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DEFENSIVE TACTICS IN LIZARDS AND SNAKES: THE POTENTIAL CONTRIBUTION OF THE NEOTROPICAL FAUNA

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Lizards and snakes are particularly good subjects to explore specific and general questions in vertebrate behavioral biology (see several examples of this potential in Huey *et al.*, 1983, Feder & Lauder, 1986, Seigel *et al.*, 1987, Seigel & Collins, 1993, and Vitt & Pianka, 1994), although this potential is poorly explored in regard to defensive strategies (see, e. g., Greene, 1988).

A comprehensive review of antipredator mechanisms in reptiles was made by Greene (1988). Several examples of defensive tactics in lizards and snakes are also found in classical texts on defense and predator-prey relationships (e. g., Cott, 1940; Wickler, 1968; Edmunds, 1974; Curio, 1976; Owen, 1980; Endler, 1986), as well as in reviews focused on specific aspects of defense in reptiles (e. g., Greene, 1973; Jackson et al., 1976; Vitt et al., 1977; Bechtel, 1978; Schoener, 1979; Vitt, 1983; Bellairs & Bryant, 1985; Arnold, 1988; Pough, 1988a, b; Savage & Slowinsky, 1992). General herpetology books also provide brief reviews on defense (e. g., Parker & Grandison, 1977; Mattison, 1986, 1989; Zug, 1993).

Although apparently well documented, a general scarcity of information on defensive tactics of lizards and snakes in the literature is easily realized in Greene's (1988) review. For instance, less than 10% of all lizard species are cited by this author as having at least one published account on defensive tactics. The picture is similar when considering Neotropical lizards and snakes (see also "Conclusions and suggestions for further studies").

The purposes of this paper are (1) to briefly review the current knowledge of predators and defensive tactics of lizards and snakes, (2) to present two case studies showing the potential of the Neotropical fauna in searching for patterns and understanding the evolution of defense in these animals, and (3) to suggest future work on the subject.

Predators of lizards and snakes

This section is intended to show the diversity of predators of lizards and snakes and which are the main predators of these animals, in order to understand to what kind of detection and handling capabilities of the predators the defensive tactics employed by lizards and snakes are directed.

Curiously, although many lizards and snakes feed exclusively or frequently on invertebrates, these animals may, in turn, be preyed upon by some carnivorous arthropods (e. g., centipedes, spiders, scorpions; see a review in McCormick & Polis, 1982). In some circumstances, these invertebrates may exert a relatively strong predation pressure on lizards and snakes. Martins (1993) described a possible predation of a snake by ants and suggested that carnivorous ants (for their cooperative foraging behavior) and tarantulas (for their large size) may be responsible for most of the predator pressure on the ground level that apparently lead many vertebrates (even terrestrials) to avoid sleeping on the ground in Central Amazonian forests. Additional observations in this region indicate that small leaf litter lizards are a common prey of tarantulas (Theraphosinae; pers. obs.).

Several carnivorous vertebrates prey upon snakes and lizards. As suggested by Greene (1988), fishes are probably unimportant in the evolution of defensive tactics in lizards and snakes, since few of these animals are aquatic. However, some small aquatic lizards and snakes may face a strong predation pressure by large carnivorous fish and thus may have developed defensive tactics directed to these potential predators. The semiaquatic lizard, *Kentropyx altamazonica*, inhabits several aquatic habitats in Central Amazonia (see also Ávila-Pires, 1995). In “várzea” habitats this species is frequently seen running very quickly over deep water within “islands” of floating meadows (pers. obs.). These areas of lakes and rivers are inhabited by several large carnivorous fishes that commonly take prey that fall on the water surface. Thus, the locomotor behavior exhibited by the lizards may have evolved as a consequence of the presence of these carnivorous fishes (in fact, an individual of *K. altamazonica* that accidentally fell in the water in a lake was immediately grasped by a large carnivorous fish, *Cichla* sp.; pers. obs.). As another possible example, *Helicops angulatus*, a common aquatic snake in ponds and lakes in Central Amazonia, has a brown, spotted dorsum (probably cryptic) and a ventral color pattern that resembles that of coral snakes (yellow or red ground with large black spots). This ventral pattern, that presumably mimics coral snakes, may serve to startle predators approaching the snake from below (e. g., fish).

Amphibians seldom feed on lizards and snakes (see a review in Duellman & Trueb, 1986), but some large carnivorous species such as the voracious Neotropical leptodactylid frogs of the genus *Ceratophrys* may eat small lizards relatively often. Obviously, amphibians are not important in the evolution of defensive tactics in snakes and lizards.

Several reptiles feed frequently on lizards and snakes, including many cases of specialization. The best known examples are some varanids that are lizard specialists and many snakes that are either lizard or snake specialists (see Greene, 1982, 1988). In the forests of Central Amazonia, lizards and snakes are eaten by 53% and 17% of the 59 snake species found there, respectively (Martins, 1994; pers. obs.). Opportunistic predation may also occur: I caught an adult individual of the insectivorous, semi-aquatic tropidurid lizard, *Uranoscodon superciliosum*, that had just eaten a wormsnake (*Leptotyphlops*, total length ca. 100 mm). Reptiles (mainly snakes) may exert an important predation pressure on snakes and lizards, and thus are relatively important in the evolution of defensive tactics in these animals (Greene, 1988; Martins, 1994). When searching for prey, some reptiles use specific cues (e. g., chemoreception, termoreception) that are not common in vertebrates, although many reptiles also use the widespread sense of vision (e. g., several diurnal snakes).

Birds are certainly important predators of lizards and snakes and thus, many of the defensive tactics observed in these latter animals are directed to the former (Greene, 1988). Several instances of birds preying upon snakes and lizards from all over the world were reviewed by Greene (1988). Some birds, especially falconiforms (see Sazima, 1992; Martins, 1994), may be very important predators of Neotropical lizards and snakes, including some cases of specialization (see examples in Sick, 1985). It is important to note here that birds are mainly diurnal, visually oriented predators.

Finally, few mammals prey regularly on lizards and/or snakes (Greene, 1988). However, some carnivorous species (e. g., cats, dogs, mustelids) may be relatively important predators of lizards and snakes (see, e. g., Greene, 1988; Sazima, 1992; Martins, 1994). Carnivorous mammals that feed on snakes and lizards tend to be nocturnal and may use mainly olfaction and audition to locate their prey.

In summary, as noted by Greene (1988), several lizards and snakes face a large number of predators (mainly vertebrates) with diverse capabilities for prey detection and handling. Although one would expect that diurnal species that are active above the ground are more vulnerable to predators (see, e. g., Greene, 1988), fossorial and nocturnal species may also suffer a high predation pressure (e. g., fossorial snakes are commonly preyed upon by ophiophagous snakes). It is important to note that diurnal lizards and snakes that face diurnal predators (e. g., birds of prey) when active by day, may also be preyed upon when resting or sleeping at night (e. g., by snakes or mammals; see Greene, 1988). Thus, to avoid being eaten, lizards and snakes may develop defensive tactics against a diversity of predators and, most importantly, tune these tactics to the various senses their predators use to locate prey.

An overview of defensive tactics in lizards and snakes

In this paper I follow the functional approach of Endler (1986; see also Edmunds, 1974) in presenting the diversity of defensive tactics exhibited by snakes and lizards. A predatory event may be divided in five stages (Endler, 1986): detection, identification, approach, subjugation, and consumption. The defensive tactics exhibited by lizards and snakes, assumed to have evolved as a way to avoid being consumed (or killed or injured during an aborted predatory event), may interrupt the sequence of the predatory event in any stage, reducing the probability that the sequence will go to completion (see Endler, 1986). As one can realize in the review by Greene (1988), most defensive tactics described for lizards and snakes are supposedly directed to visually oriented predators (especially birds and mammals). This may in part be due to the fact that visually oriented predators exert a strong predation pressure on lizards and snakes, but it also may be a consequence of sampling bias, since vision is our most used sense (Greene, 1988; see also Edmunds, 1974). This apparent bias may be kept in mind when searching for patterns in defensive tactics of snakes and lizards.

Considering the initial stages of a predatory event, lizards and snakes may avoid being consumed by avoiding being detected by their potential predators. Inaccessibility seems to be the most obvious way to avoid detection. For instance, some terrestrial snakes and lizards sleep on the vegetation in Central Amazonia, supposedly to avoid contact with terrestrial predators (Martins, 1993). However, other important defensive tactics seem to have evolved to prevent detection, such as the widespread concealing coloration (including crypsis, masquerading, countershading, and obliterative marks; Greene, 1988) and immobility. For example, nearly all diurnal snakes in the forests of Central Amazonia possess a cryptic color pattern (Martins, 1994) and some may also exhibit immobility and cryptic behavior when approached. The combination of cryptic color pattern, immobility, and cryptic behavior makes some snakes especially difficult to detect by day (e. g., *Chironius fuscus*, *Oxybelis aeneus*, and *Xenoxybelis argenteus*; Martins, 1994).

After being detected by a potential predator, to avoid identification as an edible prey, snakes and lizards may use confusion (random or unpredictable movements, polymorphism, etc.), aposematism, and Batesian and Mullerian mimicry. The subtle movements that several species of coral snakes, *Micrurus* spp., exhibit when approached by day (e. g., Martins, 1994) may confound potential predators. Polymorphism in color pattern, that supposedly makes difficult the formation of search images by predators (see, e. g., Endler, 1986), is found in some lizards and snakes. The polychrotid lizards, *Anolis fuscoauratus* and *Anolis nitens*, have both a “normal” color pattern and another with a middorsal stripe (see, e. g., Ávila-Pires, 1995) and the colubrid snake, *Liophis typhlus*, exhibit at least three color patterns in the Manaus region (the dorsum may be green, reddish orange or bluish gray; pers. obs.). All species of *Micrurus* possess contrasting color patterns (combinations of black, red, yellow or white rings or ventral spots) that are considered to be aposematic (e. g., Greene & McDiarmid, 1981, Pough, 1988a, b, Savage & Slowinsky, 1992, Brodie, 1993, Brodie & Janzen, 1995; but see an alternative hypothesis in Vitt, 1992, and a discussion on the possibility of crypsis instead of aposematism in Pough, 1988a). Even the predominantly black aspect of some *Micrurus* (the species allocated in *Leptomicrurus* by some authors; see a picture of *Micrurus narducci* in Campbell & Lamar, 1989) may be aposematic. A possible argument in favor of this hypothesis is the existence of several similarly colored colubrids that seem to be mimics of these venomous snakes (curiously, this hypothesis was developed independently by Savage & Slowinsky, 1992, and Martins & Oliveira, 1993). Mimicry seems to be a widespread defensive tactic in snakes (see comprehensive reviews by Pough, 1988a, b). Batesian mimicry seems to be relatively common in snakes (see, e. g., Pough, 1988a, b, Savage & Slowinsky, 1992) and apparently rare in lizards (see, e. g., Huey & Pianka, 1977, Vitt, 1992). Several colubrid snakes are considered Batesian mimics of venomous elapids and viperids (e. g., Pough, 1988a, b, Savage & Slowinsky, 1992; but see Vitt, 1992, for an alternative hypothesis for the supposed coral snake mimics), some examples being very compelling (see, e. g., pictures of *Bothrops jararaca* and *Waglerophis merremii* in Sazima, 1992, and *Bothrops asper* and *Xenodon rhabdocephalus* in Campbell & Lamar, 1989). Mullerian mimicry may occur in venomous coral snakes (*Micrurus* spp.) and several viperids (see Pough, 1998a), although the resemblance of these snakes may simply reflect phylogenetic affinities.

After being identified as an edible prey, to avoid being approached, a lizard or a snake nearly invariably flees (locomotor escape), although it may also use other tactics such as confounding (including “Protean behavior”; see Curio, 1976) and startling behaviors (see Edmunds, 1974). Locomotor escape is widespread in lizards and snakes (see, e. g., case studies below). Several defensive behaviors seem to startle potential predators (see Greene, 1988). Many lizards and snakes, for instance, open widely the mouth (gape) when approached by a predator (well known Neotropical examples are some polychrotid lizards of the genus *Anolis* and *Enyalius* and the colubrid snakes, *Leptophis ahaetulla* and *Oxybelis aeneus*). The false strikes of *Leptophis* spp. and the dark lining of the mouth of some snakes (e. g., *O. aeneus*) seems to reinforce the startling potential of gaping.

After being approached and grasped by a predator, lizards and snakes may impede or interrupt subjugation by escaping, using mechanical methods, being noxious, and retaliating (see several examples in Greene, 1988). Thrashing vigorously the body seems to be the commonest method for interrupting subjugation; this behavior is extremely common in lizards and snakes (see first case study below). Another widespread escape tactic used by several lizards and a few snakes is tail autotomy or breakage (see a review by Arnold, 1988). The Neotropical colubrid snake, *Dendrophidion dendrophis*, may break its tail when handled (Martins, 1994; see also Duellman, 1978). Well known mechanical methods that may impede subjugation are the hard spines of many lizards. Noxiousness, especially in the form of cloacal discharge (e. g., feces, uric acid, urine, glandular products) seems to be relatively common in snakes and less so in lizards. Egler *et al*. (1996) observed a pitviper (*Bothrops atrox*) insistently rubbing the mouth on the substrate after biting the cloacal region of a colubrid snake (*Atractus torquatus*). Biting as a form of retaliation is very common in lizards and snakes (see Greene, 1988) and in some cases may impede subjugation. Several venomous snakes and the venomous helodermatid lizards may even envenomate their predators during subjugation. Other forms of retaliation include scratching with claws in several lizards (e. g., several large teiids) and constriction in some snakes (e. g., boids and *Clelia clelia*).

Virtually no defensive tactic exhibited by snakes and lizards are evidently directed to avoid consumption. However, the cloacal discharges observed in several snakes and lizards and the external gland discharges and supposed noxious flesh of some species (see Greene, 1988) may function as emetic substances. However, for such a defensive tactic to evolve, the prey may be still alive after regurgitation.

In summary, the defensive tactics exhibited by snakes and lizards may interrupt the sequence of the predatory event in any stage. Furthermore, a single species may exhibit defensive behaviors that act in two or more stages of the predatory event; these may even act together to decrease the chances of being eaten. For instance, the diurnal colubrid snake, *Chironius fuscus*, sleeps on the vegetation at night (inaccessibility) and is cryptically colored (being very similar to a twig; cf. “masquerading”, Edmunds, 1974); when approached by day it freezes (immobility); when touched both by day and at night it flees very quickly (locomotor escape) and when handled it rotates and thrashes the body (escape), vibrates the tail (startling?), inflates the gular region (startling), and may occasionally bite (retaliation) (Martins, 1994; pers. obs.; see also the second case study below).

Case studies on Neotropical lizards and snakes

Two case studies are summarized below to illustrate the potential of Neotropical species to explore specific and general questions in snake and lizard defensive biology. One deals with a snake community (synecological) and another with a single lizard species (autecological).

A forest snake community from Central Amazonia

The natural history and ecology of a snake community was studied from 1991 to 1994 in primary forests around Manaus, State of Amazonas, Brazil (Martins, 1994; unpublished data). Fieldwork was carried out in several localities, mostly at Reserva Ducke (RFAD), a 100 km^2 primary forest reserve. The main snake searching method used was visual search along forest trails. Most sampling was made at night. Each snake found was handled for marking and every defensive tactic exhibited by these snakes (before, during, and after handling) were recorded in the field; some defensive behaviors were documented with photographs.

Similar numbers of species were found active during daytime and at night. The proportions of species found in each microhabitat were also similar during the day and at night. Defensive data was obtained for 57 species (based on over 500 snake findings), totaling 33 different tactics (Table 1). Several trends are apparent in these results, some of them highly expected. For instance: (1) virtually all species use inaccessibility, employing various methods to achieve it (see also Martins, 1993); (2) the most used (and probably primitive) tactics are fleeing, thrashing the body, and biting; (3) all diurnal species are cryptically colored, except the aposematic venomous species and their supposed mimics; (4) almost all snakes that are diurnal or with no defined activity period (i. e., they may be active both during daytime and at night) used locomotor escape when approached; (5) the supposed coral snake mimics use several defensive tactics used by *Micrurus* spp. (as already shown by Sazima & Abe, 1991, for species from southeastern Brazil, and corroborating the coral snake mimicry hypothesis; see, e. g., Greene & McDiarmid, 1981); (6) head triangulation occurs in supposed mimics of common pitvipers (*Bothrops* spp.), in the green species that are supposedly mimics of the green pitviper (*Bothrops bilineatus*; see Campbell & Lamar, 1989), and, surprisingly, in two supposed coral snake mimics (*Rhinobothryum* and *Tripanurgos*).

A cluster analysis (data from Table 1, Euclidean distances, UPGMA) for defensive tactics (Fig. 1) shows groups formed either by closely related species (most groups; e. g., vipers, several colubrines, and all *Micrurus* are each grouped at the left third of the dendrogram) or by distantly related species that converge in defensive strategies (e. g., all coral mimics are grouped together and close to *Micrurus*) or in habitat use (and probably share potential predators; e. g., *Tripanurgos compressus*, *Rhinobothryum lentiginosum*, and *Leptodeira annulata*, grouped in the center of the dendrogram). In general, these results indicate that phylogeny is a strong determinant factor for the occurrence of defensive tactics in Neotropical snakes, although shared potential predators may lead to convergent defenses. In other words, it is possible to preview with some certainty the set of defensive tactics exhibited by a given species by knowing its phylogenetic affinities, its habitat and microhabitat, and even its eventual mimetic relationships.

Most data on defensive tactics gathered by Martins (1994) were previously unreported. As far as I know, except for Sazima & Abe's (1991) study on the defensive tactics of *Micrurus* and their supposed mimics in southeastern Brazil, this was the first attempt to analyze several Neotropical snakes from various phylogenetic lineages based on defensive tactics. Thus, only further similar analyses would confirm or refute the apparent trends delineated above. Furthermore, about three fourths of the 45 categories of snake antipredator mechanisms defined by Greene (1988) occur in the assemblage, showing the evident potential of Neotropical snakes to answer theoretical questions in snake defensive biology.

Table 1 - Summary of defensive tactics observed in 57 forest snakes of the Manaus region, Central Amazonia (Martins, 1994; unpublished data). Detailed descriptions of defensive tactics are in Greene (1988), except rotate body (see text). Defensive tactics not observed, but cited by Greene (1988) are marked with an asterisk. Species abbreviations are in the Appendix.

defensive tactics	**species**
inaccessibility	all
locomotor escape	AC,AL,AM,AN,AP,AS,AT,BA,CS,DA,EM,LD,LR,MA,MB,MH,ML,MS,MU,OF,OM,OO,PN,PP,PS,TB,TN
immobility	CF,CM,DP,IC,OA,PS,XA
concealing coloration	CE,CF,DC,DD,LH,LR,LT,MB,OA,OF,PP,PS,PV,TB,XA
aposematic coloration	MA,MH,ML,MS,MU
mimicry	AL,AP,AS,CS,EA,OM,OO,RL
tail display	AL,AP*,AS,EA,EC,MA,MH,ML,MS,MU
tail vibration	BA,CF,DC,DD,LM*,MB,OM,PP*,PS*,RL,TC
tail breakage	DD
hide head	AC,AM,AN,AP,AS,AT,BA,EC,DA,DP,LT,MA,MH,ML,MS,MU,
form ball	CE,EC,SC
inflate body	DD,LM,LR
coil body	BA,HA,MH,ML,MS,MU
dorsoventral body compression	AL,AP*,AS,DP,EA,HA,LR,LT,ML,MS,MU,XS
rotate body	CE,CF,CM,CS,DC,DD,HA,HH,IC,MB,OA,OF,PP,PS,TC
body thrash	AC,AL,AM,AN,AO,AP,AT,CF,CM,CS,DA,EA,EC,HA,HH,IC, LB,LD,LH,LR,LT,MA,MB,MH,ML,MS,MU,OA,OF,OM,OO, PN,PP, PS,PV,SC,TC,TM,TN,TR,TS,XA,XS
subtle thrashes	AL,DA,DP,EA,HA,MA,MH,ML,MS,MU
rub cloaca	DP
S-coil	BA,BC,CC,CE,CM,CS,EC,EM,LA,LH,LM,MB,OA,OF,PP,PS, PV,TC
gape	HA,LH,OA,PP,PV
gular inflation	CF,CM,CS,PP,PS
head enlargement	DP,HA,LA,LH,OF,PV,PS,RL,TC
false strikes	LA,LH,PP
hiss	BC,EM,PP*
coiling	BA,LM
frontal display	BA,LM,OF,PP,PS,PV
bite	BA,BC,CC,CE,EA,EC,EM,HA,LB,LH,LM,LR,MB,OA,OF,PP, PV,MA,MH,ML
strike	BA,CM,CS,EM,LH,LM,MB,OA,OF,PP,PV,TC
constrict	BC,CC,CE,EM,HA,PN,CL
press with tail spine	AO,LD,TB,TR,TS
cloacal discharge	AS*,AT,CM,DD,DP,DA,EM,IC,LA,LD,LR,LT,OA,TB,XA
evert hemipenis	EA,IC

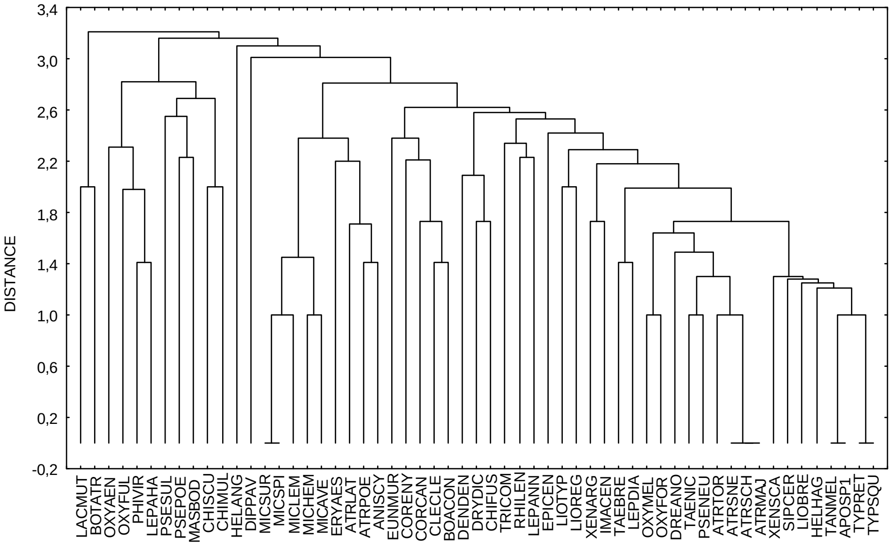

Figure 1 - Dendrogram resulting from a cluster analysis for defensive tactics exhibited by 57 forest snakes from Central Amazonia (Martins, 1994, and unpublished data). Species abbreviations are the three first letters of genera and species (see Appendix).

A lizard in a sandy beach of southeastern Brazil

During a study on the population biology of the tropidurid lizard *Liolaemus lutzae*, at Restinga de Maricá, a sandy beach in Rio de Janeiro, Rocha (1993) recorded the defensive tactics of this lizard under various situations. During eight months (in 1986-1987), the author marked lizards in an area of approximately 1.4 ha. During each visit (every two weeks), Rocha (1993) attempted to catch every lizard observed. Captured individuals were handled for marking and all defensive tactics exhibited during approach, capture, and handling was recorded. To evaluate tail breakage effectiveness, twenty lizards were seized at a similar position of the tail using a forceps. Additionally, twenty lizards were seized and pressed against the substrate by their forebody or head also with a forceps. Rocha (1993) also recorded each predation instance or capture attempts by potential predators on the lizards.

Guira Cuckoos, burrowing owls, and ghost crabs were observed attacking *L. lutzae* in the sandy beach (the Aplomado Falcon was also observed preying upon a *L. lutzae*; reference in Rocha, 1993). As primary defenses (see Edmunds, 1974), Rocha (1993) described concealing coloration (associated with long motionless periods) and disruptive marks. For the 231 lizards observed, he described as secondary defenses locomotor escape, caudal autotomy, tail waving, threat displays, and tonic immobility. Rocha (1993) quantified all these tactics. For instance, locomotor escape was exhibited by 88% of the lizards when approached. These lizards fled to the vegetation (47.5%), dived into the sand and became immobile (23.5%), hid under debris (21.6%), or fled to its burrow (7.4%). A summary of the defensive tactics used by *L. lutzae* is presented in figure 2.

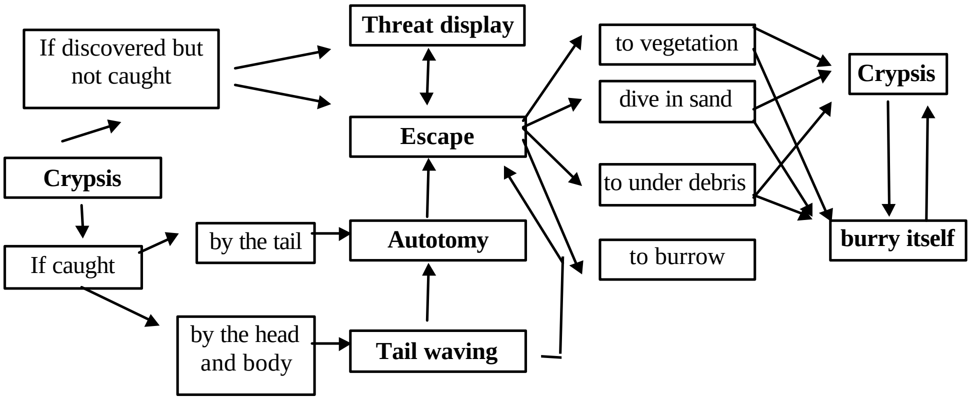

Figure 2 - A summary of the defensive tactics used by the tropidurid lizard *Liolaemus lutzae* in a sand beach in southeastern Brazil (modified from Rocha, 1993).

Expertly analyzing and interpreting the results, Rocha (1993) concluded that *L. lutzae* “developed a set of morphological and behavioral characteristics that may increase the chance of avoiding or escaping predation at the open beach habitat” (Fig. 2). Furthermore, Rocha (1993) suggested that these tactics may act simultaneously, increasing the chances of survival. This is the most detailed study on the defensive tactics of a South American lizard I am aware. This case shows clearly that a well designed study on a common species, associated with intensive fieldwork, may result in invaluable data for interpreting the evolution of defensive tactics in lizards and snakes.

Conclusions and suggestions for further studies

Although an important part of the strategies used by Neotropical lizards and snakes during their “struggle for survival” (e. g., birth, finding food, growing, mating; see Endler, 1986), defense against predators is surprisingly a secondary or ignored aspect in many natural history and ecological studies on these animals (e. g., for Amazonian lizards and snakes, Hoogmoed, 1973, Cunha & Nascimento, 1978, Duellman, 1978, 1987, Dixon & Soini, 1986, Martins, 1991, Vitt, 1993; but see Beebe, 1944a, b, 1945, 1946, Howland et al., 1990, Martins, 1994, Ávila-Pires, 1995).

Why are defensive tactics of lizards and snakes so much ignored? Several reasons may be involved, although two may be responsible for most of this lack of information in the literature. First of all, many of these studies were based on dead specimens preserved in museum jars (in such a condition, lizards and snakes do not behave defensively). Second, people with experience with live lizards and snakes apparently tend to give little importance to the several defensive tactics exhibited by these animals. To obtain detailed data on defensive tactics of snakes and lizards, it is necessary to encounter in the field and/or handle a few to several animals of each species to be studied. In fact, this was the case in the relatively few studies that provide detailed information on defense in South American reptiles (e. g., Beebe, 1944a, b, 1945, 1946; Howland et al., 1990; Sazima, 1992; Rocha, 1993; Martins, 1994; Ávila-Pires, 1995).

A thorough analysis on the problems and prospects in the study of defense in reptiles was made by Greene (1988); here I present only selected aspects (some based on my own experience with the animals). Several possible studies may be envisaged to explore the poorly known defensive tactics of Neotropical snakes and lizards, both in the field and in the laboratory. Although not as a primary purpose, defensive tactics can be intensively studied in long term field studies, both autecological and synecological. The case studies above are good examples. However, defense-oriented field studies with common species may also be promising. For instance, we know virtually nothing about the defensive behavior of very common Neotropical lizards and snakes (e. g., *Ameiva ameiva*, *Anolis* spp., *Tropidurus* spp., *Bothrops* spp.). Simple, well designed field and laboratory studies during short periods could provide insightful results (see, e. g., Brodie, 1993). Laboratory studies (see examples of methods in Ford, 1995) may include detailed descriptions of certain behaviors (that may greatly benefit from slow motion video analyses) and comparative studies of several defensive tactics among different species. These latter may provide insights on the evolution of defensive mechanisms in a given phylogenetic lineage if the systematics of the group is well known (see Brooks & McLennan, 1991). Additional promising studies (Greene, 1988) include staged encounters between predators and prey (see, e. g., Sazima, 1989), experimental studies on the costs and benefits of certain defensive tactics (e. g., Vitt et al., 1977), the relationships between injuries and defense (e. g., Schoener, 1979, Jaksic & Greene, 1984), and variation in defensive tactics (ontogenetic, geographical, etc.; see, e. g., Schall & Pianka, 1980).

A few recommendations may help those interested in studying defense in lizards and snakes. As in all fields of biology, well planned steps of the research on defense can make the gathering of good data highly predictable (Huey & Bennett, 1986). First of all, objective, clearly constructed questions and a good choice of methods are essential. During the gathering of field or laboratory data, a carefully elaborated form may help a lot in standardizing the aspects observed and making the data comparable between individuals, populations, and/or species. A careful quantification of the data is also important for several analyses (e. g., Rocha, 1993). Finally, documenting defensive tactics with good photographs and/or video may greatly help in describing and interpreting these tactics (this documentation may also serve as a substantiation for exotic, unexpected behaviors).

In summary, the rich Neotropical lizard and snake faunas have a high potential for providing good data on various aspects of antipredator mechanisms. Greene (1988) stated that “paradoxically, the most spectacular and complex defensive repertoires are often found in tropical species [...], for which rarity and other factors frequently make detailed studies difficult”. In this context, easily undertaken studies on common species and a proper documentation of defensive tactics in rare species and rich assemblages may certainly render insightful results that will surely help in understanding the evolution of defensive strategies in animals.

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Summary

Lizards and snakes are good subjects to explore specific and general questions in vertebrate behavioral biology. However, their potential for understanding vertebrate defensive strategies is relatively poorly explored. In fact, a general scarcity of information on defensive tactics of lizards and snakes is evident in the literature. In this paper I briefly review the current knowledge of predators and defensive tactics of lizards and snakes, present two case studies showing the potential of the Neotropical fauna in searching for patterns and understanding the evolution of defense in these animals, and suggest future work. Except for a few cases, defense against predators is surprisingly a secondary or ignored aspect in many natural history and ecological studies on Neotropical lizards and snakes. Easily undertaken field and laboratory studies (particularly with common species) and proper documentation of defensive tactics in rare species and rich assemblages may render extremely insightful results that will certainly help in understanding the evolution of defensive strategies in animals.

Resumo

Embora sejam bons objetos de estudo para explorar questões específicas e gerais em biologia comportamental de vertebrados, lagartos e serpentes são relativamente pouco explorados em relação à defesa contra predadores. De fato, a literatura sobre defesa em lagartos e serpentes é limitada. Neste artigo eu apresento uma breve revisão do conhecimento atual sobre predadores e defesa em serpentes e lagartos, dois estudos de caso mostrando o potencial da fauna neotropical na busca de padrões e no entendimento da evolução das estratégias defensivas nestes animais e, por fim, sugiro estudos futuros. Com poucas exceções, táticas defensivas são um aspecto surpreendentemente secundário ou ignorado em diversos estudos sobre a história natural e ecologia de lagartos e serpentes neotropicais. Estudos de fácil execução em laboratório e no campo (especialmente com espécies comuns) e uma documentação adequada de táticas defensivas em espécies raras e comunidades ricas podem render resultados extremamente úteis para o entendimento da evolução de estratégias defensivas em animais.

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Appendix

Abbreviations for species in table 1. *AC, Atractus schach; AL, Atractus latifrons; AM, Atractus major; AN, Atractus snethlageae; AO, Apostolepis* sp.; *AP, Atractus poeppigi; AS, Anilius scytale; AT, Atractus torquatus; BC, Boa constrictor; BA, Bothrops atrox; CC, Corallus caninus; CE, Corallus enydris; CF, Chironius fuscus; CL, Clelia clelia; CM, Chironius multiventris; CS, Chironius scurrulus; DA, Drepanoides anomalus; DC, Drymoluber dichrous; DD, Dendrophidion dendrophis; DP, Dipsas pavonina; EA, Erythrolamprus aesculapii; EC, Epicrates cenchria; EM, Eunectes murinus; HA, Helicops angulatus; HH, Helicops hagmanni; IC, Imantodes cenchoa; LA, Leptodeira annulata; LB, Liophis breviceps; LD, Leptotyphlops diaplocius; LH, Leptophis ahaetulla; LM, Lachesis muta; LR, Liophis reginae; LT, Liophis typhlus; MA, Micrurus averyi; MB, Mastigodryas boddaerti; MH, Micrurus hemprichii; ML, Micrurus lemniscatus; MS, Micrurus spixii; MU, Micrurus surinamensis; OA, Oxybelis aeneus; OF, Oxybelis fulgidus; OM, Oxyrhopus melanogenys; OO, Oxyrhopus formosus; PN, Pseudoboa neuwiedii; PP, Pseustes poecilonotus; PS, Pseustes sulphureus; PV, Philodryas viridissimus; RL, Rhinobothryum lentiginosum; SC, Siphlophis cervinus; TB, Taeniophalus brevirostris; TC, Tripanurgos compressus; TM, Tantilla melanocephala; TN, Taeniophalus nicagus; TR, Typhlops reticulatus; TS, Typhlophis squamosus; XA, Xenoxybelis argenteus; XS, Xenopholis scalaris.*

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