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Reproductive Strategies of the Golden Lancehead, *Bothrops insularis*, from Queimada Grande Island

Constraints and Challenges

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Introduction

Queimada Grande is a small island (0.43 km²) located approximately 33 km off the coast of São Paulo state, southeastern Brazil (24°30' S, 43°42' W). It is a rocky, craggy island with no beaches and, therefore, difficult to access when the sea is rough (Amaral 1921; Martins *et al.* 2019). Most of the island is covered by vegetation typical of the Atlantic Forest. The climate is humid subtropical. Warmer temperatures occur from spring (October–December) to summer (January–March) and are associated with higher rainfall, whereas lower temperatures occur from autumn (April–June) to winter (July–September) and are associated with lower rainfall (Martins *et al.* 2019). The island has no source of fresh water besides rainfall (Amaral 1921).

Several seabirds and 41 perching birds are seen on the island, but most of them are seasonal migrants for short periods (Marques *et al.* 2012). Only two passerine birds seem to reside on the island: the House Wren, *Troglodytes aedon*, and the Bananaquit, *Coereba flaveola* (Marques *et al.* 2012). The island also harbors two species of bats (the molossids *Nyctinomops laticaudatus* and *N. macrotis*) but no terrestrial mammals. Other vertebrates inhabiting the island include two anuran amphibians (*Haddadus binotatus* and the endemic *Scinax peixotoi*), three small lizards (the gymnophthalmid *Colobodactylus taunay*, the scincid *Mabuya macrorhyncha*, and the introduced gekkonid *Hemidactylus mabouia*), two worm lizards (the amphisbaenids *Amphisbaena hogei* and *Leposternon microcephalum*), and two snakes (the dipsadid *Dipsas albifrons* and the viperid *Bothrops insularis*).

Bothrops insularis, commonly known as Golden Lancehead, is endemic to Queimada Grande. This species has been studied *in situ* and *ex situ* for more than 100 years, and some peculiarities of its biology were observed already in the first studies (Kasperoviczus and Almeida-Santos 2012). One intriguing peculiarity of this species

is that most, if not all, females exhibit hemipenes and associated retractor muscles (Hoge *et al.* 1959; Kasperoviczus 2009). The level of development of these structures varies among individual females (Kasperoviczus 2009; Garcia *et al.* 2022). Whereas some females have vestigial or malformed hemipenes and retractor muscles, others have hemipenes and retractor muscles similar to males (Figure 3.1A–E), suggesting that at least some females can evert and retract the hemipenes. Indeed, we recently observed a captive female everting the hemipenis and moving it from side to side (Figure 3.1F). It remains unclear whether the female hemipenes have been selected for some function or fixed in the population by genetic drift. Nevertheless, female

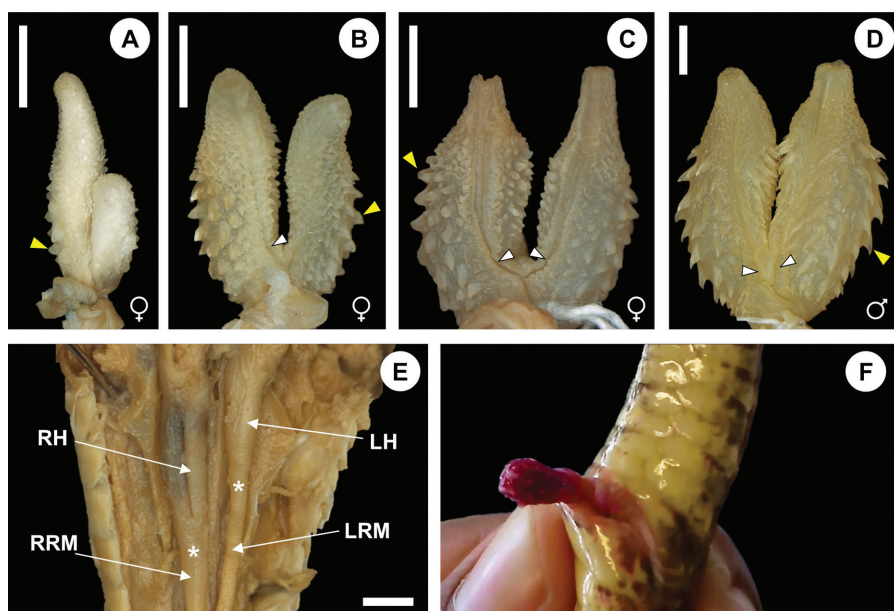


Figure 3.1 Hemipenes and retractor muscles of the Golden Lancehead, *Bothrops insularis*. (A) Female hemipenis with a malformation in one of the lobes. Note the absence of spermatic grooves and fully formed apices and the presence of spines with blunt and poorly formed tips. (B) Female hemipenis with slightly more developed spines and incomplete spermatic grooves but still showing malformation in one of the lobes. (C) A more developed female hemipenis, with complete spermatic grooves but also showing blunt spines. (D) Male hemipenis with complete spermatic sulcus, spines in greater number, and sharp spines. (E) Dissection of the tail of a female showing the hemipenes and retractor muscles. Asterisks indicate the point of origin of the retractor muscles. (F) Hemipenial eversion in a captive adult female. White arrowheads: Spermatic sulcus. Yellow arrowheads: Spines. RH: Right hemipenis. LH: Left hemipenis. RRM: Right retractor muscle. LRM: Left retractor muscle. Scale bar = 3 mm.

Photographs by Karina Kasperoviczus (A–E) and Kelly Kishi (F).

Golden Lanceheads have ZW sex chromosomes and are considered genetically female (Beçak 1965; Beçak *et al.* 1990).

Bothrops insularis exhibits many biological, ecological, and morphological divergences compared to its closest mainland relative, the Jararaca Lancehead, *B. jararaca*. Many of these divergences are consequences of insularity and are predicted by the island syndrome (Novosolov and Meiri 2013; Novosolov *et al.* 2013). For example, *B. insularis* occurs at a much higher population density than *B. jararaca*, showing one of the highest population densities recorded for snakes in the world (Marques *et al.* 2002; Martins *et al.* 2008; Guimarães *et al.* 2014; Abrahão *et al.* 2021). This high population density presumably reflects their coexistence with no interspecific competitors and few potential predators. Another difference from its mainland relative is the adult body size, which is, on average, much smaller (620 mm in males and 721 mm in females; Marques *et al.* 2013) than that of *B. jararaca* (760 mm in males and 1,115 mm in females; Almeida-Santos 2005).

Island environments also impose changes in the dietary niche and may even lead to the use of novel resources. Juvenile *B. jararaca* and *B. insularis* feed on small ectothermic prey (Martins *et al.* 2002). Adult *B. jararaca* feed primarily on small terrestrial mammals (Martins *et al.* 2002). Inasmuch as such prey type is lacking on the island, adult *B. insularis* have adapted to feed almost exclusively on passerine birds (Marques *et al.* 2002, 2012; Martins *et al.* 2002). Accordingly, *B. insularis* has evolved not only arboreal and diurnal habits but also morphological traits commonly found in arboreal snakes, such as long tails and more cranially positioned hearts than *B. jararaca* (Wüster *et al.* 2005). However, the island's resident passerine birds seemingly have evolved predation avoidance, and adult *B. insularis* feeds almost exclusively on two species of migratory passerine birds (*Elaenia chilensis* and *Turdus flavipes*) that visit and spend a few days on the island (Marques *et al.* 2012). In other words, adult *B. insularis* rely heavily on a highly seasonal resource to obtain energy to fuel reproduction. How male and female *B. insularis* manage such a seasonal and scarce energy source to reproduce is a great challenge that we describe here.

Temporal Dynamics of Food Availability and Feeding Activity

The White-crested Elaenia (*Elaenia chilensis*) and the Yellow-legged Thrush (*Turdus flavipes*) compose approximately 95% of the items consumed by the Golden Lancehead (based on a sample composed almost exclusively by adults; Marques *et al.* 2012). These migratory birds reach Queimada Grande Island in different seasons. The White-crested Elaenia visits the island in late summer, and the Yellow-legged Thrush visits the island during winter (Marques *et al.* 2012). However, adult *B. insularis* feed mainly in late summer on the White-crested Elaenia and to a lesser extent in winter on the Yellow-legged Thrush (Marques *et al.* 2012). Outside the migratory seasons of these birds, adult Golden Lanceheads may face a fasting period, as no migratory birds

appear on the island in substantial numbers and other prey types compose a minor portion of the adult diet (Marques *et al.* 2012).

To gain insights into sex differences in feeding activity, we revisited the dietary data from Marques *et al.* (2012), separating individuals by sex and considering only adults. Both male and female Golden Lanceheads prey on the White-crested Elaenia during late summer (Figure 3.2). Males seemingly stop feeding in autumn-winter, whereas some females prey on the Yellow-legged Thrush and other unidentified birds in late autumn and early winter (Figure 3.2). It is noteworthy, however, that even during the summer, when the feeding peak occurs, the frequency of males and females that consume some food seems relatively low, ranging from 20–29% of the individuals sampled (Figure 3.2). Moreover, only two of the 47 (*i.e.*, 4.3%) individual *B. insularis* that were found to contain food items by Marques *et al.* (2012) had eaten more than one bird. Both snakes were females; one had eaten two White-crested Elaenia in late summer (March), and the other had eaten two Yellow-legged Thrushes in early winter (July). These observations suggest that annual energy acquisition by adult individuals of *B. insularis* is quite low, such that a substantial number of individuals may acquire only 1–2 food items each year.

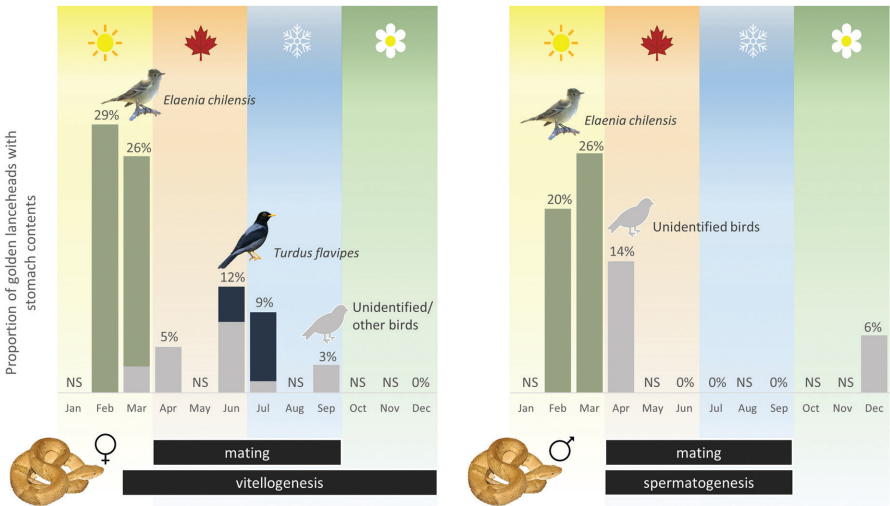


Figure 3.2 Seasonal timing of feeding and reproductive phenology of males (left) and females (right) of the Golden Lancehead, *Bothrops insularis*, from Queimada Grande Island. Green bars indicate the White-crested Elaenia (*Elaenia chilensis*), dark blue bars the Yellow-legged Thrush (*Turdus flavipes*), and gray bars other or unidentified birds. Values above the bars indicate the percentage of individuals found with stomach contents per month. NS: No sampling done in the month. Photographs of the birds by Arthur Macarrão (*Elaenia chilensis*) and Claudia Brasileiro (*Turdus flavipes*). Photograph of *Bothrops insularis* by Ricardo Sawaya.

The Reproductive Phenology of the Golden Lancehead is Largely Driven by the Seasonal Timing of Prey Availability

The reproductive phenology is relatively conserved phylogenetically across *Bothrops*. Male *Bothrops* studied thus far show one of two seasonal patterns of spermatogenesis: spring–summer or summer–autumn (reviewed in Silva *et al.* 2020). Mainland *B. jararaca*, in particular, shows a spring–summer spermatogenesis pattern (Almeida-Santos and Salomão 2002; Almeida-Santos 2005; Kasperoviczus 2013). Regardless of the timing of spermatogenesis, mating season occurs in autumn in most *Bothrops* species, synchronously with the onset of vitellogenesis. Therefore, female *Bothrops* must store sperm in their oviduct until ovarian follicles reach ovulatory sizes, which occurs primarily in spring. Parturition occurs between summer and early autumn in most *Bothrops* species (Almeida-Santos and Salomão 2002).

Bothrops insularis also reproduce seasonally, like the mainland *B. jararaca* and most congeners. However, the timing of many reproductive events of *B. insularis* differs widely from its congeners. In spring–summer, when male *Bothrops* have testes producing spermatozoa, male *B. insularis* have inactive testes (Kasperoviczus 2009). Spermatogenesis in *B. insularis* starts in autumn and proceeds until early spring and is therefore delayed compared to its congeners (Figure 3.2; Kasperoviczus 2009). In early autumn, viable sperm can already be found in the ductus deferentia (Kasperoviczus 2009; Silva *et al.* 2015). As with other congeners, mating occurs in autumn, when some females are at early vitellogenesis. Therefore, female *B. insularis* must also store sperm in their oviduct until ovarian follicles reach ovulatory sizes later in the year. However, the mating season of *B. insularis* extends to late winter (Figure 3.2) and is, therefore, much longer than the autumnal mating season observed in most congeners. Some female *B. insularis* have enlarged, preovulatory-sized follicles in early winter and ovulate in late winter (Marques *et al.* 2013), much earlier than female *B. jararaca*, which have enlarged, preovulatory-sized follicles in early spring and ovulate in mid-spring (Almeida-Santos 2005). However, between late winter and late spring, many female *B. insularis* still have small to mid-sized (10–15 mm diameter) vitellogenic follicles (Marques *et al.* 2013), while female *B. jararaca* have no small to mid-sized follicles since mid-autumn (Almeida-Santos 2005). Parturitions, however, have been recorded between mid-summer and early autumn (Marques *et al.* 2013), as in most *Bothrops* species (Almeida-Santos and Salomão 2002).

Why does *B. insularis* show this distinctive reproductive pattern compared with other congeners? We suggest that the reproductive strategies of male and female Golden Lanceheads are largely driven by the seasonal timing of bird availability. Energy intake and storage are required to initiate sperm production and vitellogenesis (Olsson *et al.* 1997; Shine 2003). Because male *B. insularis* feed essentially in late summer (when spermatogenesis begins or peaks in other congeners), spermatogenesis is pushed to begin in autumn (Figure 3.2), only after males have acquired energy

reserves. Histological analyses have detected sperm in the posterior oviduct of early vitellogenic females in April (Kasperoviczus 2009), thus confirming that mating occurs as soon as early autumn. Between late autumn and early winter, males are still actively searching for females to copulate. In an expedition in late autumn, for example, 40% of the males we observed were crawling, a proportion much higher than the maximum of 9% observed in other periods (Marques *et al.* 2013). In fact, our group has already observed seven interindividual interactions on the island between late autumn and early winter (Figure 3.3), most of them lasting 3–4 hours (Marques *et al.* 2013). In one of the records (sex unrecorded), the courting individuals had similar body sizes (Figure 3.3B), contrasting with other courtship observations in which the male was much smaller than the female (Figure 3.3C). Interestingly, none of the interactions recorded between late autumn and early winter resulted in mating (Marques *et al.* 2013).

All females that courted during late autumn and early winter observations had no vitellogenic follicles detectable by palpation (Marques *et al.* 2013), suggesting they



Figure 3.3 Courtship behavior in the Golden Lancehead, *Bothrops insularis*, on Queimada Grande Island. (A) A pair observed on a tree branch in mid-autumn (May 30, 2018). (B) A pair (sex unrecorded) found in early winter (July 1995). Note that, unlike in C, both individuals are similar-sized. (C) A male inspecting a female using tongue flicking while aligning his body to hers (late autumn, July 2007). No copulation was observed. Photographs by Ligia Graziely dos Santos Amorim (A), Paulo Lara (B), and Otavio Augusto Vuolo Marques (C).

were non-reproductive. Given the high cost required to sustain vitellogenesis and the relatively low proportion of female *B. insularis* that feed in summer (26–29% of the sampled females; Figure 3.2), it is plausible that only a few females are able to obtain enough energy reserves during the feeding activity in summer. We suspect that most females acquire insufficient (if any) energy stores in summer feeding activity to fuel vitellogenesis, and, consequently, they are not receptive to mate between autumn and early winter. Moreover, females had stomach contents in three of the six male–female interactions observed between late autumn and early winter, indicating recent feeding (Marques *et al.* 2013). Indeed, in this period, some females feed on Yellow-legged Thrushes visiting the island (Figure 3.2). Non-receptiveness after feeding has been reported in an arboreal congener, the Two-striped Forest Pitviper *B. bilineatus* (Turci *et al.* 2009). Thus, some female Golden Lanceheads may devote their time during late autumn and early winter to foraging rather than mating. Between mid- and late winter (August–September), mating has been recorded in free-ranging or recently captured *B. insularis* (Amaral 1921; Amorim *et al.* 2019). Therefore, by feeding on thrushes in late autumn–early winter, some females may acquire the required energy, or even gain “extra” energy, to fuel vitellogenesis and increase their chances of reproducing. This feeding activity in late autumn–early winter may also explain why many female *B. insularis* are still at early to mid-vitellogenesis between late winter and spring. Follicular growth beginning and proceeding between late winter and early spring is also suggestive that mating stimulates ovarian folliculogenesis (Whittier and Crews 1986).

To increase reproductive success, males may have evolved an extended mating season (compared with mainland relatives) to track this irregular and asynchronous vitellogenesis in females. As there may be few females accessible (*i.e.*, in estrus) during the mating season, it may be advantageous for males to employ some mechanism to ensure their paternity once they manage to copulate. On some occasions, males have been found on top of females during the mating season (Figure 3.4). Unfortunately, we cannot assure whether these individuals did mate, but on one occasion, the female had an enlarged cloaca (Figure 3.4A–B), suggesting recent mating. Nevertheless, the finding of males coiled on top of females is highly suggestive of mating guarding or vigilance behavior to prevent rival males from approaching and attempting to mate with the female (Luiselli 1993; Almeida-Santos *et al.* 1999). A similar interaction has been described in the Two-striped Forest Pitviper, *B. bilineatus*, in which a male coiled over a female after courtship on a tree trunk (Turci *et al.* 2009).

Reproductive Output

The reproductive output of *B. insularis* differs enormously from that of *B. jararaca*. Potential litter size (estimated by the number of enlarged vitellogenic follicles) is significantly smaller in *B. insularis* (mean = 8.2 ± 4.2 , range = 3–20) than in *B. jararaca* (mean 19.6 ± 6.3 , range = 11–36) (Marques *et al.* 2013). Moreover, female *B. insularis* exhibit a

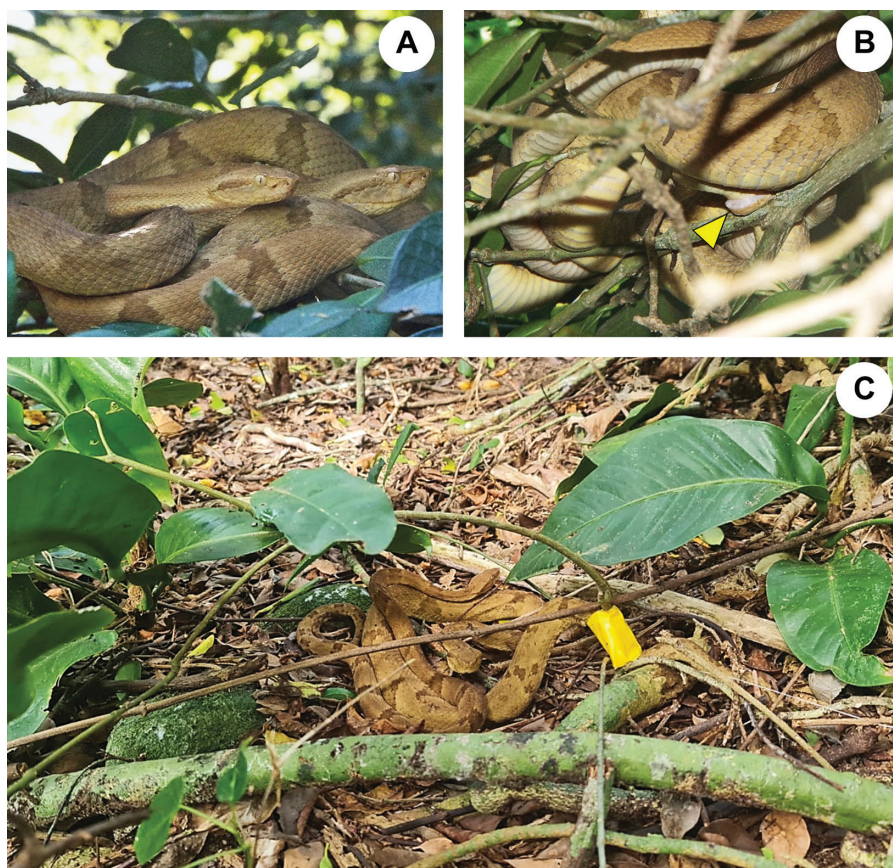


Figure 3.4 Potential mate guarding or post-mating vigilance behavior by male Golden Lanceheads, *Bothrops insularis*, during the mating season on Queimada Grande Island. (A) A male coiled on top of a female on a tree in late autumn (June). (B) A closer photo of the couple depicted in A showing the female's enlarged cloaca (arrowhead), suggesting recent mating. (C) A male on top of a female found on the ground in early winter (July). Photographs by Flora Roncolato Ortiz (A–B) and Karina Rodrigues da Silva Banci (C).

high (~45%) incidence of undeveloped oviductal eggs (Marques *et al.* 2013), presumably decreasing their reproductive output. However, the small litter size of *B. insularis* seems to reflect the smaller body size it reaches relative to *B. jararaca* because the interspecific difference in potential litter size disappears after the effect of maternal body size on litter size is taken into account (Marques *et al.* 2013). Data from free-ranging individuals brought to our laboratory show that female *B. insularis* produce smaller offspring than female *B. jararaca* (unpaired *t*-test: $t = 8.22$, $df = 221$, $p < 0.0001$); offspring size averages 229.0 ± 19.5 mm (range = 190–275 mm) in *B. insularis* and 254.3 ± 19.9 mm (range = 181–290 mm) in *B. jararaca*. However, unlike what was observed

for litter size, the offspring size in *B. insularis* is still smaller than in *B. jararaca* after accounting for the interspecific variation in maternal body size (ANCOVA with maternal SVL as the covariate: $F_{1,20} = 6.67$, $p = 0.018$). The frequency of reproductive female *B. insularis* observed per year averages 15%, varying from 0% to 50% (Marques *et al.* 2013). These values suggest that females show triennial or longer cycles. In contrast, approximately half of the females of mainland populations of *B. jararaca* reproduce annually, indicating a biennial reproductive frequency (Sazima 1992; Almeida-Santos 2005). Moreover, the proportion of newborns sampled in the population of *B. insularis* (0.6%) is much lower than that of mainland *B. jararaca* (17.8%), suggesting a lower rate of newborn recruitment (Marques *et al.* 2013). Therefore, female *B. insularis* produce smaller litters of smaller offspring at much longer intervals than their mainland closest relative, *B. jararaca*. Even with this low reproductive output, *B. insularis* shows a much higher population density than its sister species (*B. jararaca*), presumably reflecting the occurrence of few potential predators on the island.

The divergence in reproductive output between *B. insularis* and *B. jararaca* has been suggested to result from physiological constraints on gravid females or the effects of prolonged inbreeding in *B. insularis* (Wüster *et al.* 2005). Alternatively, the low reproductive output of *B. insularis* may directly or indirectly reflect its low annual rate of food intake (see also Marques *et al.* 2012). The limited energetic resources available on the island may have favored the evolution of smaller body sizes in *B. insularis* compared with *B. jararaca* (see Chapter 4, this volume), which in turn influences their smaller litter size. As female snakes usually do not feed during pregnancy, female Golden Lanceheads likely miss the feeding peak in summer and have little opportunity to feed during the years they are pregnant. Additionally, the low feeding rate of Golden Lanceheads may lengthen the time required to accumulate sufficient energy reserves for reproduction. Unfortunately, we do not know whether and to what extent the number of migrating birds varies annually, but a high resource fluctuation among years may be the source of the great year-to-year variation in the reproductive frequency of *B. insularis*. Female Golden Lanceheads kept in our laboratory as part of a breeding and conservation program have been fed mice monthly and observed to reproduce every other year (S. M. Almeida-Santos, unpublished data). Thus, the low reproductive frequency of *B. insularis* may result from the low annual food intake on the island.

Conclusion

Animals living on islands often show divergent traits compared to their mainland relatives. Despite its relatively recent origin, the island endemic Golden Lancehead, *B. insularis*, also differs in many traits from its mainland relatives, including its reproductive phenology and reproductive output. We argue here that the divergence in reproductive traits is largely due to the low and highly seasonal feeding activity of Golden Lanceheads on the island.

The discussion herein raises several questions for future studies. Answering these questions requires experimental tests in nature, captivity, or a combination of both. Future studies should manipulate food intake by Golden Lanceheads in captivity to test if the reproductive divergences described here reflect phenotypic plasticity or local adaptation. Preliminary observations indicate that, under a constant food intake regime, female Golden Lanceheads are able to reproduce biennially, like their mainland relative, *B. jararaca*. It is unclear, however, how litter size and offspring size will respond to a constant food intake regime. The same is true for male reproductive phenology. Would the timing of spermatogenesis change (resembling that of mainland relatives) in individual males kept on a constant food intake regime but mimicking the climate conditions on the island?

The potential tradeoff between feeding and mating in winter also warrants further investigation. Specifically, do males trade feeding opportunities for mating, while females trade mating opportunities for feeding? Or does this pattern merely reflect a limitation of male Golden Lanceheads to consume the Yellow-legged Thrush, which is larger than the White-crested Elaenia? An intriguing feature of *B. insularis* that has yet to be explained is why females produce so many nonviable eggs compared to their congeners and other snakes. Does the species' low annual feeding rate also influence the high frequency of nonviable eggs? Does the high frequency of nonviable eggs reflect the deleterious effects of prolonged inbreeding?

In addition, many questions on the reproductive behavior of the Golden Lancehead remain to be answered. For example, our suggestion of mating guarding or vigilance behavior by males requires confirmation. Do males and females mate once or more than once during the extended mating season? Moreover, does the female hemipenis show some role during reproductive interactions? These questions may also be assessed *in situ* and *ex situ*; however, given the high population density and extended mating season, *in situ* observations should be relatively straightforward to make and have the advantage of eliminating any captivity-induced behavioral anomaly. Ultimately, a comprehensive understanding of the reproductive biology of the Golden Lancehead is crucial to implementing informed and successful conservation strategies.

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