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PREDATION IN DIFFERENT PHENOTYPES OF VENOMOUS SNAKES IN THE ATLANTIC FOREST OF PARAÍBA, NORTHEAST BRAZIL

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RESUMO

Predação em diferentes fenótipos de serpentes venenosas na Floresta Atlântica da Paraíba, Nordeste do Brasil. Estudos sobre predação de serpentes têm sido conduzidos em condições naturais principalmente utilizando réplicas construídas e similares a diferentes fenótipos de serpentes. Estas são excelentes para acessar a frequência de ataques de predadores naturais sobre diferentes formas ou padrões de cor. O objetivo deste trabalho foi verificar as taxas de predação em diferentes fenótipos de serpentes venenosas em uma área de Floresta Atlântica do Nordeste do Brasil, a fim de verificar vantagens anti-predatórias de fenótipos de serpentes venenosas em comparação a serpentes inofensivas. Várias marcas foram encontradas nas replicas e aves foram os principais predadores. Nossos resultados indicam que os predadores são capazes de discernir os fenótipos antes do ataque e réplicas sem padrão de coloração foram mais atacadas que as de padrão venenoso. Além disso, o padrão de serpentes corais foi mais evitado que o de cascavel ou jararaca, indicando uma vantagem ao padrão colorido das serpentes mais tóxicas. Nós não encontramos diferenças nos ataques direcionados a cabeça ou corpo das réplicas, e a vantagem anti-predatória de serpentes viperídeas deve funcionar melhor com a combinação de várias estratégias, como a triangulação da cabeça, os padrões de cor e o comportamento agressivo.
Palavras-chave: Aposematismo; Coloração; Elapidae; Viperidae.

ABSTRACT

Predation in different phenotypes of venomous snakes in The Atlantic Forest of Paraíba, Northeast Brazil. Studies about predation on snakes have been conducted under natural conditions using clay-model replicas that resemble different snake phenotypes. These replicas are excellent to assess the frequency of attacks by natural predators on color pattern or body morphology. The aim of this work was to assess predation rates on different phenotypes of venomous snakes in an area of Atlantic Forest of Northeast Brazil to verify antipredatory advantages of venomous snake phenotype comparing with harmless snakes. Several imprints were found in replicas, and birds were considered the main predators that attacked the snake clay-models. Our results showed that predators were able to discriminate phenotypes prior to attack and plain replicas were attacked more than venomous morphs. Also, coral snakes morph were more avoided than rattlesnake or pitviper morphs, indicating an advantage of the colorful phenotype of the extremely venomous coral compared with the snakes of the Viperidae family. We did not find differences in attacks directed to head or body portion of the replicas, and the antipredatory advantage of viperid snakes should work better with the combination of multiple strategies such as triangulation of the head, color patterns and aggressive behavior.

Keywords: Aposematism; Coloration; Elapidae; Viperidae.

INTRODUCTION

The interaction between predator and prey has been the target of many ecological studies for more than a century (KUNO, 1987). This predator-prey relationship produces one of the strongest bases for the understanding of natural selection, and co-evolved populations of predators and preys varying their morphology, physiology and behavior for better capture or escape (STEVENS and RUXTON, 2012). One of the best antipredatory mechanisms for preys that have some dangerousness to predators is the aposematism. Despite aposematism is most commonly known in the context of warning coloration, this antipredator adaptation encompasses all “advertising” signals that are associated with the unprofitability of a prey item to potential predators (RUXTON *et al.*, 2004).

The aposematism in snakes is mainly recognized in the diverse Neotropical clade of venomous coral snakes (Elapidae), which present bright coloration in bands of red, yellow, black and white along all body extension (ROZE, 1996; CAMPBELL and LAMAR, 2004). However, another family of extremely venomous snakes, the Viperidae (pitvipers and rattlesnakes) also present morphology and coloration that can be called as aposematic. The vipers do not present bright colors, but usually shows triangular head shape and dorsal patterns of blotches in zigzag, triangle, diamond, or similar draws, that can be perceived by a predator as a warning signal (WÜSTER *et al.*, 2004; VALKONEN *et al.*, 2011).

Despite the facility to classify an aposematic snake, it is difficult to observe predatory events on aposematic or non-aposematic snakes in natural conditions and, consequently, it is hard to measure the advantage of a given color or pattern. Since 1970’s, a series of experimental works have been conducted using replicas with different colors of snakes to determine and quantify predation rates in snakes (for literature reviews see FRANÇA, 2008; PFENNIG and MULLEN, 2010; VALKONEN *et al.*, 2011). The use of non-toxic clay-models (or replicas) has been particularly useful to these studies, because it allows the recognition of predators (mostly birds or mammals) due to pecks and bite impressions in the models, and also the position of attacks in the model, and differences in predation rates in different phenotypes or in different habitats (MADSEN, 1987; BRODIE, 1993; BUASSO *et al.*, 2006; FRANÇA, 2008).

In Northeast Brazil, particularly in the Atlantic Forest, all pitviper and rattlesnake species present dorsum pattern composed by triangle or diamond blotches in grey or brown coloration, while coral snakes show conspicuous pattern of stripes in red, black and white (CAMPBELL and LAMAR, 2004). Herein, we assess predation rates on different phenotypes of venomous snakes in a rich snake area of Atlantic Forest to test the following hypothesis: i) There is no difference in the amount of attacks between natural predators, therefore the predation rate by birds is the same as by mammals; ii) Predators avoid attacking aposematic snakes, therefore the number of attacks on red and black clay models is lower than attacks on the plain models; iii) There is no difference in the amount of attacks between coral models and pitvipers/rattlesnakes models, therefore the predation rate is the same on these models; iv) Predators direct their attacks to the head of the preys, therefore the predation rate in the head region is higher than the body.

MATERIAL AND METHODS

Our experiment was conducted in the Guaribas Biological Reserve, SEMA III division, (06º40’53’’S, 35º09’59’’W), a 327 ha protected area located in Rio Tinto, Paraíba State, at the northern end of the Atlantic Forest in Northeast Brazil. The known snake assemblage of Rio Tinto is composed by 25 snake species, of which three are venomous: the pitviper *Bothrops leucurus*, and the coral snakes *Micrurus* aff *ibiboboca* and *Micrurus potiguara* (FRANÇA *et al.*, 2012). Despite that we did not record the rattlesnake *Crotalus durissus* there, this species has historical records for the area, and we have some records in neighboring municipalities, therefore we included it in the replicas.

Snakes replicas were made using pre-colored nontoxic plasticine (Acrilex clay references 507, 519, 520 and 531) threaded onto a plastic tube and a wire to create an S-shape (method follows BRODIE, 1993). Replicas were 1.5 cm in diameter and 20 cm in length, and each replica had a “head” representing the anterior end of the snake and the posterior end was anchored into the ground by a wire (Fig. 1). Five snake clay-models with different patterns were constructed: 1) uniformly gray control morph (similar to non-venomous colubrid snakes of the genera *Chironius*, *Liophis*, or *Philodryas*), 2) uniformly brown control morph (similar to non-venomous colubrid snakes of the genera *Chironius*, *Liophis*, or *Philodryas*), 3) coral snake morph (tricolor pattern in red, black and white, characteristic of venomous coral snakes *Micrurus*), 4) pitviper morph (pattern with triangular blotches similar to *Bothrops* species), 5) rattlesnake morph (pattern with diamond blotches presented by *Crotalus durissus*).

To evaluate predation rates on the different mimic patterns, we used 500

Figure 1. Plasticine replicas and examples of imprints attacks on clay-replicas: A) Toothmarks of opossum, B) Bill marks from birds, C) Incisor marks form rodent e D) and claw imprints from birds.

clay replicas (100 of each pattern) randomly distributed in different transects, all in forest environment, between December 2011 and May 2012. All clay-models in each transect were in place for 15 consecutive days, after which we checked replicas for evidence of predator attacks. We considered only bird (V- and U-shaped) and carnivorous (Canidae, Didelphidae, Mustelidae – Teeth-shaped) marks as predator attacks (Fig. 1). Marks made by rodents and arthropods were ignored. Replicas with evidence for more than one predator attack were considered a single predator, based on BRODIE (1993). All marked replicas were stored for future inspection.

We did not attempt to compensate for the relative conspicuousness of the morphs based on their placement in the environment, because previous works on aposematic snakes have demonstrated that both aposematic and cryptic replicas are attacked at the same frequency or more frequently when placed directly on the leaf litter compared to a high contrast background (BRODIE, 1993; BUASSO *et al.*, 2006; WÜSTER *et al.*, 2004).

We performed a Logistic Regression to model differences in predation rates among patterns and estimate the odds of being predated for each pattern. We polled attacks in the two control morphs in only one control to best fit in logistic regression. Also, we used chi-square analysis to determine if the body region attacked by predators differed among patterns, and the 2 x 2 contingency table to determine differences in attacks of birds or mammals. All analyses were performed in R (R Development Core Team, 2010); logistic regression was done using *lmr* function of rms package (HARRELL, 2011).

RESULTS

Of our 500 clay-models, 41 (8.2%) were attacked by predators of snakes. Among these attacks, 34 (83%) corresponded to attacks by birds, whereas 7 (17%) corresponded to attacks by carnivorous mammals. In addition to marks left on the plasticine models, other evidence of predators such as foot imprints, feathers or fur could be seen near some models. The predation rate by birds in all models was significantly higher that attacks by mammals (Chi-square = 15.11; $P< 0.005$).

We recorded attacks on 3 clay-models of coral snake morph, 7 of rattlesnake morph, 9 of pitviper morph, and 22 in controls (16 in brown pattern and 6 in gray) (Fig. 2). Logistic regression showed that the predation rate are different among the patterns (Likelihood Ratio X^2=10.27, df = 5, p = 0.0164), and also indicated that pattern significantly affected the probability of being predated (AIC = 234.12, df = 3, p < 0.0001) and estimated the odds of being attacked for each pattern (Table 1).

We did not record difference in attacks between head (22 attacks) or body (18) for all models (chisquare = 0.4; P = 0.6332) and neither for any pattern: *rattlesnake model* (4 attacks in head: 3 in body - chisquare = 0.1429; P = 1.0); *pitviper model* (5:4 - chisquare = 1.2857; P = 0.4408); coral model (3:0 - chisquare = 3; P = 0.2644); control (7:9 - chisquare = 0.1818; P = 0.8271).

DISCUSSION

We observed that replicas with the three venomous morphs were less attacked than plain replicas. These differences in the proportion of attacks suggest that vertebrate predators were able to discriminate between phenotypes of venomous or harmless snakes prior to attack, as seen in other studies that use clay-models of snakes (BRODIE, 1993; BUASSO *et al.*, 2006; WÜSTER *et al.*, 2004; NISKANEN and MAPPES, 2005).

The mistake in predator attack directed to a venomous snake might cause the predator injury (BRUGGER, 1989; HECKEL *et al.*, 1994), and this can lead to harmless snakes possess color and patterns (even imperfect) that resemble venomous snakes (GREENE and MCDIARMID, 2005). The clay-models were constructed to maintain maximum resemblance of venomous snakes present in the study area

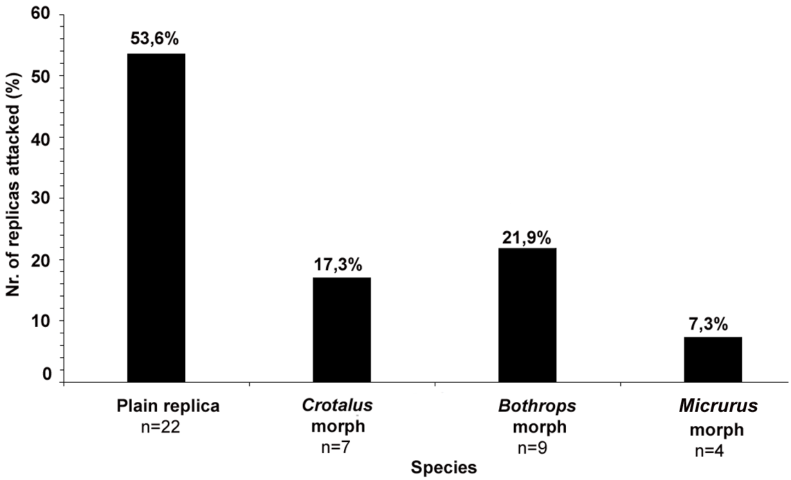

Figure 2. The number of attacks by natural predators (birds and carnivorous mammals) on each phenotype of Atlantic Forest's snakes.

Table 1- Summary of the Logistic regression results of predation rates in snake models

	Coef	S.E.	Wald Z	Pr(>|Z|)	Odds Ratio
Intercept	-1.6582	0.2728	-6.079	<0.0001	0.02
Crotalus morph	-0.6554	0.4433	-1.479	0.13927	1.58
Bothrops morph	-0.9285	0.4775	-1.944	0.05185	2.41
Micrurus morph	-1.8179	0.6466	-2.812	0.00493	2.90

(*Micrurus* aff. *ibiboboca*, *Bothrops leucurus* and *Crotalus durissus*), not only in color pattern but also in body morphology.

The replicas with coral snake phenotype were less attacked than pitviper and rattlesnake morphs. Snakes of the family Elapidae have high toxicity when compared to the poison of serpents from family Viperidae (CARDOSO *et al.*, 2003), and this may be the reason why the predators avoid the color pattern of coral snake.

We did not find preferences for attacks in the "heads" of the replicas; however, the two attacks in coral snake morph were in the head, suggesting more caution of predators to attack this phenotype. It is interesting that vipers have triangle heads and it is usually recognized as a dangerous morph, and consequently many harmless snakes can mimic this head morphology (DELL'AGLIO *et al.*, 2012; VALKONEN *et al.*, 2011). Accordingly, predators that attack venomous vipers (or mimics) should direct the attacks to the head of these snakes to avoid any injury. We did not find significant difference in attacks between head and body of pitviper/rattlesnake morphs. The lack of advantage of head shape of snakes was presented by GUIMARÃES and SAWAYA (2011; 2012), which did not find differences in attacks in replicas with oval- or triangular-shaped head. However, the importance of head shape plus color pattern, body morphology and behavior provides advantage to viper snakes and its mimics.

Birds are known as the main predators of snakes, and they are very useful in clay-model works due to their visual orientation. We recorded a higher number of imprints in replicas with pecking in "V" shape or claws of birds, as previously found in other studies (BRODIE, 1993; BUASSO *et al.*, 2006; WÜSTER *et al.*, 2004; NISKANEN and MAPPES, 2005). VALKONEN and MAPPES (2012) indicated that only bird attacks should be computed in clay-model studies. However, we also recorded carnivorous mammals imprints and used these attacks in analysis due to some reasons: first, carnivorous mammals (fox, raccoon, opossum, skunk) are also know as snake predators, even venomous snakes (RODRIGUES, 2005; REIS, 2006); also, other previous clay-model studies recorded carnivorous marks as "U" shape of bites with tooth imprint (BUASSO *et al.*, 2006; HARPER and PFENNIG, 2008); finally, discarding attacks by ants, other arthropods and rodents, the use of all true attacks can provide better results for clay-model studies.

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