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Research article

To be (cryptic) or not to be? Variation in detectability by prey explains the diet of an ambush predator

Xavier Glaudas[1,2], **Eletra de Souza**[1,3], **Fabio Schunck**[2], **Karina Banci**[3], **Andrés Rojas**[1], **Erika Hingst-Zaher**[2] **and Marcio Martins**[1]

[1]Departamento de Ecologia / Instituto de Biociências, Universidade de São Paulo, São Paulo, SP, Brazil
[2]Museu Biológico, Instituto Butantan, São Paulo, SP, Brazil
[3]Laboratório de Ecologia e Evolução, Instituto Butantan, São Paulo, SP, Brazil

Correspondence: Xavier Glaudas (glaudasx@gmail.com)

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Differences in detection of cryptic predators by different animal groups are largely unstudied, limiting our understanding of how variation in detectability may affect the diet of ambush predators and their interactions with other animals. Using a combination of radiotelemetry and fixed videography, we monitored encounters between *Bothrops* snakes and other vertebrates in an Atlantic Forest community of Brazil. We also assessed snake detection by animal types and characterized snake feeding habits using multiple data sources. Our results showed that animal encounters occurred more frequently during daytime than nighttime, because birds, which are largely diurnal, encountered the snakes more often than the typically nocturnal mammals. We found dramatic differences in snake detectability between animal types: birds detected snakes in 89.2% of encounters compared to only 5.3% for mammals. All predatory strikes targeted mammals and snakes never struck at birds. Further, *Bothrops* fed almost exclusively on mammals (96.3% of diet), despite birds representing 61% of simulated prey encounters. The detectability bias we observed provides a mechanistic explanation for why birds are severely underrepresented in *Bothrops* diet relative to their encounter frequency. Our findings indicate that predator detectability can be a key factor shaping the realized diet of cryptic ambush predators.

Keywords: animal behaviour, *Bothrops*, camouflage, community ecology, detection, predator–prey interactions

Introduction

Camouflage is an adaptation that prevents animals from being detected or recognized (Darwin 1794, Merilaita and Stevens 2011), and the importance of predation as the main driver of camouflage evolution has been heavily documented (Endler 1978, Grant 2012). Camouflage evolves from selective pressures operating on prey to avoid predation and on predators to evade detection by prey, particularly in ambush hunters (Pembury Smith and Ruxton 2020).

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Ambush predators lie in wait for prey to pass by, and being undiscovered until prey is close enough to be caught is critical to their foraging strategy. Some use structures in the environment to conceal themselves, for example trapdoor spiders (Buchli 1969) or mantis shrimps (deVries et al. 2012), while others have evolved camouflage strategies including background-matching and disruptive colouration, masquerade (i.e. the mimicking of inanimate objects), and aggressive mimicry, where an organism resembles another one to dupe potential prey (reviewed by Pembury Smith and Ruxton 2020). These adaptations for ambush-hunting are astonishing textbook examples of evolution by natural selection.

Despite the widespread occurrence of camouflage in ambush predators, historically, most research examines the crypticity of prey rather than predator camouflage (Pembury Smith and Ruxton 2020, Yu et al. 2024). Notable exceptions to this pattern include study systems on crab spiders, which can adjust their colouration to colourmatch the flower they forage on (Heiling et al. 2005, Théry 2007, Yu et al. 2022), and on primate detection of cryptic predators (Coss et al. 2005, de Moraes et al. 2025). That said, the heavy focus on cryptic prey and the lack of knowledge about cryptic predators hinder the development of unbiased theories and applications in animal camouflage overall (Yu et al. 2024), calling for more research on cryptic predators.

A particularly understudied aspect of predator camouflage is how the effectiveness of crypsis varies among diverse types of potential prey or other community members. Although certain predators are dietary specialists, many are generalist opportunists, implying that the latter interact with a diversity of prey species with different perceptual abilities. Moreover, crypsis itself is a relative concept since an animal can be well hidden from one observer but conspicuous to another with different sensory capabilities (Endler 1992). This raises intriguing questions: does a predator's crypsis work equally well among various prey types? If not, how might these differences influence predator diet composition? For venomous predators, the first question can also be extended to other non-prey animals. Because they can actively inject venom into any approaching animal, venomous organisms should not be trivial to other animal community members, warranting a broader investigation of detectability across animals as a whole (i.e. prey or non-prey).

Here, we addressed these questions in free-ranging *Bothrops* vipers in an Atlantic Forest community of Brazil. Vipers are a typical group of ambush-foraging venomous snakes, which select hunting locations next to the trails of prey where they 'sit-and-wait' for them to come by (Roth et al. 1999). They are often visually cryptic, exhibiting a combination of background matching and disruptive colouration, which presumably conceals them from most other animals. Additionally, vipers represent an ideal system to study predator–prey interactions in nature. Because they rely on crypsis to forage and as their first line of defence, they can easily be approached with little disturbance, allowing researchers to set up continuously recording video-cameras at their foraging locations (i.e. fixed videography) to monitor interactions with other animal community members (Clark 2006, Glaudas and Alexander 2017a).

Using data collected via a combination of radiotelemetry, fixed videography, and a compilation of feeding records, we aimed to 1) present an encounter analysis between our radio-equipped *Bothrops* and other vertebrate animals; 2) establish whether taxa from different taxonomic classes (i.e. mammals, birds) vary in *Bothrops* detection; and 3) examine the link between the types of prey encountered and those eaten. Our research design allowed us to examine variation in snake detection by different animal types, and ultimately, to investigate potential discrepancies between prey encounter rates and the realized diet in a typical ambush predator.

Material and methods

Study system

We conducted our research at Etá Farm located in the municipalities of Sete Barras and Eldorado in the state of São Paulo, Brazil (~ 50 m a.s.l.; 24°19′13″S, 48°07′03″W). The farm is in the Vale do Ribeira, part of the Serra do Mar, in the Atlantic Forest biome, and most of the farm's area consists of largely untouched dense ombrophilous forest, with patches of agricultural fields, mostly peach palm plantations (cf. Fig. 1 in Fiorillo et al. 2020 for a detailed map). At this site, *Bothrops* snakes, which are highly venomous snakes commonly referred to as fer-de-lance or lanceheads, are the most commonly observed snakes. Two species of large-sized *Bothrops*, typically associated with the Atlantic rainforest realm (Sazima 1992, Martins et al. 2002), are found at the field site: *Bothrops jararaca* and *B. jararacussu*.

Snake capture, instrumentation, and tracking

We implanted small radio-transmitters, weighing a maximum of 5% of the snake body mass (but generally 2–3%; models SB-2 and SI-2; Holohil), into the body cavity of one opportunistically caught adult *B. jararaca* and five adult *B. jararacussu* following established procedures (Reinert 1992). Prior to surgery, we recorded standard morphometric data (snout–vent length [SVL], mass) and determined sex using a probe. All individuals were females. At the initiation of the study, the *B. jararaca* measured 1485.0 mm in SVL and weighed 738.0 g, and the five *B. jararacussu* measured 1009 ± 203.1 mm and weighed 835.6 ± 432.3 g (means ± SD). We released four of these snakes at their exact capture location within 5–6 days following surgery, but two *B. jararacussu* were translocated to our study site from neighbouring areas ~ 4 km away, to avoid potential human–wildlife conflicts in agricultural areas. Following an initial period of exploration at their new locations, these translocated snakes settled and established home ranges in their new environment. After release, we located the snakes using a radio receiver (model R1000; Communications Specialists) and a Yagi antenna (model RA-23K; Telonics) once or twice a day during our visits to the field site, where we typically spent two to three weeks per month from August 2022 to July

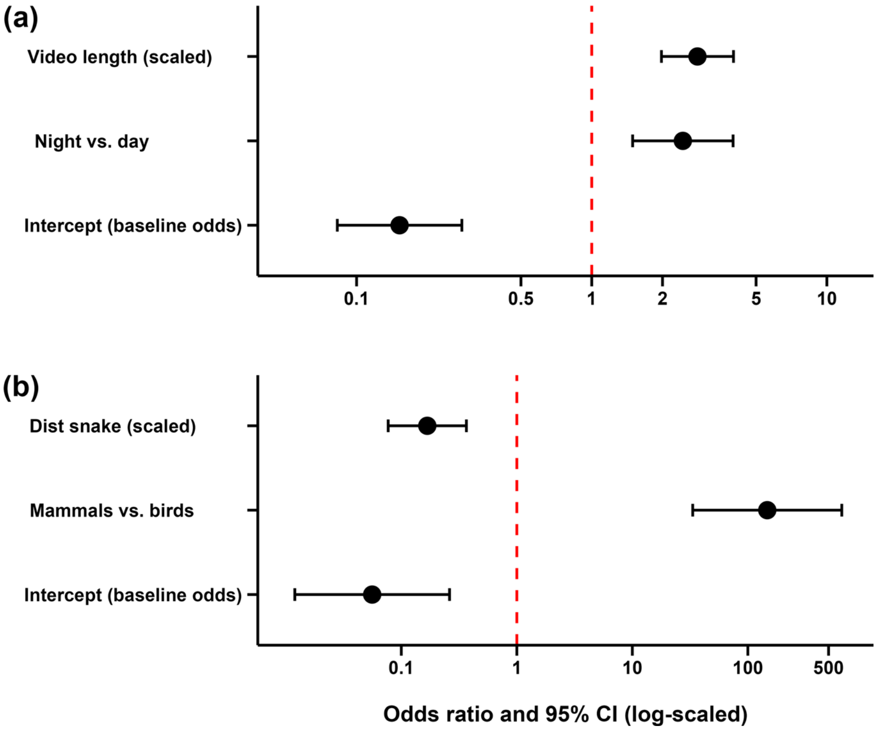

Figure 1. Odds ratios (points) and 95% confidence intervals (CI; horizontal lines) for the fixed effects from the best fitting generalized linear mixed models predicting the odds of (a) animal encounters and (b) snake detection. For (a) the intercept represents the baseline odds of encountering an animal during the reference category (night) at average video length, and for (b) the baseline odds of the snake being detected by the reference category (mammal) at average distance to the snakes. Values greater than 1 indicate increased odds, while values less than 1 indicate decreased odds relative to the reference level or per unit increase in the predictor. Confidence intervals crossing 1 indicate non-significant effects at the 95% level. For (b), Dist snake refers to the continuous predictor, distance to the snake.

2024. Overall, snakes were tracked 161.3 ± 70.1 times over a period of 255.3 ± 92.4 days.

Fixed videography

Bothrops spp. are sedentary ambush predators (Martins et al. 2002) that can easily be approached in nature with little disturbance. This characteristic allowed us to use fixed videography on the radio-equipped snakes, a powerful approach to observe how animals interact with other community members (Clark 2006, Glaudas and Alexander 2017a, 2017b, Glaudas et al. 2017a, 2017b). We located the radio-equipped snakes twice per day (generally between 7:00–9:00 and 18:00–20:00 h) and set up continuously recording video camera units ~ 1–3 m from the snakes. We generally recorded data on one snake at a time, and rarely two. Each video camera unit (XP9 Ultrafire, Reconyx) was powered by a 12-V sealed lead-acid battery and video data were recorded in high-definition (1080 p) on SD cards. The cameras recorded in colour during daylight hours and automatically switched to nighttime vision using built-in infrared LEDs at low light levels. During each snake relocation we replaced the 12-V batteries, collected and replaced the memory cards, and whenever necessary, repositioned the video cameras if snakes had moved on. We then reviewed the videos to record encounters and their outcomes between our snakes and other community members.

Video data extraction

We carefully reviewed video footage to monitor any vertebrate animals that entered the field of view at the snake's foraging locations. We excluded from our analysis small amphibians, which were difficult to identify reliably, and a few instances of fish foraging in leaf litter along water canals, where one of our snakes sometimes foraged. We recorded the identity of other vertebrates to the lowest possible taxonomic level and classified them into 'functional' groups:

1) Prey = any animal that *Bothrops* would potentially eat, based on body size and known dietary preferences from our feeding record compilation. This included small marsupials (i.e. *Monodelphis* sp.), rodents (with the exception of the large-sized *Cuniculus*), amphibians (with the exception of bufonid toads that are seemingly safe from predation due to their toxicity), birds of the orders Columbiformes and Passeriformes, and all non-*Bothrops* snakes (with the exception of one that was too large to be considered prey); 2) predator = any animal known to feed on snakes, which included members of Canidae and Felidae; 3) ambiguous = animals difficult to assign to either prey or predator categories. For mammals, this included an otter *Lontra longicaudis*, larger-sized marsupials (i.e. *Didelphis*, *Metachirus*), species of the order Cingulata (i.e. armadillos), and for birds, green ibises *Mesembrinibis cayennensis*; 4) 'neighbours' = animals not considered as likely predator or prey, including toads, tinamous,

pacas, and a *Hydromedusa* turtle (see the Supporting information for details).

We recorded proximity to the snakes as the closest distance between the two protagonists during an encounter. While reviewing videos, we took screenshots of the closest distances between our snakes and other animals. After snakes moved on, we used these screenshots in the field to estimate the closest distance using a measuring tape. In each case, we used the snake's snout as a point of reference and recorded the distance to the closest body part of the encountered animal, rounding our measurement to the nearest 5 cm increment (e.g. 30, 35 cm).

For our analysis, we defined an encounter based on two criteria. First, the animal had to approach within 200 cm of the snake while the snake was visible. In most cases, snakes were coiled and exposed on the forest floor and, more rarely, partially hidden in vegetation or positioned at or near the entrance of a burrow. Except for one individual, all snakes were large, with coiled diameters approximating 30–40 cm (comparable to the size of a large plate), and we are confident that, within 200 cm, they were generally noticeable. Second, we considered observations independent when they occurred at 60 min intervals, minimizing the risk of pseudo-replication from potential repeated visits by the same individuals.

We also created a subset focusing on potential feeding opportunities. To qualify for this prey encounter dataset, an observation had to meet additional criteria: 1) the animal had to be considered a potential prey item; and 2) it had to come within 40 cm of the snake, which was the longest offensive (i.e. feeding) strike we observed throughout the study. Our intent was to model close-range encounters that could realistically result in an offensive strike by the snake, effectively representing feeding opportunities.

For all encounters, we assessed whether the animals detected the radio-equipped *Bothrops*. Most animals entering the field of view were birds and mammals that generally had stereotypical responses to the snakes, including ignoring the snake (as if not detecting it), cautious behaviour, investigation, or fleeing. When initially reviewing the videos, the first author (XG) observed variation in snake detection, which led to the formulation of the research questions examined herein. To minimize potential bias in scoring snake detection, three of us independently scored it, including two authors (FS and KB) who were blind to this article's research questions. For each encounter, we answered the following question: is there evidence that the snake was detected? We were conservative in our scoring, and when in doubt, scored detection as 'unknown'. After independently reviewing all videos, we met to compare our observations and scored detection only for cases where we reached consensus.

We also recorded whether the snakes moved during encounters. We considered any noticeable movement by the snake as movement (excluding shallow breathing), either while the encountered animal was in the field of view or approaching, which could sometimes be detected acoustically. Therefore, for each encounter, we answered the question: is there any obvious movement by the snake? In case a snake struck (see definition below), the motion of the snake starting at the launching of the strike was not classified as movement.

Finally, we recorded the outcomes of encounters. We never recorded a predation event on snakes, despite a few occasions when potential predators approached closely. Therefore, our outcomes included only predation attempts by the snakes, which we defined as an effort to envenomate prey via a strike (i.e. any quick, sudden forward movement of the snake toward an animal with apparent intent to bite). We considered a predatory strike successful when snakes gripped prey in their mouth and in cases of strike-and-release bites, when snakes embedded their fangs into prey, which was always followed by snakes exiting the field of view to trail the bitten prey (Glaudas et al. 2017b).

Diet data

To supplement the few videotaped *Bothrops* feeding observations (n = 6), we compiled feeding records from multiple sources. Some radio-equipped snakes defecated in their containers during captive housing, and we collected and examined their feces for hair, feathers, and/or scales to determine recent consumption of a mammal, bird, and/or reptile. We also examined prey items regurgitated by snakes not used in our study but caught near our field site. Finally, we compiled unpublished feeding records collected by examining gastro-intestinal contents of preserved museum specimens and reviewed the literature for published feeding records (Marques and Sazima 2004, Fiorillo et al. 2020).

Because all videotaped snakes were adult females, we restricted our diet compilation to adult females. We minimized biases associated with potential geographic variation in diet by including only snakes from the watershed where we conducted our study, the Vale do Ribeira. When published records lacked information on sex, maturity status and or the geographic origin of the snakes, we contacted authors to obtain these details.

Statistical analyses

We used several datasets depending on the questions addressed, which were: 1) what factor(s) affected the odds of an animal encountering the snake? 2) Were some types of animals more likely to encounter the snakes, and if so, what factors affected these odds? 3) Did snake detectability vary by animal type? And 4) what types of prey are most encountered, and how is this reflected in snake diet?

We considered several biologically and methodologically relevant factors in our analyses depending on the questions. Biologically relevant factors included 'season' (dry versus wet; reference level = dry), 'time of day' (night versus day; reference level = night), and 'snake movement during the encounter' (no versus yes; reference level = no) as categorical variables and 'closest distance to the snake' as a continuous variable. For the season predictor, we classified data collected from 1 April to 30 September as the dry season, and data from 1 October to 31 March as the wet season, reflecting the precipitation regime in the Atlantic Forest of southeastern Brazil (de Oliveira et al. 2016). For time of day, we categorized our video footage as nighttime (18:00 to 06:00 h) and daytime (06:00 to 18:00 h), roughly corresponding to the diel cycle. Methodologically relevant factors included two continuous variables, 'length of video footage' and 'camera distance to the snake,' because both could affect the odds of monitoring an encounter, the latter because of increased field of view. The shortest video footage where we observed an encounter was 19 min. Therefore, we included all videos ≥ 19 min in our analysis. We did not systematically record the other continuous predictor 'camera distance to the snake', which reduced our dataset by 22%. We initially ran an analysis with this reduced dataset, which included this predictor, but decided to not consider it further, because the results of the analyses with or without this predictor were similar (see the Supporting information for detailed reporting). Finally, for models that included animal identity, we categorized encounters into their respective classes (i.e. amphibians, birds, mammals, reptiles). Due to small sample sizes for amphibians ($n = 9$) and reptiles ($n = 10$), we focused analyses on birds and mammals. In all cases, we used mammals as the reference level.

For most analyses, we used general linear mixed models (GLMMs) fit by maximum likelihood with a logit link to model the probability of an event occurring (i.e. a binomial response variable; Bolker et al. 2009). We reported statistical results as odds ratio (OR) and their 95% confidence intervals (CI), calculated from the log-odds model coefficients. ORs provide an effective measure of effect size by estimating how likely an event is to occur compared to a baseline reference level: an OR > 1 indicates increased odds, while an OR < 1 indicates decreased odds (Nakagawa and Cuthill 2007). Effects were considered statistically significant when the 95% CI of the OR did not include 1. Whenever meaningful, we converted OR to probabilities to further facilitate interpretation.

We entered snake identification (ID) as a random factor to account for multiple observations on the same individuals and estimated the intraclass coefficient (ICC), which indicates how much of the total variation is explained by individual differences (e.g. an ICC of 0.1 indicates that 10% is explained by snake ID). The analyses reported include data from snakes of both species. We tested whether the data collected on the single *B. jararaca* differed from those of the *B. jararacussu* individuals by statistically examining the random effect of snake ID. The single *B. jararaca* did not differ from the *B. jararacussu* individuals, except in one case where one *B. jararacussu* differed from three other snakes, including the *B. jararaca* (see the Supporting information for a graphical inspection of statistical differences). Based on this, we considered it reasonable to pool data from both species in our analyses, and all statistical tests but one proved to be similar when we used data from *B. jararacussu* only (see Supporting information).

To investigate which types of prey are more frequently encountered and how it compares to their realized diet (question 4), we ran a computer simulation to extrapolate prey encounter rates for 100 hypothetical snakes. The simulation used the log-odds of bird encounters from a normal distribution based on the model's fixed effect. To account for individual variation, we added random intercepts drawn from a normal distribution. The rationale for this simulation was to predict prey encounters for a broader population of snakes (i.e. generating one data point per simulated snake) to compare these predictions to the diet records we were able to retrieve for this study.

Whenever appropriate, we estimated the quality of different models using the Akaike information criterion adjusted for small sample size (AIC_c; Burnham and Anderson 2002). We selected the most plausible models from all candidates using those with a $\Delta AIC \leq 2$ and statistically tested the selected models against the null model to establish significance. We also generated marginal (r^2_m) and conditional (r^2_c) r^2 values as recommended for mixed effects models (Nakagawa and Schielzeth 2013): r^2_m indicates the portion of variance explained only by fixed effects, while r^2_c incorporates the total variance (fixed + random effects) explained by a model. We conducted all statistical analyses in R ver. 4.4.3 (www.r-project.org). We used the R packages 'lme4' (Bates et al. 2015) and 'jtools' (Long 2022) to conduct the GLMMs, 'DHARMa' to check assumptions of GLMMs (Hartig 2020), and 'MuMIn' for model comparisons and selection (Barton 2014). We tested statistical assumptions of models prior to testing and transformed variables if necessary. Values given are means ± SE unless otherwise mentioned and all reported p values are two-tailed. Significance for all tests was set at $\alpha = 0.05$.

Results

We gathered a total of 3012 hours (i.e. 125.5 days) of video footage on six snakes (one *B. jararaca* and five *B. jararacussu*). The number of videos (i.e. footage ≥ 19 min in length, $n = 433$; 72.2 ± 25.2 per snake, range = 20–188) and the total amount of footage (hours) varied substantially between snakes (480.8 ± 174 h, range = 153–1289), but mean video length did not differ between individuals (one-factor ANOVA; $F_{5,427} = 0.9$, $p = 0.48$; $p \geq 0.66$ for all pairwise contrasts between individuals).

Determinants of encounters

Two thousand eight hundred and eighty-five hours (out of 3012 hours) qualified for our encounter analysis (footage ≥ 19 min in length). We observed an encounter with at least one animal in 27.2% (118/433) of videos. We modelled determinants of encounters by fitting a GLMM considering three predictors: season and time of day and their interaction as categorical predictors, and (log- and z-transformed) length of video footage as a continuous variable. The best model ($r^2_m = 0.23$; $r^2_c = 0.28$) was significantly better than the null model ($\chi^2 = 51.3$, $df = 2$, $p < 0.0001$) and included two significant factors: time of day and video length (Fig. 1a). No other candidate models had a ΔAIC score ≤ 2 (Table 1a). The odds of an encounter significantly increased from nighttime

Table 1. Metrics of AIC$_c$-ranked general linear mixed models considered as candidates for the response variables examined in this study. For (a), vid refers to video length and TOD to time of day. For (b), class refers to animal class, dist snake to the animal distance to the snake and movt to snake movement. Terms in parentheses identify the interactions of terms included in the models. Significant variables at $p \leq 0.05$ are indicated by asterisks.

MODEL	AIC$_c$	ΔAIC	Weight
(a) Determinants of encounter			
vid* + TOD*	461	0	0.589
vid* + TOD* + season	463	2.04	0.213
vid* + TOD* + (TOD × season) + season	463.2	2.21	0.195
vid*	472.1	11.14	0.002
vid* + season	474.2	13.17	0.001
TOD	508.2	47.21	0.000
(b) Detectability			
class* + dist snake*	137.2	0	0.45
class* + dist snake* + movt	138.1	0.90	0.285
class* + dist snake* + (class × dist snake)	139.2	2	0.164
class* + dist snake* + (class × dist snake) + movt	140.1	2.91	0.104
class* + movt	169.1	31.88	0
class*	169.4	32.2	0

to daytime (OR = 2.44, 95% CI = 1.49–3.99, $p < 0.0001$) and with longer video length (OR = 2.82, 95% CI = 1.98–4.01, $p < 0.0001$). At mean video length (400 min), these odds translated into a 13.2% (95% CI = 7.9–21.3) probability of observing an animal encountering snakes at night, which increased to 27.1% (95% CI = 18.3–38.2) during the day. The intraclass correlation coefficient (ICC) was 0.06, indicating low variability in baseline encounter odds across individuals.

Encounters by animal type

The snakes were encountered by a total of 216 animals (see Supporting information), including 128 birds and 69 mammals, which were included in our analysis (Fig. 2). For birds, 111 individuals were considered potential prey, 13 neighbours, and four ambiguous; for mammals, 43 were classified as prey, three as predators, three as neighbours, and 20 as ambiguous. We fitted a binomial GLMM with a logit link to assess the probability of observing birds compared to mammals. We first tested the null model that included only the random effect of snake ID and the intercept to assess whether the overall frequency of encounters differed between birds and mammals. The model intercept was statistically significant (log-odds = 0.89, SE = 0.35, $z = -2.53$, $p = 0.011$), indicating that the odds of observing birds were significantly higher than for mammals (OR = 2.43, 95% CI = 1.22–4.82). This corresponded to a 71% probability of observing a bird (95% CI: 55–83%). The ICC (0.10) indicated a relatively minor effect of individual variation on encounter probability.

Second, we fitted the full model to our data by including the variables season, time of day, and their interaction. However, due to quasi-complete data separation (mammals observed almost exclusively at night, birds during the day), the model was unstable (e.g. singular fit warnings, reported standard errors and p-values very large). Visual inspection showed no obvious seasonal effects of season or

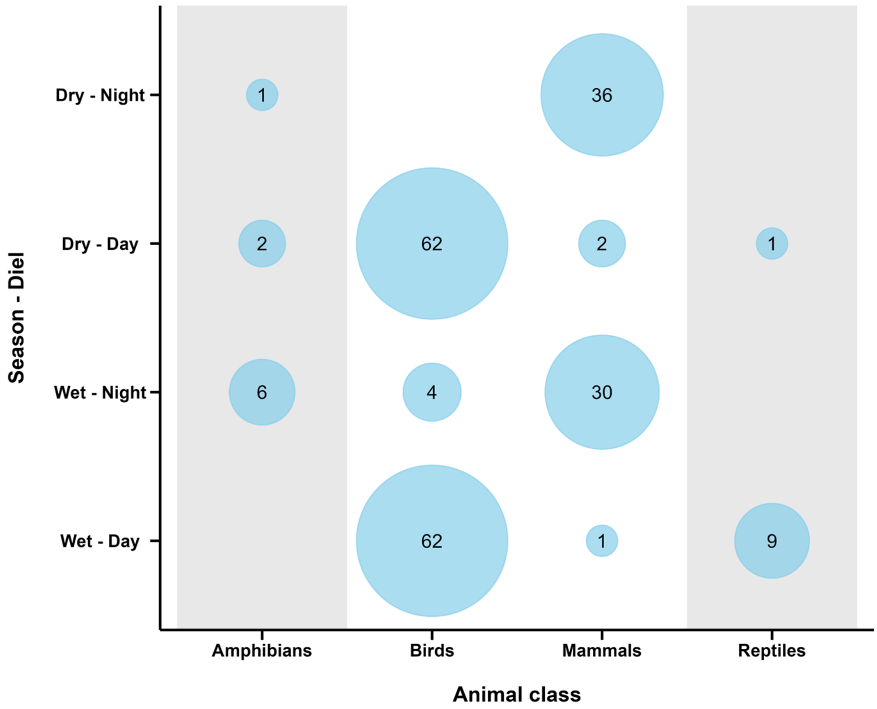

Figure 2. A summary of the animals that encountered the snakes by class, season and time of the day (diel). The areas shaded in grey on the graphs show the animal groups that were excluded from the analysis due to relatively small sample sizes.

an interaction with time of day (see Supporting information). Therefore, we fitted a simple model with only time of day as a predictor, which showed a dramatic increase in the odds of observing birds during daytime (OR = 1025.2, 95% CI = 153.9–6830.4), consistent with the diurnal nature of most birds versus the nocturnal activity of most mammals. This model explained a substantial portion of the variance in bird encounters ($r^2_m = 0.73$; $r^2_c = 0.78$) and was significantly better than the null model ($\chi^2 = 192.7$, df = 2, $p < 0.0001$). We observed moderate but meaningful variation in baseline probability across snakes, with an ICC indicating that 18% of variation was explained by individual variation (snake ID).

Detectability

We assessed snake detection for 170 of the 197 bird and mammal encounters (108 birds, 62 mammals). The best model included two significant predictors: animal class and (z-transformed) distance to the snake (Fig. 1b). Two other candidate models had a ΔAIC score ≤ 2, but none of the additional variables were significant (snake movement: $p = 0.29$; animal class × distance to the snake: $p = 0.73$) and therefore we considered the top model only (Table 1b). The model explained a substantial portion of the variance in detection outcomes ($r^2_m = 0.64$; $r^2_c = 0.74$) and was significantly better than the null model ($\chi^2 = 104.7$, df = 2, $p < 0.0001$).

The odds of detection dramatically increased when the animal was a bird compared to a mammal (OR = 147.2, 95% CI: 33.3–650.4, $p < 0.0001$) and significantly decreased with increasing distance from the snake (OR = 0.17, 95% CI: 0.08–0.37, $p < 0.0001$). At mean distance to the snake (58.4 cm), these odds corresponded to a 5.3% (95% CI = 1.2–20.8) probability of detecting the snake for mammals, which increased to 89.2% (95% CI = 70.2–96.6) for birds (Fig. 3). The large ICC value (0.29) indicated that snake ID strongly influenced detection. Similar results were obtained when restricting analyses to potential prey only (n = 130; $OR_{(\text{animal type})} = 249.2$, 95% CI: 40.1–1547, $p < 0.0001$; $OR_{(\text{dist to the snake})} = 0.27$, 95% CI: 0.12–0.62, $p = 0.002$; Supporting information).

Prey encounters, strike outcomes, and diet composition

We examined whether the frequency of close-range encounters with potential prey differed between animal classes. Among the 50 encounters that met our criteria, birds (n = 31) and mammals (n = 19) were equally likely to be observed (OR = 1.74, 95% CI = 0.67–4.51, $p = 0.25$; ICC=0.12).

Three snakes (one *B. jararaca* and two *B. jararacussu*) struck at prey 10 times and successfully hit prey 5 times (50% strike success rate). All strikes targeted mammals (10 strikes out of 19 encounters) and snakes never struck at birds (0/31). Additional strikes (excluded from the analyses) included a successful strike at an *Erythrolamprus miliaris* snake, and two strikes at the 'ambiguous' marsupials *Metachirus myosuros* and *Didelphis aurita.*

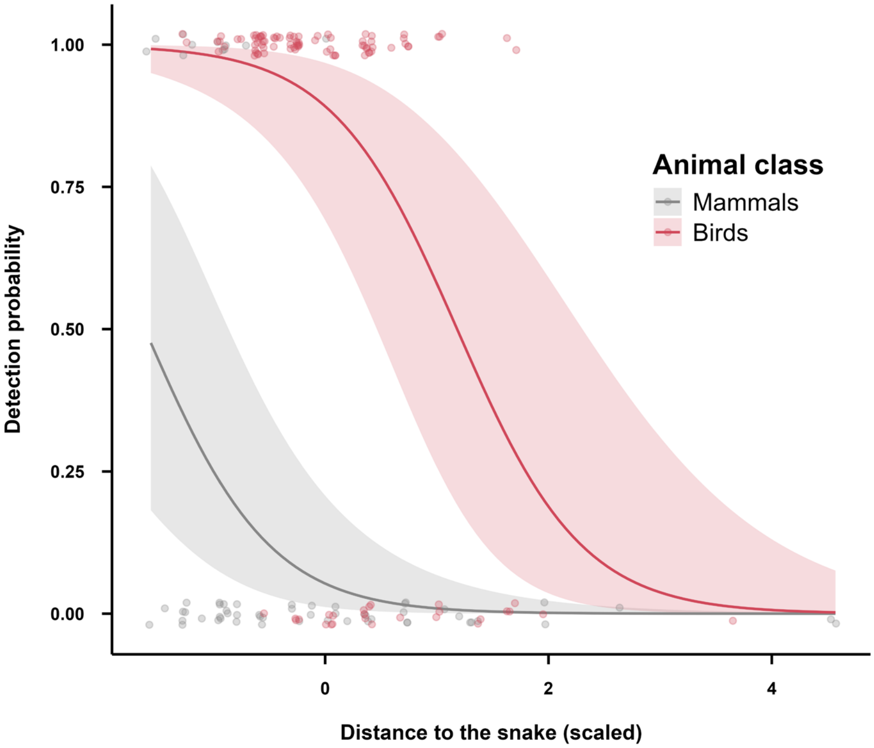

Figure 3. Observed data (jittered points) and predicted probabilities (solid lines) with 95% confidence intervals (shaded areas) from the top model of snake detectability. The graph illustrates the relationships between the (z-transformed) statistically significant continuous predictor distance to the snake and detectability by animal class.

We gathered a total of 38 prey items from adult females of *B. jararaca* (n = 14) and *B. jararacussu* (n = 24) from our study region (see Supporting information). These included 10 records during this study (i.e. videoed snakes, prey remnants in feces, and regurgitated items from captured snakes), 14 from literature records, and 14 from unpublished data (12 provided by one of us, MM, and two from O. Marques). We reduced this dataset by excluding amphibians and reptiles (n = 3). When multiple prey records existed for the same individual, we randomly selected one item. The final dataset included 28 prey items: 11 for *B. jararaca* and 17 for *B. jararacussu*. Fisher's exact test showed no statistical difference in diet composition between the two species (p = 0.39). Therefore, we combined the records, which showed that birds accounted for only 3.6% (1/28) of snake prey items.

We then compared observed diet records to simulated prey encounters for 100 hypothetical snakes. The computer simulation incorporated the fixed effect (mean = 0.55, SE = 0.48) and estimated among-snake variation (SD = 0.66) from our prey encounter model and predicted that 61% of prey encounters would involve birds and 39% mammals. Statistical comparison revealed that birds were significantly underrepresented in snake diet relative to their encounter frequency (Fisher's exact test; OR = 0.02, 95% CI: 0.0006–0.16, $p < 0.0001$; Fig. 4).

Discussion

We used fixed videography on free-ranging *Bothrops* snakes to monitor animals that encountered our radio-equipped snakes, mostly potential prey species. We demonstrated that animal encounters occur more frequently during daytime than nighttime, because birds, which are largely diurnal, are more commonly encountered than the typically nocturnal mammals. We also examined the detection abilities of different animal types and found a strong bias in snake detectability with birds greatly outperforming mammals. This bias in detectability provides a potential mechanistic explanation for the underrepresentation of bird prey, relative to their encounter frequency, in the diet of *Bothrops* snakes, which consequently may be restricted to feeding primarily on mammals.

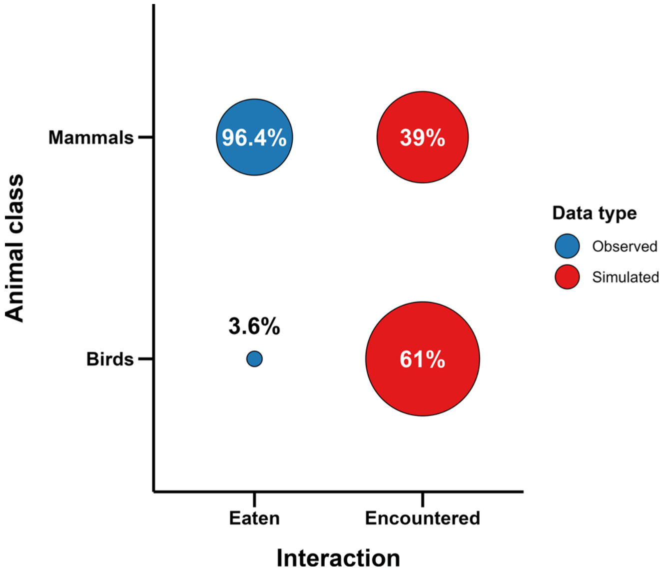

Figure 4. The discrepancy between simulated prey encountered for 100 hypothetical snakes and the observed prey animals eaten (birds versus mammals; n = 28) by *Bothrops* snakes expressed as percentages.

Considering all 'functional' groups (prey, predators, neighbours, ambiguous), birds encountered snakes more often than mammals, and our observations suggest this is partly due to detectability differences. The videos showed that birds often came to investigate snakes, circling around them, sometimes for extended periods. Snake detection could be enhanced by their 'bird's eye view', which could facilitate spotting snakes on the forest floor. However, this is not the sole reason. The most observed bird was the rufous-capped antthrush *Formicarius colma* (25.7% [33/128] of all birds), a strictly ground-foraging species that did not benefit from an aerial perspective. Furthermore, on occasion snakes were well-hidden in vegetation, negating the benefits of an elevated vantage point.

Birds are highly visual organisms with tetrachromatic colour vision (Bowmaker 2008, Martin 2022), and vision is likely the primary sensory modality that allows them to detect snakes. Because snake movement did not affect detectability, this suggests that *Bothrops* snakes have a visual signature that birds are able to perceive. Some birds can see into the higher end of the electromagnetic spectrum (up to the ultraviolet range; Martin 2022) – including Passeriformes that were the most observed birds (77/108 birds) – which may allow them to easily notice snakes. This idea is supported by a recent study which showed that many snakes, including all the *Bothrops* species that were investigated, reflect UV light, and that birds were markedly the best receivers of snake UV reflectance (Crowell et al. 2024).

Considering potential prey – individuals that came ≤ 40 cm of snakes – mammals and birds were encountered at statistically similar frequencies, with birds representing 62% of cases (31/50). These birds apparently maintained a relatively safe distance while examining snakes, because snakes never struck at them. Hence, birds are an example of the 'hard to catch prey' of optimal diet models (MacArthur and Pianka 1966). The snakes were probably aware that they had been discovered, eliminating the element of surprise critical to the ambush-foraging strategy, and may have decided not to spend valuable energy on a predatory attempt. All strikes we monitored targeted mammals, and therefore it is possible that snake offensive striking range for birds is shorter, as snakes are known to exhibit prey-specific foraging strategies (Glaudas and Alexander 2017a).

It could be argued that birds are not part of the diet of *Bothrops*. Yet our feeding data indicate that they occasionally eat them, because we recorded birds in the diet of *B. jararaca* and of male *B. jararacussu* (Sazima 1991, 1992; see Supporting information). Another possibility explaining the rarity of birds in their diet is that snakes do not feed during the day, when birds encounter them. Our data show this is unlikely, because 50% (3/6) of the successful predation attempts we monitored on videos occurred during the day (one *Erythrolamprus miliaris* snake by *B. jararaca* and two *Monodelphis* marsupials by *B. jararacussu*). Snakes clearly exhibited a shift to foraging behavior at sunset, yet they are opportunistic predators that will feed during the day (Marques and Araújo 2011). Collectively, our results demonstrate that – given the comparatively similar encounter frequencies of bird and mammal prey with snakes – birds are strongly underrepresented in the diet of *Bothrops* (see Martins et al. 2002 for feeding habits of several other *Bothrops* species), due to their excellency at detecting them (see videos in the Supporting information). The rarity of birds seems to be a general trend in snake diets, which has been attributed to the difficulty in capturing them (Shine et al. 1996), and our findings provide a possible explanation for it.

Mammals were encountered almost exclusively at night, with exceptions being three *Monodelphis* marsupials, including the two successfully predated individuals noted above. Overall, mammals were poor at detecting snakes, with an average detection probability of 5.3% (compared to 89.2% for birds; see videos in the Supporting information). Our mammal dataset included prey, representing the bulk of our mammal observations (58% [36/62]), but also included potential predators, such as *Leopardus* cats and a crab-eating fox *Cerdocyon thous*, and ambiguous cases, like opossums (*Didelphis aurita*; see the Supporting information). Although our observations of predators were limited ($n = 3$), in all cases these predators stepped very close to the snakes (20–40 cm) and failed to detect them, despite snakes adjusting their body positions to face the approaching animals. This failure of all senses, including olfaction – which is important to nocturnal predatory mammals (Hughes et al. 2010) – suggests that these vipers may employ not only visual but also chemical crypsis as part of their anti-detection system (Ruxton 2009; see Miller et al. 2015 for a case of chemical crypsis in an African ambush-foraging viper).

These observations also apply to 'ambiguous' mammal cases, particularly *Didelphis aurita*, which often encountered snakes (12 cases) but only detected them on a few occasions (four cases). Snake detection involved cases at very close range (20–35 cm), with two observations including snakes approaching the opossums to investigate them. Notably, the relationship between *Didelphis* and *B. jararacussu*, one of the larger-sized members of the genus, is not clear. Although the context is unknown (i.e. predation or scavenging events), there are records of *B. jararacussu* eating *Didelphis* (Fiorillo et al. 2020; our own data). Further, *Didelphis* species are known to predate snakes, including venomous ones, because they are resistant to their venoms (Voss and Jansa 2012, Drabeck et al. 2020, 2022). Yet the typical reaction (3/4) of *Didelphis* to large-sized *B. jararacussu* individuals was defensive and triggered escape. In the other case, a *Didelphis* came extremely close to a *B. jararacussu*, prompting the only snake defensive strike monitored in the study. We are unsure whether the marsupial attempted predation or if it simply did not notice the snake until it was directly adjacent to it. In any case, the snake was caught off guard and defensively struck repeatedly without hitting.

Notwithstanding their poor ability to detect snakes (a consistent pattern even when considering prey encounters only), mammal prey, specifically rodents, are not a guaranteed meal for these *Bothrops*. Snakes successfully struck 50% (5/10) of the time. Our sample size of striking snakes was small ($n = 3$), but rodents seem reasonably skilled at dodging an incoming strike. Anecdotally, after detecting a snake, a *Nectomys* rat demonstrated the confidence to repeatedly approach the snake closely (15–25 cm), dodging three consecutive strikes. Extrapolating our results to rodent–viper systems overall and assuming that rodents may be generally poor at detecting ambushing vipers, we speculate that strong positive selection operates on their evasive reflexes, particularly given their poor snake detection skills (see Freymiller et al. 2019, Whitford et al. 2019 for the remarkable reflexes evolved by North American rodents to evade rattlesnake strikes). The same reasoning could also explain the physiological resistance to viper venoms exhibited by various rodent taxa (Holding et al. 2016, Robinson et al. 2021, Balchan et al. 2024).

From the perspective of an opportunistic ambush-hunting predator like *Bothrops*, we might expect that crypsis would be optimized (balanced) to thwart detection by various types of animals. This is particularly relevant for mammals and birds, because both groups include major snake predators and prey: birds of prey and carnivorous mammals are among their main predators (Greene 1997), and rodents and smaller birds are clearly potential prey items, with rodents forming the basis of the diet of many species (Martins et al. 2002). Yet our findings suggest that the evolution of crypsis in *Bothrops* may be primarily driven by the perceptual limitations of mammals rather than birds. This putative role of mammals as a driver of snake phenotypic evolution has also been suggested in coral snake mimicry systems of the Atlantic Forest (Banci et al. 2020). That said, because we cannot separate the effect of animal class from time of day (birds and mammals were largely encountered during daytime and nighttime, respectively), diel cycle may also play a role as a driver of crypsis evolution if the different environmental conditions experienced by snakes between day and night affect the efficacy of crypsis: crypsis may be constrained during the day, for example due to the snake scale physical properties (e.g. UV reflectance), and the selective pressure shaping crypsis evolution may be nighttime concealment.

Our research also raises an intriguing question: how does the critically endangered *B. insularis* sustain itself mostly on a bird diet? This snake, which is the sister species of *B. jararaca* (Carrasco et al. 2023), inhabits the mammal-free island of Queimada Grande off the São Paulo coast, Brazil. It mostly feeds on two migrating birds that stop on the island for a few weeks twice a year, which are generally ambushed from trees (*Elaenia chilensis* and *Turdus flavipes;* Marques et al. 2012).

We wonder about its ability to rely mostly on birds as prey: are they easily detected by birds? If not, what adaptations did *B. insularis* evolve to remain undetected? Are there differences in snake detectability across bird species given the diversity of avian visual systems (Martins 2022)? Could bird fatigue resulting from migration or their strong drive to feed on fruits during brief stopovers (Schunck unpubl.) explain costly errors on their part? Interestingly, both most common island resident bird species have never been recorded in their diet (Marques et al. 2012), and we observed one of these birds (*Troglodytes aedon*) staring at a *B. insularis* and avoiding getting close to it (Martins et al. 2019). While our study will not answer these questions, it highlights a fascinating avenue for studying predator–prey interactions in this unique island ecosystem.

We also ponder about the broader applicability of our results to other viper species. This group of snakes has a set of unifying characteristics, such as ambush-foraging strategy, cryptic phenotype, and generally rare representation of birds in their diets (Glaudas et al. 2019a, 2019b; but see Nilson et al. 1999, Shine et al. 2002 for notable exceptions, all of them island species). We speculate that the strong bias in snake detectability we demonstrated herein possibly extends to many other vipers. We hope that our findings will stimulate similar research to investigate our hypothesis and ultimately answer important questions regarding the ecology and evolution of predator–prey interactions and feeding habits in ambush-foraging snakes.

In conclusion, our study provides novel mechanistic insights into how differential detectability by prey types can shape the realized diet of cryptic ambush predators. The striking contrast in detection abilities between birds (89.2%) and mammals (5.3%) offers a compelling explanation for the predominance of mammals in *Bothrops* diet despite frequent bird encounters. These findings highlight the importance of considering predator detectability – not just prey availability – when interpreting diet patterns in cryptic predators and underscore the likely complex sensory ecology underlying predator–prey interactions in natural communities.

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Author contributions

Xavier Glaudas: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Visualization (lead); Writing – original draft (lead). **Eletra de Souza**: Formal analysis (supporting); Investigation (supporting); Visualization (supporting); Writing – review and editing (equal). **Fabio Schunck**: Formal analysis (supporting); Investigation (supporting); Writing – review and editing (equal). **Karina Banci**: Formal analysis (supporting); Investigation (supporting); Writing – review and editing (equal). **Andrés Rojas**: Formal analysis (supporting); Visualization (supporting); Writing – review and editing (equal). **Erika Hingst–Zaher**: Formal analysis (supporting); Investigation (supporting); Resources (supporting); Writing – review and editing (equal). **Marcio Martins**: Funding acquisition (lead); Investigation (supporting); Project administration (lead); Resources (lead); Supervision (lead); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.83bk3jb50 (Glaudas et al. 2025).

Supporting information

The Supporting information associated with this article is available with the online version.

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