

Geographic variation in the probability of being born with and retaining contrasting tail tip colour (tail luring) in the Common Lancehead *Bothrops jararaca*

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Abstract

In snakes that are known to be ambush predators, tail luring, in which the movement of a snake’s tail resembles that of a worm or insect larva and is used to attract prey, has emerged as a complementary hunting strategy. In certain species, some individuals may present a conspicuously bright colour at the tail tip, which eventually disappears with age. Some authors argue that the bright colour enhances the resemblance of the snake’s tail with a potential food item, increasing the success of capture. Here, we tested the influence of geographic variation, sex, and environmental factors on the probability that Common Lanceheads *Bothrops jararaca* (Wied-Neuwied, 1824) from southeastern Brazil were born with this contrasting tail tip and whether snakes retain this trait throughout adulthood. None of the predictors affected the probability of births with a contrasting tail tip. However, a higher proportion of individuals from the coastal populations retained this trait into adulthood. The absence of difference in the probability of being born with this trait indicates that there are other factors influencing tail tip colour, such as phylogenetic correlates, rather than intrinsic or environmental factors. A higher proportion of ectothermic prey in the diet of coastal populations may explain why this population retains tail luring throughout adulthood.

Key words: *Bothrops jararaca* (Wied-Neuwied, 1824), aggressive mimicry, caudal luring, pit viper, feeding, population ecology

Introduction

Throughout their life histories, snakes have evolved a series of intriguing strategies to hunt and capture prey. The major methods vary from active foragers, which generally search for prey and simply seize it (e.g., constrict or use venom to immobilise, kill, and then swallow prey), to ambush predators that select a site potentially used by their prey and then “sit and wait” until the target comes within striking distance (Greene 1997; Beaupre and Montgomery 2007; McDiarmid 2012). In addition to these main hunting strategies, other complementary methods have emerged, such as using the tail as a lure, known as tail luring (also “aggressive mimicry”; Pasteur 1982), to attract prey and bring them towards the snake.

This behaviour consists of a waving movement of the tail to resemble potential prey (e.g., mimicking an insect larva or worm), which stimulates the interest of some ectothermic prey such as frogs and lizards that approach the snake’s tail lure looking for a meal, only to become a meal themselves (Neil 1960; Heatwole and Davison 1976). Additionally, some

species often present a conspicuous brightly coloured tail tip (Heatwole and Davison 1976; Carpenter et al. 1978), in contrast to the cryptic colour of the body (hereafter contrasting tail tip (CTT)). Some authors argue that the CTT is advantageous because it enhances the resemblance of the tail lure with a worm or insect larvae and, compared to non-coloured tail tips, reduces the probability that the snake’s prey will detect the attachment of the lure to the snake’s body (Rabatsky 2008), potentially increasing feeding success and snake fitness (see Rabatsky 2008, for a detailed discussion of this assumption).

CTT arose independently in distinct phylogenetic lineages of snakes and appears to be affected by intrinsic factors such as sexual dimorphism in which a given pattern is more closely linked to males or females (Burger and Smith 1950; Heatwole and Davison 1976; Tesler et al. 2019), age/size, where the contrasting colour tends to disappear as the snake grows (Burger and Smith 1950; Murphy et al. 1978; Andrade et al. 1996), and geographic distribution, where the presence/absence of conspicuous markings differs between pop-

ulations (Neil 1960). Therefore, if the presence of a CTT provides more advantages than disadvantages to individuals in a group or population, it is expected that this trait will become fixed.

Tail luring is widespread in crotaline snakes, including pit vipers of the genus *Bothrops* Wagler, 1824 (Burger and Smith 1950; Greene and Campbell 1972; Andrade et al. 1996, 2010; Martins et al. 2002; Fonseca et al. 2019). The Common Lancehead *Bothrops jararaca* (Wied-Neuwied, 1824) inhabits the Atlantic Forest in Brazil (Campbell and Lamar 2004), and undergoes a marked ontogenetic change in diet. Adults feed mostly on endothermic prey such as birds and small mammals, while juveniles, which exhibit tail-luring behaviour, feed mainly on ectothermic prey, such as frogs and lizards (Sazima 1992, 2006). There are at least three morphotypes of tail tips in this species: two conspicuous colours, whitish or blackish that contrast with the body, and one inconspicuous mottled brownish colour that is similar to the body colour (Sazima 1991). The CTT is found in juveniles and fades and merges with the body colour of the snakes as they grow (Sazima 2001).

In the Neotropical region, juvenile *B. jararaca* prey activity is positively correlated with climatic factors, mainly temperature and rainfall, for both anurans (Boquimpani-Freitas et al. 2007; Canelas and Bertoluci 2007; Vasconcelos et al. 2010; Ximenes and Tozetti 2015; Schalk and Saenz 2016) and lizards (Bergallo and Rocha 1993; Vrcibradic and Rocha 1998; Filogonio et al. 2010; Maia-Carneiro et al. 2012). Additionally, juveniles from a coastal population (subject to more rain and higher temperatures) consume more ectothermic prey than those from a highland population, and the ontogenetic shift from ectothermic to endothermic prey occurs more slowly in the former (Moraes 2008). Accordingly, we assumed that frogs and lizards from areas with warmer temperatures and higher precipitation would be more active and a higher proportion of *B. jararaca* individuals would therefore be likely to present CTT.

Despite the large number of studies on tail luring in snakes, most of them are not hypothesis-based. In this study, we evaluated two main hypotheses focusing on adaptations that may occur between *B. jararaca* populations. Based on the premise that study populations are subject to different environmental pressures, such as climate and prey availability, and that these pressures result in different phenotypes, we tested the hypothesis that a higher proportion of individuals from coastal populations are born with CTT than in the highland population. Second, considering that ontogenetic changes in morphology and feeding habits may differ between study populations, we tested the hypothesis that a higher proportion of coastal individuals retain CTT throughout adulthood than in the highland population. Additionally, we evaluated the influence of intrinsic (sex and body size) and climatic factors on the prevalence of CTT.

Materials and methods

A total of 209 *B. jararaca* individuals were used in this study. A total of 110 individuals were obtained from the coastal pop-

ulation (59 females and 51 males) and 99 from the highland population (50 females and 49 males). All specimens were housed in the Herpetological Collection of Richard Alphonse Hoge, at the Institute of Butantan, São Paulo, Brazil. We classified the specimens belonging to each population based on their elevational distribution, with individuals from 0 to 80 m.a.s.l. belonging to the coastal population and those above 600 m.a.s.l. as the highland population (cf. Siqueira et al. 2022).

The body sizes of the specimens ranged from 165 to 1265 mm in coastal areas and from 242 to 1248 mm in highland populations. For each individual, we recorded three variables: sex (determined by sexual size dimorphism, an inspection of the gonads or the hemipenis erector muscle); snout-vent length (SVL), measured from the tip of the nose to the last scale before the cloacal scale; and tail tip colour, which was categorised as CTT absent (the same colour as the body) or CTT present (conspicuous tail tip, lighter or darker than the body). Specimens with incomplete tails were excluded. The environmental data were the mean annual temperature (MAT) and mean annual precipitation (MAP), which were extracted from the Wordclim database at a resolution of 30 arc sec based on the geographic coordinates for each specimen (cf. Siqueira et al. 2022). When specific coordinates were not available, we considered the origin to be the centroid of the municipality. All variables were log-transformed before the analysis to determine the normality criterion.

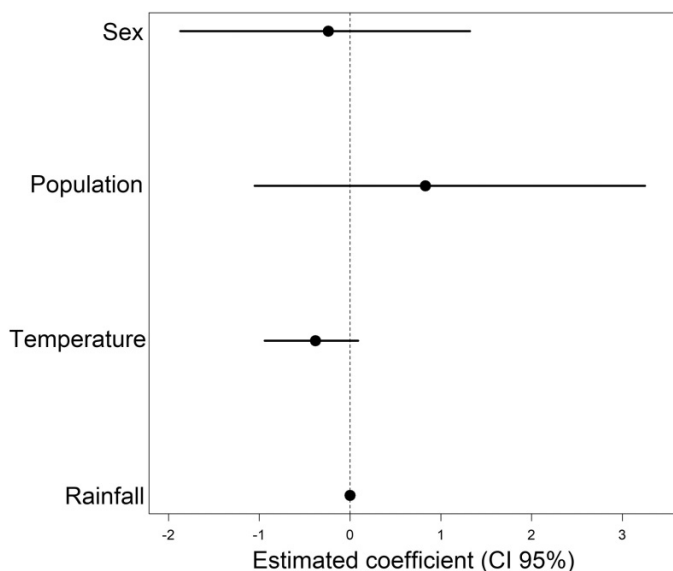
We are aware that the best way to analyse the differential chances of having or not having a contrasting colour in the tail is to examine newborns. However, because we did not have access to neonates, we arbitrarily nested our dataset on individuals with up to 350 mm SVL (juvenile dataset). Previous studies have described that *B. jararaca* newborns have approximately 250 mm SVL (range 190–275 mm SVL; Sazima 1992), and in this sense, we expected that in this size range, the chance of losing CTT at this stage would be negligible.

The data were analysed using two approaches: For the first hypothesis, we tested the effect of intrinsic (sex and population) and environmental predictors (MAT and MAP) on the probability of being born with CTT by means of exact logistic regression using the *elmr* function from the *elmr* package (Zamar et al. 2007). Exact logistic regression is especially well suited to testing this hypothesis because of the binomial nature of our response variable (absent = 0 and present = 1, CTT) and the small sample size resulting from our 350 mm SVL cut. The models were based on Markov chain Monte Carlo sampling and were performed with 50 000 iterations after a 5000 burn-in period. We ran a separate model for each variable. Testing the second hypothesis followed a similar method, but a regular logistic model was used. The impact of sex, population, and SVL on the probability of maintaining CTT was tested using the complete dataset. We were especially interested in the interaction between SVL and the population to observe whether there was a different probability of the presence of CTT in individuals with larger SVLs in each population. All analyses were performed using R software version 4.2 (R Core Team 2022).

Table 1. Exact logistic model table for the juvenile dataset to test the effect of four variables on the probability of *Bothrops jararaca* individuals born with contrasting tail tips.

Factor	Estimate	p-value	p-value SE	MCMC size
Sex	-0.243	0.744	0.002	45 000
Population	0.830	0.442	0.004	45 000
MAP	-0.382	0.192	0.008	45 000
MAT	0	0.903	0.004	45 000

Note: SE, standard error for the estimate; MCMC, Markov chain Monte Carlo; MAP, mean annual precipitation; MAT, mean annual temperature; SVL, snout-vent length.

Fig. 1. Estimated coefficients from exact logistic regression testing the effect of four variables on the probability that *Bothrops jararaca* individuals are born with a contrasting tail tip. Circles are mean estimates, and the segments indicate lower and upper confidence intervals (95% CI).

Results

Considering juveniles only, 80% (8 of 10) of the individuals in the coastal population presented CTT, while 68% (17 of 25) of the individuals in the highland population presented CTT. The exact logistic model showed that none of the predictors had a significant effect on the probability of presenting with CTT (Table 1), indicating that the chance of individuals being born with this trait was independent of the population or any intrinsic or environmental factor we tested (Fig. 1).

For the complete dataset, the largest male and female exhibiting CTT in the coastal population were 776 and 814 mm, respectively, while the largest male and female exhibiting CTT in the highland population were 711 and 467 mm SVL, respectively. As for the first hypothesis, sex had no impact on the probability of presenting CTT ($z = -0.4$, $df = 207$, $P = 0.65$). Therefore, this factor was removed and a second and simpler model was then built to test the second hypothesis. In this final model, we found a significant interaction between SVL and population (Table 2). Specifically, we found

Table 2. Regular logistic model table for the complete dataset to test the probability of males and females from two *Bothrops jararaca* populations with contrasting tail tips.

Factor	Estimate	Std. error	z-value	p-value
Intercept	10.66	2.96	3.59	0.0003
SVL	-1.82	0.48	-3.79	0.0001
Population	14.33	6.58	2.17	0.0295
SVL:population	-2.31	1.04	-2.226	0.0259

Note: Statistical significance is highlighted in bold. MAP, mean annual precipitation; MAT, mean annual temperature; SVL, snout-vent length.

that in individuals with SVL < 460 mm there was a slightly higher probability of finding a snake with CTT in the highland population; at approximately 460 mm SVL, the probability was virtually the same in both populations, and above this threshold, the probability was higher in the coastal population. This means that snakes in the coastal population retained CTT throughout adulthood in a higher proportion than those in the highland population (Fig. 2).

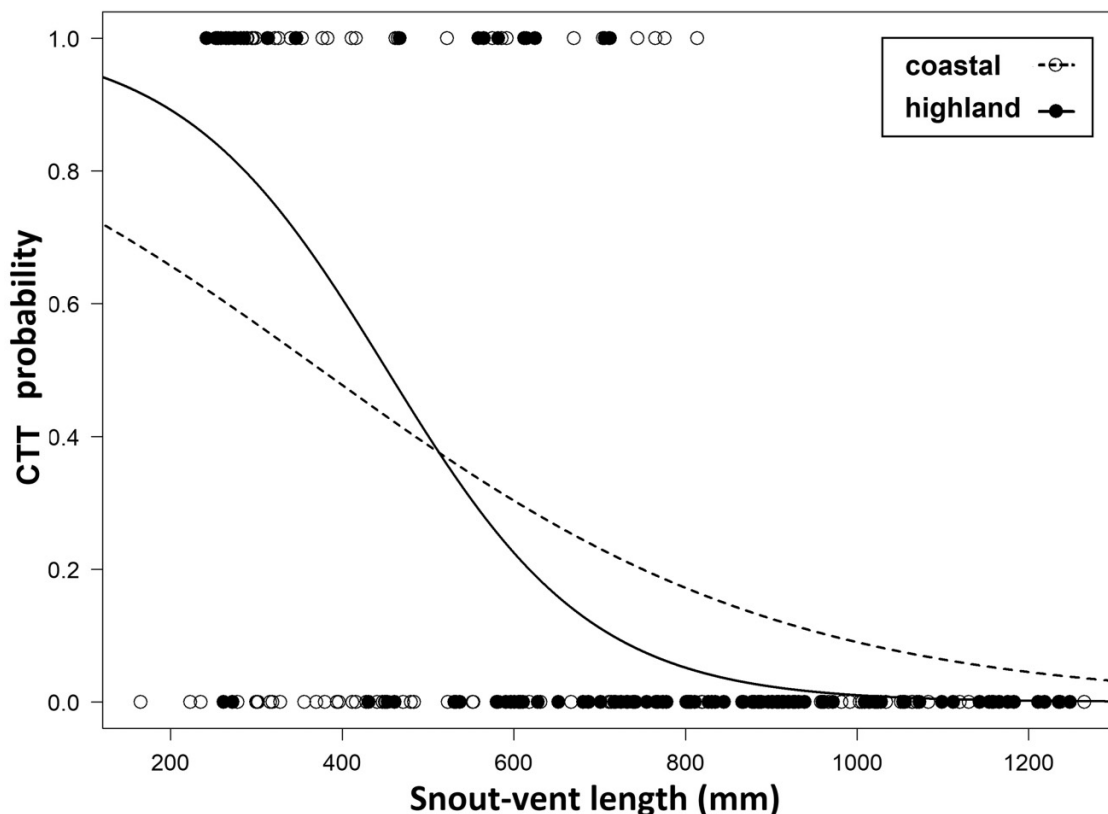
Discussion

In this study, we have shown that the chance of *B. jararaca* being born with CTT was independent of the population or other factors included in our analysis. However, a higher proportion of individuals from the coastal population retained this trait into adulthood than from the highland population. Morphology and climate impact several ecological traits of reptiles. A previous study showed that the seasonal activity of *B. jararaca* is synchronous with its potential prey and non-synchronous with its predators, with activity being higher in the rainy and warmer periods of the year (Siqueira et al. 2021). However, none of the variables we studied (MAT and MAP) affected our models, suggesting that CTT must be driven by other factors.

Martins et al. (2002) argued that the distinct tail tip colour in juveniles is a plesiomorphic character in the *Bothrops* genus and varies among group members. The absence of a distinct tail tip colour is synapomorphic for a clade of mammalian specialists; however, some juveniles in this clade do possess this trait (Martins et al. 2002). This scenario provides valuable data on the importance of evolutionary history in driving the presence/absence of CTTs in Neotropical pit vipers. Thus, we suggest that the lack of difference in the probability of presenting this trait in our interpopulation study may be a result of phylogenetic inertia.

Notably, when analysing the complete dataset, the logistic model suggested a higher proportion of juveniles with CTT in the highland population. However, one must be cautious in interpreting these results, as the exact logistic model from the first hypothesis clearly indicated no effect of population on CTT prevalence. Therefore, the small sample of juveniles from the highlands may have affected the model, and additional studies conducted with neonates from different litters are needed to better clarify this issue. Therefore, we focused our discussion on the second hypothesis, mainly for individuals > 460 mm.

Fig. 2. The effect of snout–vent length on the probability of *Bothrops jararaca* individuals from two populations retaining the contrasting tail tip (CTT) throughout adulthood. Males and females were pooled together.



We detected CTT in both sexes and age classes in our study population, except in adult females from the highlands. Although a distinct tail tip colour has been reported mainly in juveniles, this trait is frequently accompanied by caudal-luring behaviour and may persist into adulthood in several snakes, including species in the *Bothrops* genus (e.g., Greene and Campbell 1972; Heatwole and Davison 1976; Shine 1980; Parellada and Santos 2002; Stender-Oliveira et al. 2016). Thus, the use of caudal luring in adults of other species supports the idea that this behaviour may also be used by large individuals of the two studied populations of *B. jararaca*.

The loss of CTT colour is probably correlated with other ontogenetic variations in ecological traits. A study carried out in North America found that *Agkistrodon piscivorus* (Lacépède, 1789) presented a marked ontogenetic shift in several ecological characteristics, such as foraging strategy, habitat use, and diet composition, and this change was accompanied by a loss of the contrasting yellowish tail tips of the juveniles (Eskew et al. 2009). Accordingly, juveniles of *B. jararaca* are commonly found at stream edges, probably because of the abundance of frogs in these habitats, which are usually included in their diet (Hartman et al. 2003). However, adults feed mostly on small rodents, and to our knowledge, were never recorded performing tail-luring behaviour to attract this prey type (Sazima 1991, 1992).

There are several lines of evidence to indicate that species with a wide geographic distribution and broad diet often show variations in diet composition and ontogenetic shift

patterns between populations (King 1993; Daltry et al. 1998; Luiselli et al. 2001, 2005; Queiroz et al. 2001). From the 330 identified prey items of *B. jararaca*, Moraes (2008) found the most gradual inclusion of endothermic prey in the diet of the coastal population, and this trend is highly consistent with the pattern of a more gradual loss of CTT in this population. Nevertheless, the onset of an ontogenetic shift in diet and prey selection during growth may be asynchronous between populations (Natusch and Lyons 2012), and this asynchrony probably affects the timing of CTT loss in *B. jararaca*.

Some authors argue that the conspicuous colour of the tail may act not only to attract prey but also as an anti-predatory signal (Greene 1973; Booth 1990). In a previous study, we provided experimental evidence that distinct populations of *B. jararaca* are subject to different predation pressures and predator types (Siqueira and Marques 2018), but the effectiveness of conspicuous tail colour against predators remains untested.

We must consider that the colour of the lure itself may not be sufficient to determine success in prey capture. An experiment carried out with *Acanthophis praelongus* Ramsay, 1877, which exhibited a small yellowish patch on the ventral surface of the brown tail, showed that tails with painted lures (all brown or all yellow vs. natural ones) had the same efficiency in attracting lizards (Hagman et al. 2008). Another study that manipulated the tail colour of *Sistrurus miliaris* Linnaeus, 1766 in the field also indicated that conspicuous tail tips had no effect on foraging success (Farrel et al. 2011). Thus, although

the colour of the tail tip may play an important role in *B. jararaca* ecology, this trait alone may not be the only factor driving its feeding ecology.

In this study, we have resolved important questions about fixed adaptations relating to the presence of contrasting colours used for tail luring in *B. jararaca*, providing novel evidence that enhances population knowledge of the species and is directly associated with its feeding ecology and natural history. However, questions remain about how these adaptations are related to individual behaviour and this is an issue that requires further research.

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Data availability

Data generated or analysed during this study are available from the corresponding author upon reasonable request.

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Competing interests

The authors declare there are no competing interests.

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