert = 0.9, and Tundra = 0.9.

We calculated the amount of range overlap ($100 \times [\text{area of range overlap} / \text{homerange size of carnivore prey species}]$) between every possible pair of recognized carnivore species ($N = 246$ species, which reduced to 181 eventually) using range maps from IUCN (2011). The shapefiles were merged into one file

using ArcGIS 10.0 (ESRI 2011) and species with multiple range types (Extant, Probably Extant, Possibly Extant, etc.) were combined into one record. When available we included “Extinct” ranges (shapefiles) to add as much historical relevance as possible to our analyses, so our results are valid to the extent that current proportion of range overlap reflects historical proportions of range overlap. Using Model Builder in ArcGIS (ESRI 2011), we exported each species record into its own feature class of a single file geodatabase containing all species. A Python (Python Software Foundation 2010) script was used to determine the intersection of all (246×246) species ranges using the ArcPy module (ESRI 2011) *Intersect_analysis* ArcGIS function, creating a file geodatabase with individual feature classes of the range overlap of the species. To help reduce future computing time, another Python script was used to delete any feature classes with zero data, indicating no overlap between species. A third Python script using the ArcPy module (ESRI 2011) *Merge_management* ArcGIS function was then used to merge all remaining feature classes with overlapping species ranges into one feature class. This was then exported to a spreadsheet where the percent overlap of ranges for each species was calculated.

AVIAN DATA

To quantify potential predation risk from avian predators on mammalian carnivores, we gathered similar behavioral and morphological data on all bird-of-prey and owl species in the Orders Accipitriformes, Falconiformes, and Strigiformes ($N = 512$). Note that snakes are potential predators of smaller carnivores, especially burrowing species, nocturnal species, and perhaps arboreal species but, we could not test this here primarily for lack of spatial data at a global scale for snakes. Most data on body mass, body length, diet, and activity were drawn from del Hoyo et al. (1994, 1999), and missing data were filled in using secondary sources (Gross 1944; Fitch 1947; Smeenk 1974; Korpimäki and Norrdahl 1989; Birdlife International 2001; Johnsgard 2002; Olsen et al. 2002; König and Weick 2008; Birdlife International 2011; Seipke et al. 2011). Habitat information was downloaded from IUCN (2011) and sorted into the same categories described above for carnivores. Bird activity was defined as described above for carnivores. Bird diets were categorized as follows: 0 = no likelihood of taking a carnivore (e.g., insectivore or only carrion), 1 = takes vertebrates, occasionally takes small mammals (e.g., rodents), but mostly other nonmammals, 2 = takes mostly mammals, but just small rodents OR omnivorous but occasionally preys on mammals the size of rabbits or larger, 3 = eats mostly mammals where at least some are the size of rabbits or larger (≥ 1 kg) OR described specifically as eating carnivores or defended mammals (e.g., porcupines). We calculated the amount of range overlap between every possible pair of carnivore (246 species) and avian species

(512 species) using range maps (Birdlife International 2011) as described above for carnivore–carnivore pairs.

CALCULATING POTENTIAL PREDATION RISK

To estimate *potential* predation risk for mammals and predatory birds on mammalian carnivores, we assumed that for another species to pose a threat to a given carnivore species, that predator must (a) live in the same geographic range, (b) live in the same type of habitat, (c) live in the same habitat strata, (d) have a diet that includes mammals, (e) be large enough in size to be able to capture and kill that carnivore species, and (f) be active at the same time of day (see Caro and Stoner 2003; Hunter and Caro 2008). To calculate potential predation risk from each candidate carnivore species, we (a) used the percent range overlap from the carnivore–carnivore dyads ($100 \times [\text{area of range overlap}/\text{total homerange size of carnivore prey species}]$). (b) If the two species shared any habitat category in common, we multiplied the range overlap from (a) by 1; if there was no overlap in habitat, we multiplied the range overlap by 0. (c) If the two species matched in any category of arboreality or natatoriality, we multiplied (b) by 1; if one species is either “terrestrial but climbs” or “terrestrial and arboreal” and the other species is either “terrestrial” or “arboreal,” we multiplied (b) by 0.75; otherwise we judged there to be no overlap in habitat strata and we multiplied (b) by 0. (d) If the potential predator’s diet category was 3, we multiplied (c) by 1; 2, we multiplied (c) by 0.5; 1, we multiplied (c) by 0.25; 0, we multiplied (c) by 0. (e) To account for differences in body size between potential predators and prey, we assumed that as the ratio of prey body mass to predator body mass increased, the probability of the predator being able to kill the prey decreased. When mammalian carnivores kill each other (Palomares and Caro 1999), the average (μ) prey species mass to solitary predator species mass is 0.5, with a standard deviation (SD; σ) of 0.3. For group or pack hunters, which can work together to kill carnivores much larger than themselves, $\mu = 3.85$ and $\sigma = 4.5$. If the prey:predator mass ratio was μ or less (i.e., the predator was much larger than the prey), we multiplied (d) by 1. If the ratio was greater than μ , we used a normal curve equation to estimate the decreasing likelihood of predation where the maximum of the curve is 1 (at a ratio of μ) and decreases as the ratio increases following the equation $e^{-\frac{(x-\mu)^2}{2\sigma^2}}$ where x is the actual prey:predator body mass ratio. The resulting value from the equation is multiplied by (d). (f) If there was an exact match in activity category (1–4; see above) or if one species was nocturnal and the other was nocturnal/crepuscular, we multiplied (e) by 1; if one species was cathemeral and the other was nocturnal, crepuscular, or diurnal, we multiplied (e) by 0.5; if one species was diurnal and the other was nocturnal/crepuscular, we multiplied (e) by 0.2; and if one species was diurnal and the other was nocturnal, we multiplied (e) by 0. Based on several rounds of phylogenetic analyses (see

below) using different values for the multipliers described thus far (especially for activity and predator diet multiplier), we found our results to be generally robust to slight changes in how we corrected for each aspect of predation risk. For example, minor modifications to activity and diet scores yielded the same results every time. The resulting score of $(a \times b \times c \times d \times e \times f)$ is the potential predation score for that predator–prey dyad and ranged from 0 to 100. Where “correction factor” is referenced in the text regarding range maps, we refer to $(b \times c \times d \times e \times f)$, that is, everything except the geographic range. If one aspect of the required data was missing for one of the species of the dyad (e.g., activity, body mass), the potential predation risk for that predator was ignored (i.e., treated as missing data). To calculate the potential predation risk from carnivores for a given species, we summed the individual scores from all potential predator dyads for that species. A sample of well-studied undefended prey species was checked to verify estimated risks corresponded well to the predator species actually faced by these prey species. For example, naïve reintroduced black-footed ferrets (*Mustela nigripes*) suffered significant mortality from coyotes (*Canis latrans*), badgers (*Taxidea taxus*), and great horned owls (*Bubo virginianus*; Breck et al. 2006; Biggins et al. 2011), and these predators had, by far, the greatest potential predation risk scores (all 100) in our dataset relative to any other potential predators. Finally, we split the mammalian and avian predation risk scores for each prey species into daytime and nighttime risk scores (i.e., Nighttime Mammal Risk, Daytime Mammal Risk, Nighttime Avian Risk, Daytime Avian Risk) using a similar scheme as described in (f). We defined nighttime as the hours including dusk, night, and dawn; and we defined daytime as the hours including dawn, daylight, and dusk. If the prey species was strictly nocturnal, we multiplied each predation risk score by 1 to get the nighttime risk scores and by 0 to get the daytime risk scores. Nocturnal/crepuscular and diurnal species may overlap for several hours each day during dawn and dusk (i.e., diurnal species will have some nighttime predation risk). If the prey species was nocturnal/crepuscular, we multiplied each predation risk score by 1 to get the nighttime risk scores and by 0.2 to get the daytime risk scores. If the prey species was diurnal, we multiplied each predation risk score by 0.2 to get the nighttime risk scores and 1 to get the daytime risk scores. If the prey species was cathemeral, we multiplied each predation risk score by 0.5 to get the nighttime risk scores and 0.5 to get the daytime risk scores. The results of our analyses also were robust to slight variations in these multipliers.

The procedure for calculating potential predation risk from predatory birds was identical to that for carnivore predators, except for the following steps. Step (c) was skipped as birds have access to both terrestrial and arboreal environments. In step (e), there was no published μ or σ available for predatory birds killing carnivore species. We searched several general references on birds of prey (Craighead and Craighead Jr. 1969; del Hoyo et al. 1994,

1999; Johnsgard 2002; König and Weick 2008; Birdlife International 2011) and many published studies reporting specific species taken by predatory birds (Gross 1944; Fitch 1947; Schnell 1958; Storer 1966; Smeenk 1974; Korpimäki and Norrdahl 1989), and we recorded instances of predatory birds killing specific carnivore taxa (Table S1). We calculated the carnivore:bird mass ratio for each reported instance of killing; when descriptions of the carnivore prey were not specific (e.g., only mentioned “weasels” or “mustelids”), we calculated the average body mass of the carnivore species that fit that description and overlapped in geographic range (from (a)) with the predatory bird species. The average and SD of these scores were $\mu = 1.25$ and $\sigma = 1.5$. These values were then used to calculate the likelihood of the predatory bird species killing the carnivore species of interest in the same way as described above for carnivore–carnivore killing. Identical to the potential carnivore predation risk procedure, we multiplied a–f together and summed them for all carnivore–bird dyads for each carnivore species.

ANALYSES

From 10KTrees (Arnold et al. 2010), we downloaded a consensus phylogenetic tree calculated from 100 candidate trees containing all of the species for which we had data for all variables ($N = 181$ spp.). We reconstructed the ancestral states of the Spray Behavior variable using Maximum Likelihood Reconstruction routines in the *geiger* (Harmon et al. 2009) package in R. Following Stankowich and Caro (2009), we also sought to test *Conspicuousness/Exposure* in the environment as a source of predation risk, which is the product of Habitat Openness (0–1) and Log Body Mass; we simply allowed the interaction term for these two main effects to compete for a spot in each final model. We tested for the effects of Log Body Mass, Carnivory, Fossoriality, Arboreality, Natatoriality, Activity, Group Hunting, Habitat Openness, and Exposure on Predation Risk due to Mammals and Predation Risk due to Birds (not split into daytime and nighttime); we then tested for the effects of all of the above factors (including Nighttime Mammal Risk, Daytime Mammal Risk, Nighttime Avian Risk, and Daytime Avian Risk) on Spray Behavior and Social Behavior. We ran phylogenetic generalized least squares (PGLS) analyses using the *caper* (Orme et al. 2012) package in R (R Development Core Team 2012). Our goal was not to build the perfect model but instead to compare the factors and see which ones explained most of the variance; therefore, we used a forward entry method of model building, entering the factor with the smallest P -value at each step until none of the remaining factors had a P -value < 0.10 . If, when a new factor was added to the model, another factor that was already in the model fell to $P > 0.10$ as a result, we did not allow the contending factor to enter. The exception to the latter rule was for Exposure (Habitat Openness \times Log₁₀Mass): this factor was allowed to enter even if one of its main effects

became insignificant. Diagnostic plots (e.g., outlier analysis, Q-Q plots) of each model were checked to assure that data met the assumptions of linear modeling with PGLS. The complete dataset can be found archived as Supporting Information.

Results

Empirically, carnivores tend to experience either high predation risk from mammals or from birds, but not both (Fig. 1A). For example, the zorilla (*Ictonyx striatus*) has the second greatest nighttime mammal predation risk score (834.6), but has no daytime risk from birds of prey (Fig. 1B–E); conversely, the common dwarf mongoose (*Helogale parvula*) has the greatest daytime bird-of-prey predation risk score (1543.2), but is at low risk from mammals at night (37.8; Fig. 1F–I). We found a far greater potential risk of predation on smaller than on larger species (mammalian predators: $P = 3.9 \times 10^{-6}$; birds of prey: $P = 0.030$; Tables 1 and 2) and on terrestrial than aquatic carnivore species (mammalian predators: $P = 3.3 \times 10^{-5}$, birds of prey: $P = 0.004$; Tables 1 and 2). Nocturnal species are under much heavier predation risk from sympatric mammals ($P = 5.6 \times 10^{-7}$); diurnal species, however, are under much heavier risk from birds ($P = 1.7 \times 10^{-13}$). Species living in the open are at greater risk from birds of prey ($P = 0.009$), and there is a marginal trend for smaller species that live in more open environments to also be at greater risk of predation from all predators (mammalian predators: $P = 0.083$; birds of prey: $P = 0.092$; Tables 1 and 2).

Noxious spray behavior evolved several times independently in Carnivora, with rudimentary secretions appearing very early in the diversification of this order (Fig. 2). Our comparative analysis on spray ability (Table 3) shows that predation risk from mammals during the nighttime is the most important positive predictor of advanced spray defenses ($P = 0.028$) and species with spray defenses experience very low daytime avian risk ($P = 7.5 \times 10^{-4}$; Fig. 1A, Table 3). We found no effects of daytime mammal risk or nighttime avian risk. We also found that carnivore species that specialize on feeding on mammals show a marginal trend to evolve spraying behavior ($P = 0.051$, Table 3).

There was no overlap between sociality and noxious spraying: no species were both highly social and used noxious secretions in defense (*Spray Behavior* > 0 ; Fig. 2). Increased sociality is favored by increased predation risk from birds of prey during the daytime (Fig. 1; Table 4; $P = 0.003$) and by group hunting ($P = 5.7 \times 10^{-10}$); social species experience very low nighttime mammal risk ($P = 0.004$). Again, we found no effects (Table 4) of daytime mammal risk and nighttime avian risk. We found, not unexpectedly, that group/pack hunters were highly social ($P = 5.7 \times 10^{-10}$). Less carnivorous and more insectivorous species ($P = 0.002$) and species that live in burrows ($P = 0.002$) were also more likely to be more social.

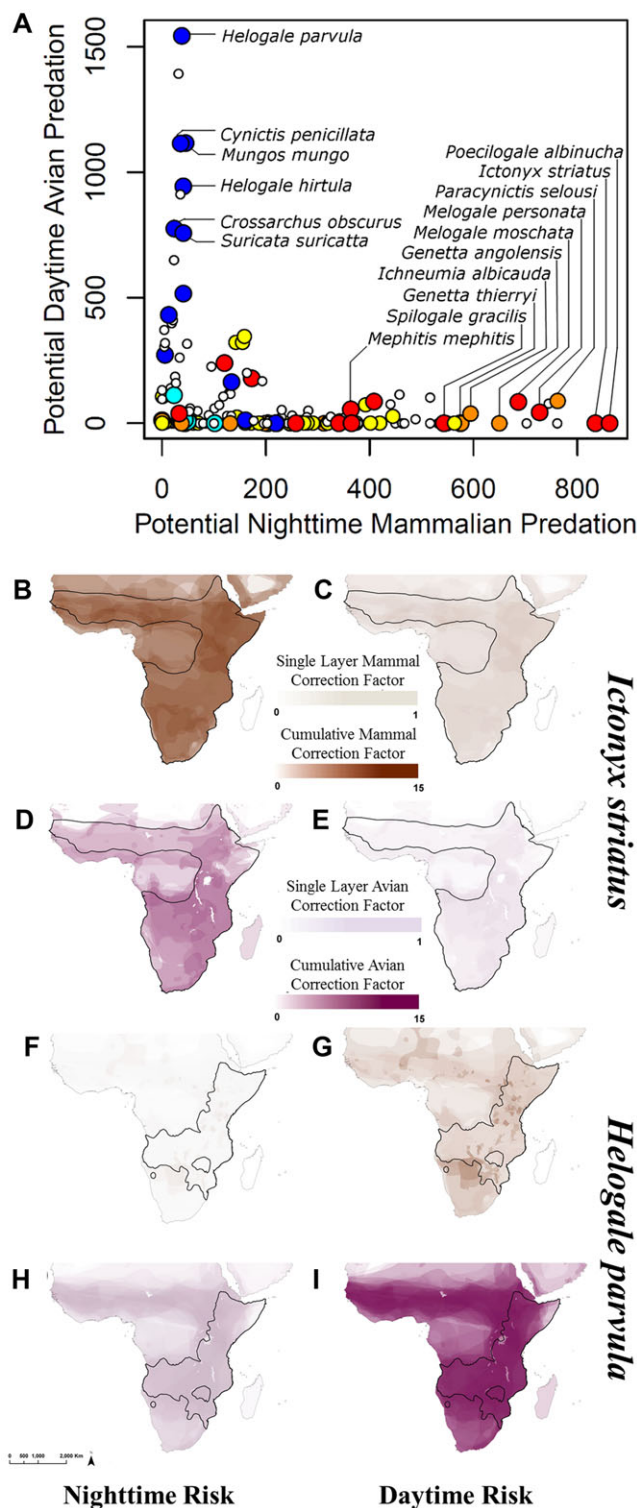


Figure 1. Relationship between potential avian and mammalian predation risk and antipredator traits. (A) Scatterplot showing relationship between potential predation nighttime risk from mammals, potential daytime predation risk from birds of prey, sociality, and the ability to spray anal gland secretions in defense ($N = 181$ species). Marker colors denote spray ability or sociality: white = no noxious secretions, yellow = foul odor or secretion, orange = squirt noxious secretions in a stream, red = ability to direct

Discussion

Our comparative results suggest that small carnivore species experience substantially greater predation risk than larger carnivores and that risk comes primarily from mammals at night and birds of prey during the day. Species with high nighttime potential risk from mammalian predators and low daytime potential risk from birds of prey were much more likely to have noxious defenses. Conversely, species with high daytime potential risk from avian predators but low nighttime risk from mammalian predators were much more likely to be highly social. Activity and source of predation risk play major roles in shaping the antipredator behavior of species that are under heavy risk of predation.

As nighttime mammal predation risk increases, the likelihood of more advanced noxious spray ability increases: of nine species with nighttime mammal risk scores over 600 (>95th percentile), six of them are able to eject their anal secretions in a stream toward the predator (Fig. 1A). As predicted, none of the nine carnivore species with very high risk of daytime predation from birds of prey (≥ 600 ; >95th percentile) use defensive secretions. Taken together, these results suggest that hypotheses (a) and (b) are both true (Table S2): the evolution of noxious weaponry in carnivores is favored by increased risk from mammalian predators that are likely more sensitive to noxious smells than birds of prey, and by greater risk during nighttime conditions where sociality brings

Figure 1. noxious secretions at predator, light blue = hunts in large prey in social packs, dark blue = lives in large social groups with no pack hunting. Markers are sized based on degree of antipredator defense due to noxiousness or sociality (small markers for undefended species) to increase clarity and highlight defended species. Enhanced noxious spray ability is favored by increased potential mammal predation risk at night and sociality is favored by increased potential avian predation risk during daylight. (B–I) Danger maps showing potential predation risk from birds of prey (purple) and mammalian carnivores (brown) for two species: *Ictonyx striatus* (B–E) and *Helogale parvula* (F–I). Maps and shapefiles provided by IUCN (2011). Nighttime risk maps are on the left (B, D, F, H); daytime risk maps are on the right (C, E, G, I). Dark black outlines show the geographic range of the featured species. Colored transparent layers show the overlapping ranges of predators for the featured species. The darkness of each layer corresponds to the correction factor for a single predator with the featured species (0–1). Due to layering of predator shapes, generally darker areas denote regions where many dangerous predators also live. *Ictonyx striatus*, a species with advanced noxious spray defenses, is under extremely high potential risk from mammalian predators at night and relatively low risk from birds of prey during the day, whereas *H. parvula*, a highly social species, is under extremely high potential risk from birds of prey during the day and relatively low risk from mammalian predators at night.

Table 1. Results of final model of forward entry phylogenetic generalized least squares analysis on potential mammal predation risk. Factors not included in the final model are listed after the factors entered in the final model (**bold**) and their corresponding statistics come from a model that includes that factor plus the entered factors (1–5).

Order entered	Factor	Coefficient	Standard error	<i>t</i>	<i>P</i>
	Intercept	490.189	102.773	4.770	3.87×10^{-6}
1	Log₁₀ Body Mass	−272.698	73.069	−3.732	2.57×10^{-4}
2	Activity	−48.988	9.423	−5.199	5.55×10^{-7}
3	Natatoriality	−226.131	53.043	−4.263	3.29×10^{-5}
4	Habitat Openness	−0.179	1.077	−0.166	0.869
5	Openness x LogMass	2.142	1.229	1.743	0.083
	Group Hunting	38.152	56.770	0.672	0.502
	Carnivory	7.070	14.545	0.486	0.628
	Fossoriality	0.348	18.633	0.019	0.985
	Arboreality	−14.882	26.344	−0.565	0.573

N = 181; adjusted R^2 = 0.3146; $F_{6, 175}$ = 17.53; λ = 0.738 (95% CI: 0.450–0.881).

Table 2. Results of final model forward entry phylogenetic generalized least squares analysis on potential avian predation risk. Factors not included in the final model are listed after the factors entered in the final model (**bold**) and their corresponding statistics come from a model that includes that factor plus the entered factors (1–5).

Order entered	Factor	Coefficient	Standard error	<i>t</i>	<i>P</i>
	Intercept	90.616	87.78	1.032	0.303
1	Log₁₀ Body Mass	−166.238	75.862	−2.191	0.030
2	Activity	84.794	10.606	7.995	1.69×10^{-13}
3	Natatoriality	−152.398	51.866	−2.938	0.004
4	Habitat Openness	3.077	1.167	2.637	0.009
5	Openness x LogMass	−2.258	1.336	−1.691	0.093
	Group Hunting	32.536	59.410	0.548	0.585
	Carnivory	−17.557	14.029	−1.252	0.212
	Fossoriality	12.516	19.529	0.641	0.522
	Arboreality	2.705	27.642	0.098	0.922

N = 181; adjusted R^2 = 0.4754; $F_{6, 175}$ = 33.63; λ = 0.416 (95% CI: 0.213–0.629).

fewer benefits of long-range predator detection, making possession of a short-range noxious defensive spray advantageous.

Species with the greatest daytime predation risk from birds of prey (≥ 600 ; >95th percentile) are all mongooses in the family Herpestidae (e.g., *H. parvula*; Fig. 1E) that seem to lack any noxious anal gland secretions (Fig. 2). Of the nine species with avian predation risk scores greater than 600, six species live in large social groups (Fig. 1A; e.g., *Cynictis penicillata*, *Suricata suricatta*, *Mungos mungo*), and members of this family are known to bunch together as a group to harass birds of prey to force their departure or save a captured pack member (Rood 1983; Graw and Manser 2007). Predation risk appears to be a key selective force promoting the formation of social groups in the mongooses due to enhanced predator detection and defensive abilities of large groups (Rood 1986), and enhanced vigilance is probably effective for both diurnal avian predators and diurnal mammalian predators. Although

possession of a defense is thought to have led to aggregation in some aposematic insects (Ruxton and Sherratt 2006), we found no evidence of noxious anal gland secretions in any of the extremely social Carnivoran species. Taken together, these results suggest that hypotheses (c) and (d) are both true (Table S1): the evolution of large cohesive social groups is favored by increased risk from avian predators that may be more susceptible to avoidance by defensive mobbing or enhanced vigilance and by greater risk during daylight conditions where the long-range visual advantages of predator detection are more useful.

Interestingly, in contrast to the findings of Arbuckle et al. (2013) for Musteloids only, we found that Carnivoran species that specialize on feeding on mammals show a marginal trend to have evolved spraying behavior possibly as a result of intraguild competition over mammalian prey items (Hunter and Caro 2008). In contrast, although many cases of sociality in carnivores can

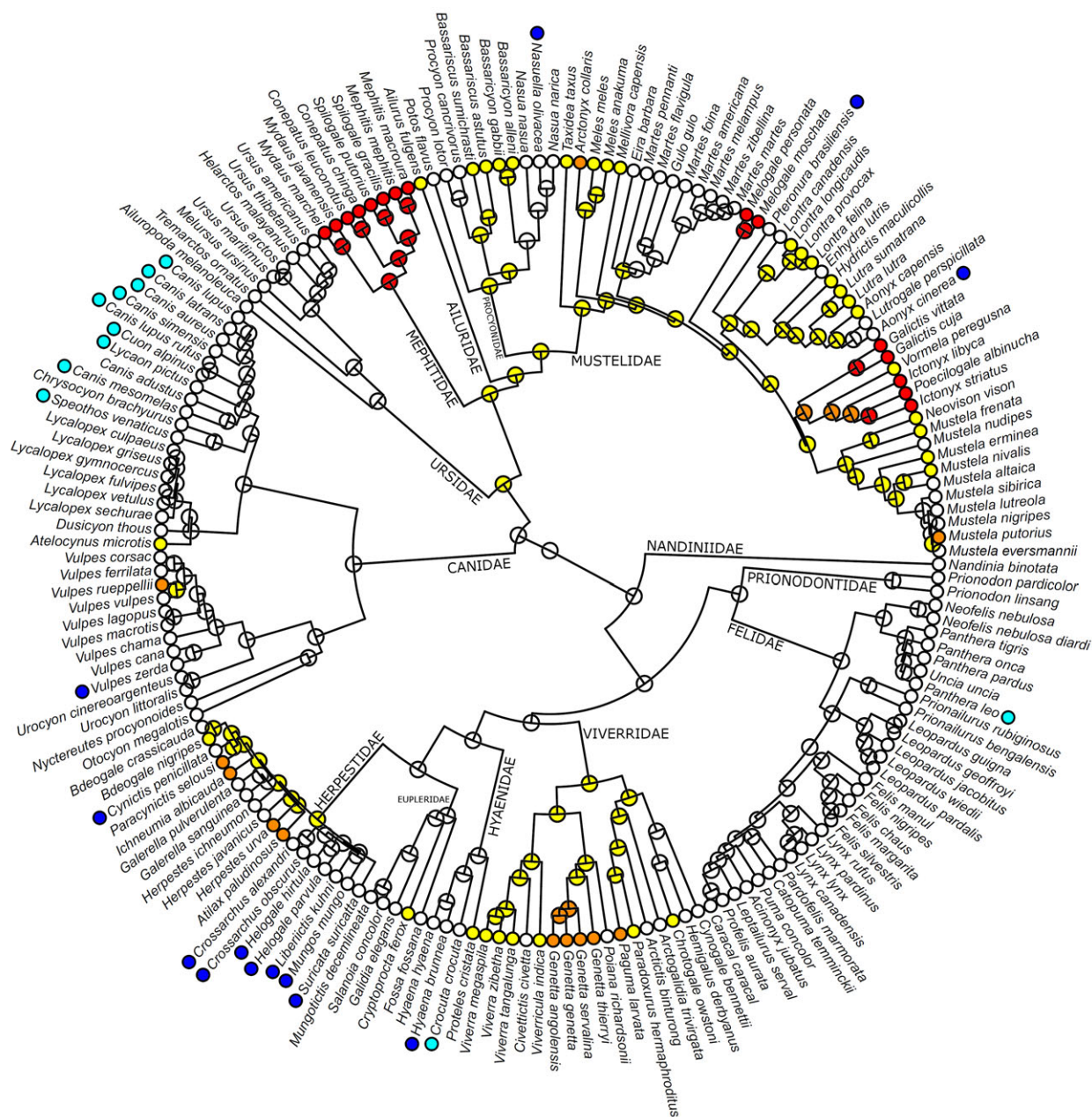


Figure 2. Consensus Carnivora tree showing evolutionary relationships of the 181 species in this study. Family names are indicated on the appropriate stem branches in all capital letters. Colored branch tips show the noxious spray ability of each species and colored nodes show the results of a maximum likelihood ancestral state reconstruction of spray ability where values have been rounded to the nearest integer state (0, 1, 2, 3). Marker colors denote spray ability: white (0) = no noxious secretions, yellow (1) = foul odor or secretion, orange (2) = squirt noxious secretions in a stream, red (3) = ability to direct noxious secretions at predator. Blue circles next to each name indicate sociality: light blue = hunts in large prey in social packs, dark blue = lives in large social groups with no pack hunting.

be explained by group/pack hunting for mammalian prey, social species that do not hunt in groups are more likely to have diets focused on insects and other small vertebrates while never or only occasionally eating other mammals. This supports Rood's (1986) assertion that insectivory may permit sociality in Herpestids, and the benefits of sociality may extend beyond collective foraging or hunting in groups to antipredator effects. Further, social car-

nivores are more likely to retreat to burrows. This phenomenon may enhance safety from attacking birds, which are less able to enter burrows than mammalian predators.

Our estimates of potential predation risk were based on a composite of several sources of data and while they provided a remarkable fit to the data for both sociality and noxious weaponry, they have their limitations. Ideally, these measures should take

Table 3. Results of final model of forward entry phylogenetic generalized least squares analysis on noxious spray behavior. Factors not included in the final model are listed after the factors entered in the final model (bold) and their corresponding statistics come from a model that includes that factor plus the entered factors (1–3).

Order entered	Factor	Coefficient	Standard error	<i>t</i>	<i>P</i>
	Intercept	0.179	0.470	0.381	0.704
1	Daytime Avian Risk	-7.19×10^{-4}	2.10×10^{-4}	-3.429	0.001
2	Nighttime Mammal Risk	5.67×10^{-4}	2.56×10^{-4}	2.219	0.028
3	Carnivory	0.131	0.067	1.961	0.051
	Daytime Mammal Risk	-3.43×10^{-4}	9.21×10^{-4}	-0.370	0.712
	Nighttime Avian Risk	3.76×10^{-4}	5.97×10^{-4}	0.631	0.529
	Log ₁₀ Body Mass	-0.200	0.171	-1.173	0.242
	Natatoriality	0.272	0.240	1.133	0.259
	Fossoriality	0.079	0.077	1.025	0.307
	Arboreality	-0.069	0.104	-0.658	0.511
	Habitat Openness	0.003	0.003	1.126	0.262
	Openness \times LogMass	-0.005	0.005	-0.955	0.341
	Group Hunting	-0.131	0.233	-0.561	0.575

$N = 181$; adjusted $R^2 = 0.1314$; $F_{4, 177} = 10.07$; $\lambda = 0.908$ (95% CI: 0.828–0.956).

Table 4. Results of final model of forward entry phylogenetic generalized least squares analysis on Social Behavior. Factors not included in the final model are listed after the factors entered in the final model (bold) and their corresponding statistics come from a model that includes that factor plus the entered factors (1–5).

Order entered	Factor	Coefficient	Standard error	<i>t</i>	<i>P</i>
	Intercept	-0.608	0.560	-1.085	0.279
1	Group Hunting	2.054	0.313	6.569	5.705×10^{-10}
2	Daytime Avian Risk	9.58×10^{-4}	3.16×10^{-4}	3.037	0.003
3	Nighttime Mammal Risk	-0.001	3.52×10^{-4}	-2.938	0.004
4	Carnivory	-0.268	0.085	-3.155	0.002
5	Fossoriality	0.321	0.103	3.103	0.002
	Daytime Mammal Risk	0.003	0.001	2.189	0.030 ¹
	Nighttime Avian Risk	6.80×10^{-4}	8.33×10^{-4}	0.816	0.416
	Log ₁₀ Body Mass	-0.029	0.223	-0.130	0.897
	Natatoriality	0.272	0.350	0.778	0.438
	Arboreality	-0.126	0.141	-0.891	0.374
	Habitat Openness	-0.001	0.004	-0.276	0.783
	Openness \times LogMass	0.005	0.007	0.783	0.435

¹Daytime Mammal Risk was not added to the final model because its addition would have left Daytime Avian Risk insignificant, violating our model selection rules (see Methods).

$N = 179$; adjusted $R^2 = 0.3148$; $F_{6, 173} = 17.36$; $\lambda = 0.688$ (95% CI: 0.239–0.902).

into account predator and even prey abundance on a spatial scale. For example, some predator species may have always been rare and therefore have contributed little to potential risk; and some areas of a species' range may have more individual predators than others. Such data could certainly be used to correct the risk estimates on a case-by-case basis where they are available. We could not, however, account for abundance of every predator species in this analysis ($N = 758$ predator species) given the paucity of abundance data. Future analyses should aim to incorporate abun-

dance data as they become more universally available for certain predator and prey groups.

In conclusion, we have shown that both the composition of predator guilds and the ability to rely on long-range predator detection during daylight hours have a significant influence on the evolution of mammalian defenses. Although we cannot yet determine the direction of causation between the evolution of diurnal/nocturnal activity and mammalian/avian predation risk, it does appear that potential risk is influenced by several ecological

factors in addition to whether a species is nocturnal or diurnal. The present data, combined with previous studies (Stankowich et al. 2011), suggest that physical and morphological defenses in plantigrade mammals are found in groups such as mephitids (Caro 2005) because they (1) are nocturnal, cannot rely on long-range visual detection of predators, and therefore are more likely to engage predators at close range; (2) encounter more mammalian predators, which are more sensitive to noxious defenses, and fewer birds of prey, which are likely insensitive to noxious defenses; (3) are small and stocky and are therefore at greater risk of predation by both carnivores and birds; (4) live in exposed terrestrial environments; and (5) that have little recourse to rapid flight or retreating to burrows. Diurnal insectivores are under reduced nighttime risk from carnivores but subject to greater daytime risk from birds of prey, and species experiencing increased daytime avian risk rely on vigilance and collective detection in social groups followed by alarm calling and retreat to burrows (especially in smaller species such as the dwarf mongoose, *H. parvula*) and frequent predator harassment (especially in larger species such as the banded mongoose, *M. mungo*, and the meerkat, *S. suricatta*: Rood 1986; Rasa 1989; Manser 2001; Graw and Manser 2007). Our data suggest that aposematic defenses and aggregation, far from being linked (Alatalo and Mappes 1996), may actually be alternative antipredator strategies and their evolution may depend strongly on the composition of the predator guild in a community operating at different times of the day.

ACKNOWLEDGMENTS

We thank the Center for Spatial Technologies and Remote Sensing (CSTARS) at UC Davis for their computing resources for this analysis, J. Blossom and the Center for Geographic Analysis at Harvard University for running the initial carnivore–carnivore geospatial analysis, C. Nunn for granting access to the unpublished Carnivora portion of 10KTrees, the Pierce Lab at Harvard University and S. Doucet for initial theoretical discussions, and the AnthroTree Workshop, which is supported by the National Science Foundation (BCS-0923791) and the National Evolutionary Synthesis Center (NSF grant EF-0905606), for training in phylogenetic comparative methods, and T. Hossie, T. Sherratt, M. Speed, W. Allen, B. Lyon, and an anonymous reviewer for comments. T. Caro was supported by a National Institute of Food and Agriculture Grant CA-D-WFB-6721-H. We, the authors, declare that we have no potential conflicts of interest.

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Associate Editor: B. Lyon

Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Table S1. Raw data from the literature used to calculate the μ or σ available for predatory birds killing carnivore species.

Table S2. Hypotheses and predictions regarding the evolution of noxious spray defenses and sociality in Carnivorans.