Does color polymorphism affect the predation risk on *Phalotris lemniscatus* (Duméril, Bibron and Duméril, 1854) (Serpentes, Dipsadidae)?

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Abstract. The snake *Phalotris lemniscatus* is a polymorphic species regarding color, which varies between light shades with a yellow predominance (pale yellow-brown) to darker shades with a red predominance (red-dark). Pale yellow-brown individuals are more frequent in coastal populations while there is a tendency of increasing the frequency of red-dark morphs in inland areas. Considering the variation in substrate color along the species distribution (light/sandy on the coast to reddish and dark/argillaceous in inland areas), we raise the hypothesis that the predation rate of each morph would be lower in sites were its crypsis potential is higher. If correct, this hypothesis would reinforce the idea that the predation risk is one of the factors influencing the spatial structuring in morph frequency distributions in populations of *P. lemniscatus*. To test this hypothesis, we performed a field experiment using plasticine *P. lemniscatus* artificial models that represent two morphs: red-dark and pale yellow-brown. The models were distributed in three localities where the following substrate types predominate: light (Coastal Site), intermediary (Lowland Site) and reddish dark (Highland Site). Our predictions were corroborated only at the coastal site, where the less cryptic morph was the most preyed one. We verified that there is a regional variation in the predation risk on different morphs. Thus, the possibility that the selective pressure by predators is a relevant element in the structuring of the frequencies of different morph populations of this species cannot be completely excluded.

Keywords. Behavior, Brazil, coral-pattern, mimetism, phenotype, snake.

INTRODUCTION

Polymorphism is characterized by the presence of different phenotypes in a population (Mayr, 1963) and does not only include the morphological features, but also those related to the life history and behavior of the organisms (Huxley, 1955; Hedrick, 2006). There are many processes behind the maintenance of different morphs in a population, and these processes are not easily identified (Calsbeek and Cox, 2012; Deitloff et al., 2013; Karpestam et al., 2016, Barnett et al., 2018).

Questions such as "how do morphs vary their

appearance and abundance in a spatial scale" and "what are the habitat components that favor the existence and sympatry of two or more morphs" would be better answered from experiments performed under natural conditions (Hoffman and Blouin, 2000; Roulin, 2004; Gray and McKinnon, 2006).

In squamates, particularly in snakes, some of the most well-documented types of polymorphism are the multiple color forms (color polymorphism). From an ecological view, morphs can be considered cryptic (when they maximize the animal's camouflage; Clarke, 1962; King and Lawson, 1995; Eizirik et al., 2003; Hoffman et al., 2006), aposematic (when they highlight a warning signal; Brodie and Brodie, 2004; Noonan and Comeault, 2009) or a combination of both (Brodie and Brodie, 1980; Wang and Shaffer, 2008; Barnett et al., 2018). Variations in the color are recorded in other taxa and are associated with an improvement in the performance of intraspecific communication, thermoregulation or as anti-predation mechanisms (Endler, 1978; Pérez et al., 2017). Snakes have many different and complex patterns of intraspecific color polymorphism, from systems with bright and contrasting colors to those with cryptic color sets or disruptive patterns (Cox and Rabosky, 2013; Holmes et al., 2017; Martínez-Freiría et al., 2017; Santos et al., 2017).

Undoubtedly, crypsis is an important factor that might bring higher survival chances to the morphotype, since the animal's color matches the color of the substrate, making it difficult to be detected by vision-oriented predators (Johannesson and Ekendahl, 2002; Venesky and Anthony, 2007). These predators are expected to find and attack more easily the more conspicuous morphs in the population, according to their crypsis (Stimson and Berman, 1990).

In southern Brazil, there are consistent records of polymorphic variations spatially structured for the Dumeril's Diadem Snake (*Phalotris lemniscatus*) (Duméril, Bibron and Duméril, 1854) (Fig. 1A and 1C). This species has different morphs with shades going from red-dark to pale yellow-brown (Ferrarezzi, 1993; Esteves, 2011; Noronha, 2012). The variations seem to be restricted to these shades, with only one record of albinism (Abegg, 2015) and no records of a melanistic form. The distribution of *P. lemniscatus* morphs is spatially structured in the following way: individuals of predominantly pale yellow-brown color occur more frequently in populations from regions of sandy substrate of the southern Brazil and Uruguay coasts, while the predominantly red-dark individuals occur more frequently in more continental regions of Brazil and Argentina (Noronha, 2012). In these more continental localities, the substrates are darker due to the predominance of organic matter and

clay in the soil (Lema, 2002; Esteves, 2011), allowing differential crypsis between the morphs.

Many snake predators in the extreme South of Brazil are visually oriented (e.g., birds: Dell' Aglio et al., 2012; Santos et al., 2013), and probably respond to variations in the level of contrast between their prey and the substrate. With this premise, we expect that predation is an important selective factor for the definition of the rare (more predated) and more frequent (less predated) morphs in each population. Thus, the predation rate of the morphs of *P. lemniscatus* should vary between regions with different substrate colors, being higher on artificial models of the red-dark type than on those of the yellow-brown type in the coastal region, and the opposite in continental regions.

Because predation events are generally difficult to observe in the wild, they have been largely studied using experimental approaches as a manner to observe the interactions between predator and prey (Brodie, 1993; Guimarães and Sawaya, 2011; Purger et al., 2017). The use of artificial plasticine models has been employed successfully in predation experiments with invertebrates (Koh and Menge, 2006), amphibians (Kuchta, 2006) and reptiles (Stuart-Fox et al., 2002; Valkonen et al., 2011; Dell´Aglio et al., 2012), with highlight on snakes (Brodie, 1993; Dell'Aglio et al., 2012; Farallo and Forstner, 2012; Santos et al., 2013; Akcali et al., 2019).

In the present study, we used models of *P. lemniscatus* to test the hypothesis that the predation rate of each morph would be lower in sites were its crypsis potential is higher. If correct, this hypothesis would reinforce the idea that predation risk is one of the factors for the spatial structuring in the distribution of morph frequencies in populations of *P. lemniscatus*.

MATERIAL AND METHODS

We distributed, in the wild, two types of artificial models of the snake: red-dark and yellow-brown (Fig. 1B and 1D). Their color was based on live specimens captured in the study area in order to accurately represent the color of the morphs that have the extremes of variation between the lighter and darker shades (Noronha, 2012; Fig. 1A and 1C). These models were manufactured with non-toxic plasticine that allowed the record and quantification of marks left by predator attacks (Brodie, 1993). The models measured 30 cm in length and 1 cm in diameter, which represents the mean size of adult animals (Carreira et al., 2012).

The samplings were performed in localities with different natural proportions in the abundance of the morphs of *P. lemniscatus*, these being: 1 – Coastal Site (32°43'2.49"S; 52°28'29.87"W) in the municipality of Rio Grande (annual mean temperature of 17.5 °C, Rossato, 2014), where the pale yellow-brown morph is more abundant; 2 – Highland Site (29°39'23.04"S; 51°23'7.40"W) in the municipality of São Francisco de Paula, where the red-
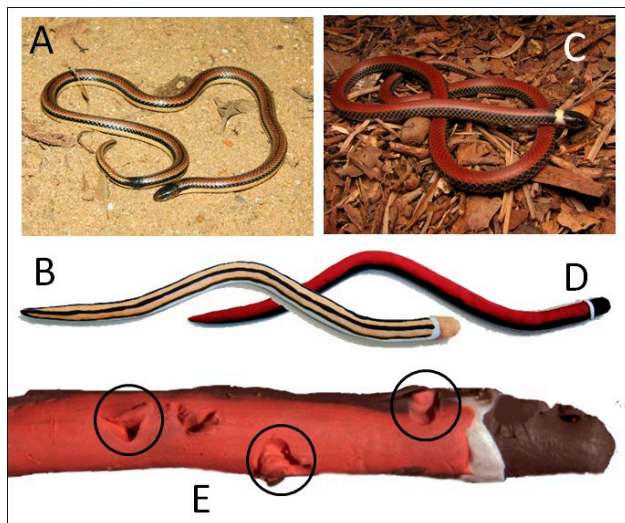
Fig. 1. General aspect of the specimens of *Phalotris lemniscatus* used as a reference to the pale yellow-brown (A) and red-dark (C) patterns and their models manufactured in plasticine (B and D, respectively). The image E show some marks considered as attacks from predators.

Fig. 2. Geographic location of the sampling sites.

dark morph is more abundant (annual mean temperature of 14.5 °C; Rossato, 2014; minimum temperatures frequently close to 0 °C in winter; Maluf, 2000); 3 – Lowland Site (29°27'0.20"S; 50°34'59.83"W) in the municipality of Capela de Santana (annual mean temperature of 17.0 °C; Rossato, 2014), where both morphs are observed in similar proportions (Noronha, 2012). The sampled localities extend in extreme points of an area of approximately 12660 km² located at least at 404 km from each other (Fig. 2). The prevailing substrates in each locality are light and sandy (Coastal Site) and dark and argillaceous (Highland and Lowland Sites), allowing the evaluation of different contrast levels between model and background.

We distributed 200 models in each locality (100 red-dark and 100 pale yellow-brown), along five transects, each 400 m long. The transects were at least 1000 m from each other and each received 40 snakes (one every 10 meters). In each transect, the two morphs were interspersed so that they had 20 red-dark and 20 pale yellow-brown models, a protocol similar to that of Dell'Aglio et al. (2012) and Farallo and Forstner (2012). We used this 1:1 ratio to avoid a possible frequency-dependent predation effect. Each model received an identification code and its position was marked with a GPS device to facilitate their monitoring. We also took the care to arrange all the transects in an area of similar vegetation cover (low and scarce vegetation with the prevalence of exposed soil) that would not provide any visual barrier to the predators. Thus, the contrast between the models and the background happened due to the color of the artificial snake and the soil.

The artificial models remained exposed in the field for 48 hours. During this time, they were inspected twice, after 24 and 48 hours since the installation. During the inspections, we recorded the presence of attack marks on the models. Each artificial model that clearly showed marks of bird attack (e.g., peck-

ings) was considered a predation event (Brodie, 1993; Dell'Aglio et al., 2012). The models showing attack marks during the first inspection were replaced by new models. It is worth highlighting that the three localities have a similar fauna of predatory birds (Fontana et al., 2008; Petry and Scherer, 2008; Accordi and Hartz, 2006), mainly of birds of prey (e.g., *Caracara plancus*, *Milvago chimango*), egrets (e.g., *Ardea alba*, *Syrigma sibilatrix*) and even some other generalist foragers (e.g., *Guira guira*).

Data analysis

Just clearly identifiable pecking marks were considered as an attack (or predation event). We quantified only the presence and not the number of marks. Thus, a model with one or more marks corresponded to one predation event. To evaluate the predation intensity of each morph, we calculated the predation rate. To do so, we divided the number of models of each morph with predation evidence (number of events) by the number of exposure hours of these models. The number of exposure hours corresponds to the total number of hours between the installation of the model and its final inspection. This calculation was done for each transect. To test the differences in predation rates of the morphs between the localities we performed an Analysis of Variance with randomization test (Pillar and Orlóci, 1996). In these analyses, we used Euclidian distance matrices between the morphs, restricting the permutations within the transects (blocks) to control possible discrepancies in factors related to the predation that were not directly verified (e.g. number and species of predators). The Analyses of Variance were performed by means of the software MULTIV v.3.34b (Pillar, 1997).

RESULTS

We recorded altogether 162 predation events, which corresponds to an overall predation rate of 1.06 events per hour. At the Lowland Site, 90 models were attacked (23%). This locality had a larger number of attacks directed to the
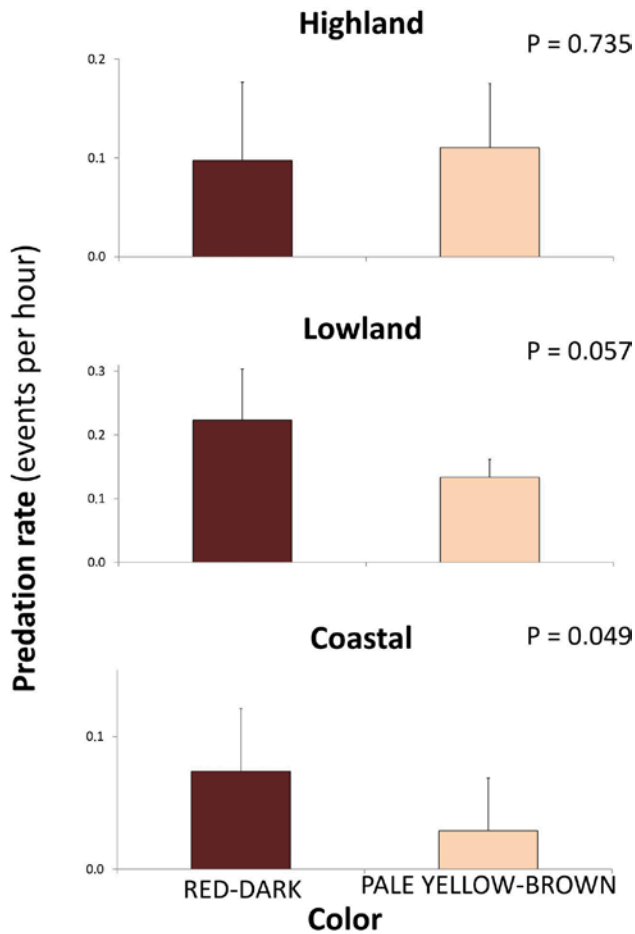
Highland

P = 0.735

Lowland

P = 0.057

Coastal

P = 0.049

RED-DARK   PALE YELLOW-BROWN

Color

Predation rate (events per hour)

Fig. 3. Mean predation rate (events per hour) on the different morphs (red-dark and pale yellow-brown) in the three areas (Highland, Lowland and Coastal).

red-dark morph (57 models; 0.22 events per hour) than to the pale yellow-brown morph (33 models; 0.13 events per hour), this difference being marginally significant (SQE = 0.02; R^2 = 41%; P = 0.057; n = 10). At the Coastal Site, we recorded 22 predation events (11%). As for the Lowland Site, the Coastal Site also showed more attacks on the red-dark models (16 models; 0.07 events per hour) than on the pale yellow-brown models (6 models; 0.03 events per hour) (SQE = 0.005; R^2 = 25%; P = 0.049; n = 10). At the Highland Site, there was no significant variation in the number of attacks between the different morphs (SQE = 0.0004; R^2 < 1%; P = 0.735; n = 10) (Fig. 3).

DISCUSSION

Our results suggest that the morphs of *Phalotris lemniscatus* have different levels of predation and the preda-

tion rate varies between areas. Our predictions regarding the importance of crypsis were corroborated only at the Coastal Site, where the predation rate was higher on the red-dark models that have higher contrast (less cryptic) in relation to the substrate of the region. Similar results were also observed for the morphs of the Mottled Rock Rattlesnake (*Crotalus lepidus lepidus*; Farallo and Forstner, 2012) and the sand hills mice (Linnen et al., 2013), both in the United States. Experiments with artificial models showed that differential crypsis and predation are the main forces of the spatial structuring of the western rattlesnake's morphs (Farallo and Forstner, 2012). Similarly, Linnen et al. (2013) pointed out that the color of the soil offers differential camouflage opportunity to sandhill mice against owls and other raptors and is determinant to the spatial structuring of their colored morphs.

However, our data show that predation does not seem to be the main factor acting on the spatial structuring of the morphs of *P. lemniscatus* since the naturally more uncommon morph in the Lowland Site was the one that suffered less predation (pale-yellow). In other words, the low frequency of the pale-yellow morph in the Lowland Site population does not seem to be the result of predation.

It is worth highlighting that all the sampled localities have a similar predator composition. However, there is a possibility of existing regional variations in the ability of these predators in detecting prey, which would have influenced the local number of attacks on each model type. Experiments showed that the capacity of predators to detect the different morphs based on motionless prey is variable and depends on their ability to generate a specific searching image according to the form, size and color of the prey (e.g., Brodie, 1993; Olsson, 1993; Gotmark, 1994).

It is reasonable to imagine that the search image established by a predator is compatible with a certain type of prey that has a higher probability of being found. Thus, the naturally rare morphs in each locality may not be part of the searching image of local predators (Dukas, 1998). In this case, they might not be easily detectable, even if their color shows more contrast with the background. Therefore, their predation rate would remain relatively low, even if their population was experimentally increased with the introduction of artificial models (Wennersten and Forsman, 2009; Karpestam et al., 2014). In addition, animals that attack potentially dangerous organisms (e.g., snakes) commonly reduce their exploratory behavior toward new and different prey morphs (Greenberg and Mettke-Hofmann, 2001), thus exhibiting a neophobic behavior (avoiding a new environmental aspect) (Greggor et al., 2016). Although possible, this hypothesis would be

applicable to the lowland and highland sites, but not to the coastal site, where the less common and less cryptical models were the most preyed ones.

Our results point toward the possibility that other factors besides crypsis interfere on the predation rate. Among those, we can mention the mimetic aposematic potential of the red morph since their bright colors are associated with poisonous or nonpalatable animals (Cuthill et al., 2005; Tarvin et al., 2017). The establishment of a parallel between our data and such studies seems convenient due to the slightly reddish pattern of one of the morphs of *P. lemniscatus*. Yet, the effectiveness of the aposematism based on coral-like coloration is questionable regarding canids (Tozetti et al., 2004) and birds (Smith, 1969). Besides the passive strategies such as crypsis and immobility (Venesky and Anthony, 2007), snakes show active defense strategies or behavioral displays such as escape (Forsman and Appelqvist, 1998; Creer, 2005; Allen et al, 2013). Additionally, *P. lemniscatus* has the antipredatory behavior called "erratic movements" (Tozetti et al., 2009), which would reduce the predation effectiveness after being detected by a predator (Forsman and Appelqvist, 1998). These behaviors may act in combination with the crypsis for the maintenance of each morph in each population.

Our study failed to obtain answers to the proposed questions. One of the reasons might be that the frequency of different morphs in each population may be related to other environmental factors such as thermoregulation (Trullas et al., 2007). In general, ectotherms from cold environments tend to have darker colors, which favor the absorption of solar radiation (Gibson and Falls, 1979; Clusella-Trullas et al., 2008; Allen et al., 2013). Considering that the Highland Site has the lowest temperatures in the distribution area of *P. lemniscatus*, there would be a positive selective pressure favorable to red-dark individuals in the Highland Site and to pale yellow-brown individuals in the Coastal Site (see Bittner et al., 2002).

Despite the weakness of our hypothesis based on our results, we verify a regional variation on the predation risk of the different morphs of this species, which does not completely exclude the possibility that the selective pressure by predators is a relevant element in the structuring of the frequencies of different morphs in populations of this species.

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