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Are plasticine models efficient to test defensive colouration of snakes?

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Plasticine models are often used to test hypotheses related to defensive colourations. However, the behaviour of natural predators is hardly ever examined in these experiments, which can lead to imperfect conclusions about the interactions. Accordingly, we ran an experiment to test whether plasticine models are an efficient tool to test Batesian mimicry, aposematism and camouflage hypotheses, using Atlantic forest snakes as a model group. We made 150 non-toxic simulacra of four snake species and two generic plasticine models. We placed cameras traps at the study sites to record the behaviour of potential predators towards the models. We classified the predator-simulacrum relations as physically interactive, interactive with no contact, or not visualised, and we examined whether mammals behaved differently from birds towards the plasticine models. We recorded 110 instances of birds or mammals approaching the plasticine models, most of them with models. Most birds presented an interaction with no contact during the day, and mammals presented physical interaction during the night. None of the model types influenced the interaction with predators, but we observed that mammals interacted significantly more with models than birds. While mammals clearly did not behave protectively when interacting with the models, some birds did behave with caution when approaching them. Our results showed that the use of plasticine models may not always result in reliable data to test predator-prey hypotheses.

Keywords: Mimicry, predation, Atlantic forest, aposematic colouration, Serpentes

INTRODUCTION

Predator-prey relationships provide a classic paradigm in animal ecology studies, frequently involving the diversification of behavioural strategies, such as defensive colourations (Barnett et al., 2018; Postema et al., 2023; Toledo & Haddad, 2009). These aposematic colouration patterns, which can be a result of sexual selection (Santos et al., 2014) acts as a warning to would-be predators by signaling the presence of toxins, unpalatable substances, or the possibility of physical counter-attack (Stevens, 2007; Toledo et al., 2011). On the other hand, some harmless or profitable organisms are specialised in production of information sought by a predator as a warning signal (Bates, 1862; Vane-Wright, 1980). These patterns were already observed in diverse taxa, such as plants (Launchbaugh & Provenza, 1993), invertebrates (Mallet & Gilbert Jr, 1995), and vertebrates (Prates et al., 2012; Toledo & Haddad, 2009). Some non-venomous snakes, such as *Erythrolamprus aesculapii*, are hypothetical colour mimics of coral snakes, such as those from the genus *Micrurus*, which potentially confuses the predator (Banci et al., 2020). From this perspective, several methods were adopted to test the function of colours, and the use of plasticine models is one of the most common approaches (e.g. Banci et al., 2020; Brodie III, 1993; França et al., 2017; Kakazu et al., 2010; Rebouças et al., 2019).

Brodie III (1993) was likely the first to employ plasticine models of snakes to evaluate predator-prey relationships. Several studies have since deployed similar experiments to explore how variations in colour aposematism (Banci et al., 2020; Husak et al., 2006; Rebouças et al., 2019; Saporito et al., 2007), body shape (Guimarães & Sawaya, 2011; Shepard, 2007) and crypsis (Kakazu et al., 2010; Vignieri et al., 2010) affect predation rates. This approach is attractive as it is low cost, and allows for identification and quantification of predation marks left on the models,

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such as bites, beak indentations and claw imprints (see Brodie III, 1993; Kakazu et al., 2010; Rebouças et al., 2019). However, this technique fails in some cases as the models are motionless and therefore problematic for studies involving predators that respond to kinetic cues (Paluh et al., 2014). The cognitive ability and behaviour of prey and predator are also frequently disregarded in this type of experiment (Beckers et al., 1996).

Since the accuracy of experiments depends on how simulated conditions reflect the natural history of the organisms involved, an observational approach is recommended for experiment construction and hypothesis testing (Guidetti et al., 2014). In experiments using plasticine simulacra, it is common to use methodically disposed models of potential prey in the field, and the marks left on these models are used as evidence of interaction to answer ecological questions (Banci et al., 2020; Bordignon et al., 2018; Paluh et al., 2014), and, consequently, can only be accounted when marks on models are visible. However, the interactions are generally not recorded at the moment of the potential predation (Beckers et al., 1996; Harmel et al., 2020), although the behaviour of predators when finding the models could provide relevant information. Consequently, we conducted a traditional experiment with plasticine prey models to answer evolutionary hypotheses about colouration patterns in snakes (e.g. Akcali et al., 2019; Banci et al., 2020), with the difference that we set camera traps to record behaviours of predators when detecting, approaching and interacting with the models. Thus, we could also test the reliability of the use of plasticine models in simulacra-predation studies.

MATERIALS & METHODS

The study was conducted between August and September 2020 in the Projeto Dacnis private reserve in the sub-district of São Francisco Xavier, municipality of São José dos Campos, São Paulo, Brazil (-22.89, -45.94; WGS-84; 700–800 m a.s.l.). The area within Atlantic forest domain presents marked seasonality, with a dry winter (between June and August) and humid summer (between December and February). The transect where the experiment was carried out is surrounded by secondary forest, with creeks and native palm trees *Euterpes edulis*, which is a common habitat for diverse snake species.

The snake species to be modelled were selected as they occur in the study site, and would be familiar to local potential predators. We used non-toxic plasticine models of the four snake species: 1) *Bothrops jararaca*, venomous and hypothetically cryptic; 2) *Xenodon neuwiedii*, non-venomous and hypothetically mimic of *B. jararaca*; 3) *Micrurus corallinus*, venomous and hypothetically aposematic; and 4) *Erythrolamprus aesculapii*, slightly venomous and hypothetically mimic of *M. corallinus*. Additionally, we tested two generic plasticine models: a brown, cryptic with the background, and a green, conspicuous with the background (Fig. 1). In total, we used 150 plasticine models with 60 cm total length, 25 for each species. We selected three sampling sites along a 3 km transect, spaced from each other by 500 m, to install the camera traps (Bushnell Trophy Cam HD-E-3), based in environmental setting and whether the camera suited to record. Once triggered by a movement, the cameras were set to record predator-model interaction for 30 seconds. Simulacra were divided in three groups to be tested separately in each point: group 1, with *B. jararaca* and *E. aesculapii* models; group 2, with *X. neuwiedii* and *M. corallinus* models; and group three, with the generic green and the generic brown. A plasticine model of each group was placed in each site about 50 cm in front of the camera trap among the leaves on the ground, with three simulacra per point. In each site, we inserted a random simulacrum of each group (e.g. point 1: *B. jararaca*, *X. neuwiedii* and generic green; point 2: *E. aesculapii*, *X. neuwiedii* and generic brown; point 3: *B. jararaca*, *E. aesculapii* and generic brown), and the model was replaced by another of the same group during the daily checking, which lasted ~5 minutes. In total, each plasticine model was randomly placed 30 times. Those models physically modified were replaced to avoid that their appearance influenced the results. Camera-recorded predator behaviour was placed in one of three categories: (1) physical interactions, when a potential predator interacted physically with the model; (2) interactions with no contact, when predators detected, visualised and ignored the model; and (3) approaches with no visualisation, when the model apparently was not seen by predator. Furthermore, we corresponded video data with marks in models and all interactions were classified in diurnal and nocturnal activity. All videos were deposited at Fonoteca Neotropical Jacques Vielliard, Museu de Diversidade Biológica (ZUEC-VID 953-967), Universidade Estadual de Campinas, Campinas, SP, Brazil (Dena et al., 2018; 2020).

To evaluate whether mammals and birds preferred any model, we employed Ivlev's electivity index (Lechowicz, 1982), through the R package 'electivity' (Quintans, 2019), which uses the availability and the interaction with each prey to evaluate avoidance (when the index range is between -1 and 0) and preference (when the index ranges from 0 to +1). We considered as "availability" the sum of non-interactive and interactions, since we were unable to evaluate if all the models in each treatment were perceived by predators, and "use" when potential predators actively interacted with the models. To avoid the influence of intrinsic characteristics of predator species in interaction frequency with the models, we separated predators into two general categories: birds and mammals. Furthermore, to evaluate if there were differences in interaction with any model, we performed a Generalised Linear Model analysis (GLM), with a binomial distribution and a logit link, considering the interaction as a response variable (non-interactive = 0, interactive = 1), and the model type (*B. jararaca*, *X. neuwiedii*, *M. corallinus*, *E. aesculapii* and those hypothetically cryptic and conspicuous, the brown and green models, respectively). We used the class of predator (bird or mammal) as response variables. To

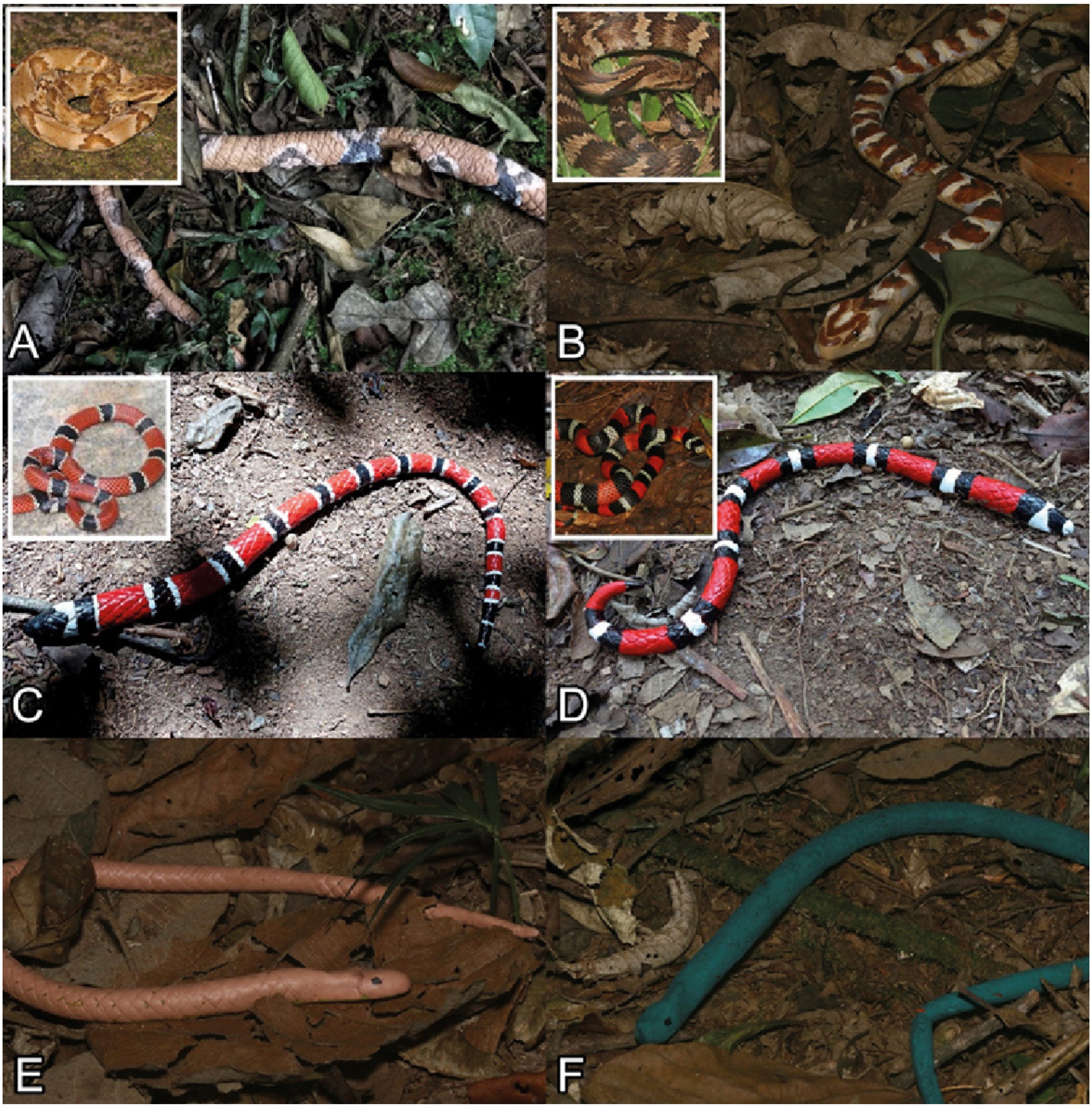

Figure 1. Plasticine models of snake species- **(A)** the venomous pitviper *Bothrops jararaca*, **(B)** Neuwied's false pitviper *Xenodon neuwiedii*, hypothetical mimic of *B. jararaca* **(C)** the venomous painted coral snake *Micrurus corallinus*, **(D)** South American false coral snake *Erythrolamprus aesculapii*, hypothetical mimic of *M. corallinus*; generic models, **(E)** brown cryptic and **(F)** green conspicuous.

determine the size effect of each variable, we used the analysis of variance type II through the function "Anova" of the R package 'car' (Fox et al., 2012). All analyses were performed in R 4.0.4 (R Core Team, 2023) with a confidence interval of 95%.

RESULTS

We recorded 110 events in which birds or mammals approached the plasticine models (Fig. 3; Table 1), of which 69.8% (n = 74) interacted with models, 28.3% interacted, but with no contact (n = 30) and 1.89% (n = 2) did not visualise the simulacra. Among interactions, 87.83% (n = 65) were displayed by mammals and 12.2% (n = 9) by birds. Among the videos where there was interaction but with no contact, 73.3% were displayed by birds (n = 22) and 26.7% (n = 8) by mammals. Only mammals did not visualise the simulacra in two instances (Fig. 2).

Most bird interactions with plasticine models occurred during the day, with 22 birds interacting with no contact (71%) and eight birds physically interacting with the models (25.81%). Only one individual presented interaction during the night, and none presented no visualising. Among mammal interactions, 71 occurred during the night, with 65 representing physical interactions (91.6%), five representing interactions with no contact (7.04%) and in only one interaction the individual did

Table 1. Models used in the experiment, their predators and observed behaviors and interaction

Plasticine prey model		Predator	Behaviour	Records	Interaction
Bothrops jararaca					
	Birds	*Baryphthengus ruficapillus*	Eating the model	2	Yes
		Crypturellus obsoletus	Foraging around the model	1	No
		Grallaria guatimalensis	Foraging around the model	2	No
		Leptotila rufaxilla	Foraging around the model	1	No
		Penelope obscura	Foraging around the model	1	No
		Trichothraupis melanops	Foraging around the model	1	No
		Turdus rufiventris	Foraging around and sitting on the model	1	No
	Mammals	*Didelphis aurita*	Eating the model	10	Yes
		Leopardus pardalis	Passed over the model	1	No
		Metachirus nudicaudatus	Eating the model	3	Yes
		Nectomys sp.	Eating the model	6	Yes
Xenodon neuwiedii					
	Birds	*B. ruficapillus*	Eating the model	1	Yes
		C. obsoletus	Foraging around the model	1	No
		Myiothlypis leucoblephara	Foraging around the model	1	No
		P. obscura	Foraging around the model	1	No
	Mammals	*D. aurita*	Eating the model	6	Yes
		Guerlinguetus ingrami	Foraging around the model	1	No
		Leopardus guttulus	Urinating on the model	1	Yes
		Nectomys sp.	Eating the model	1	Yes
Micrurus corallinus					
	Birds	*B. ruficapillus*	Eating the model	1	Yes
		G. guatimalensis	Foraging around the model	1	No
		L. rufaxilla	Foraging around the model	1	No
		P. obscura	Foraging around the model	2	No
		Turdus leucomelas	Foraging around the model	1	No
	Mammals	*D. aurita*	Eating the model	6	Yes
		M. nudicaudatus	Eating the model	7	Yes
		Nectomys sp.	Eating the model	2	Yes
Erythrolamprus aesculapii					
	Birds	*B. ruficapillus*	Eating the model	1	Yes
		G. guatimalensis	Foraging around the model	1	No
		L. rufaxilla	Foraging around the model	1	No
		P. obscura	Foraging around the model	1	No
			Eating the model	1	Yes
	Mammals	*Canis lupus familiaris*	Passed over the model	1	No
		D. aurita	Eating the model	2	Yes
		Leopardus pardalis	Passed over the model	1	No
		Nectomys sp.	Eating the model	8	Yes
Brown cryptic					
	Birds	*B. ruficapillus*	Eating the model	2	Yes
		C. obsoletus	Foraging around the model	1	No
		G. guatimalensis	Foraging around the model	1	No
		L. rufaxilla	Foraging around the model	1	No
		P. obscura	Foraging around the model	2	No
	Mammals	*C. lupus familiaris*	Passed over the model	1	No
		D. aurita	Eating the model	5	Yes
		L. pardalis	Passed over the model	1	No
		M. nudicaudatus	Eating the model	1	Yes
		Nectomys sp.	Eating the model	3	Yes
Green conspicuous					
	Mammals	*D. aurita*	Eating the model	3	Yes
		Herpailurus yagouaroundi	Passed over the model	1	No
		L. pardalis	Passed over the model	1	No
		Mazama gouazoubira	Sniffing the model	1	Yes
		Nectomys sp.	Eating the model	2	Yes

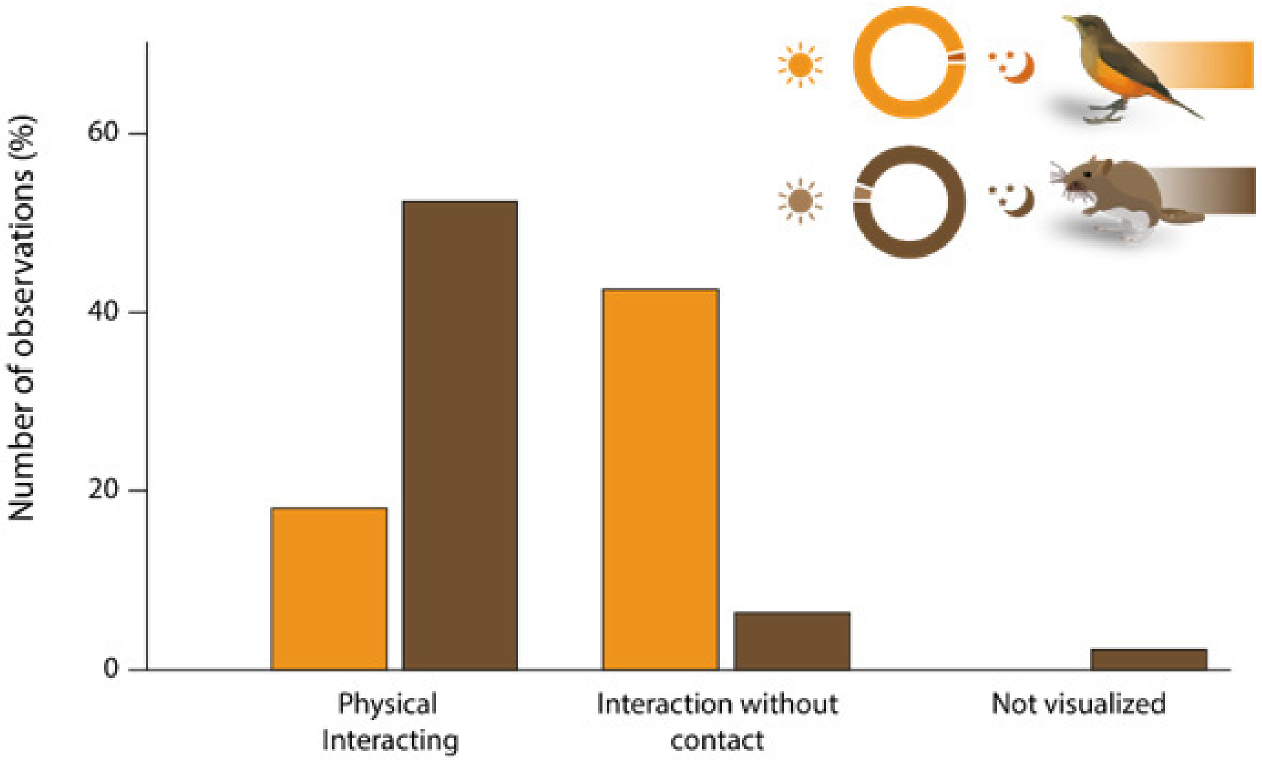

Figure 2. Number of individuals of birds (orange) and mammals (brown) observed in camera traps classified by type of interaction (interacting, interaction without contact, and not visualised). The donut chart indicates the total of interactions by period (diurnal: light colour; nocturnal: dark colour) for birds (orange) and mammals (brown).

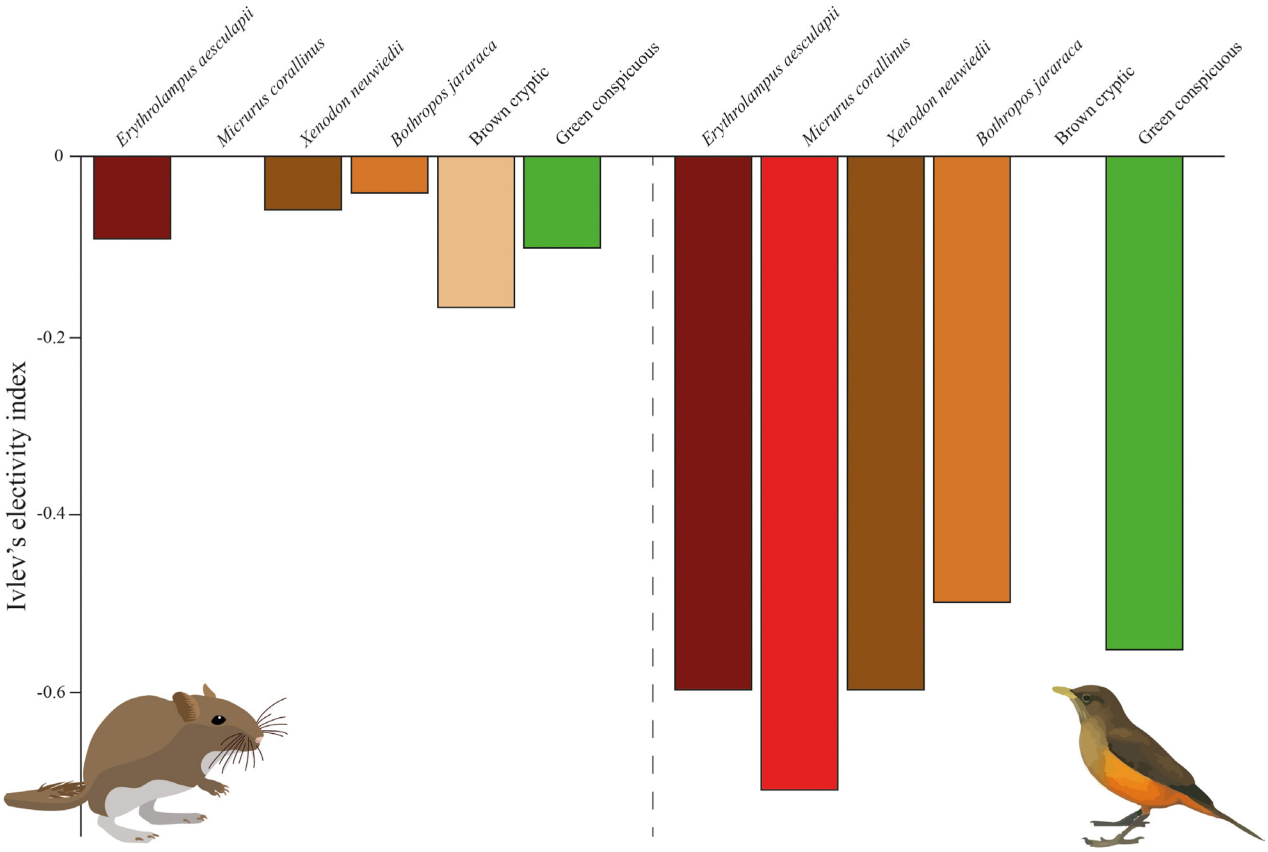

Figure 3. Ivlev's electivity index of predation by birds (left) and mammals (right) on each plasticine model

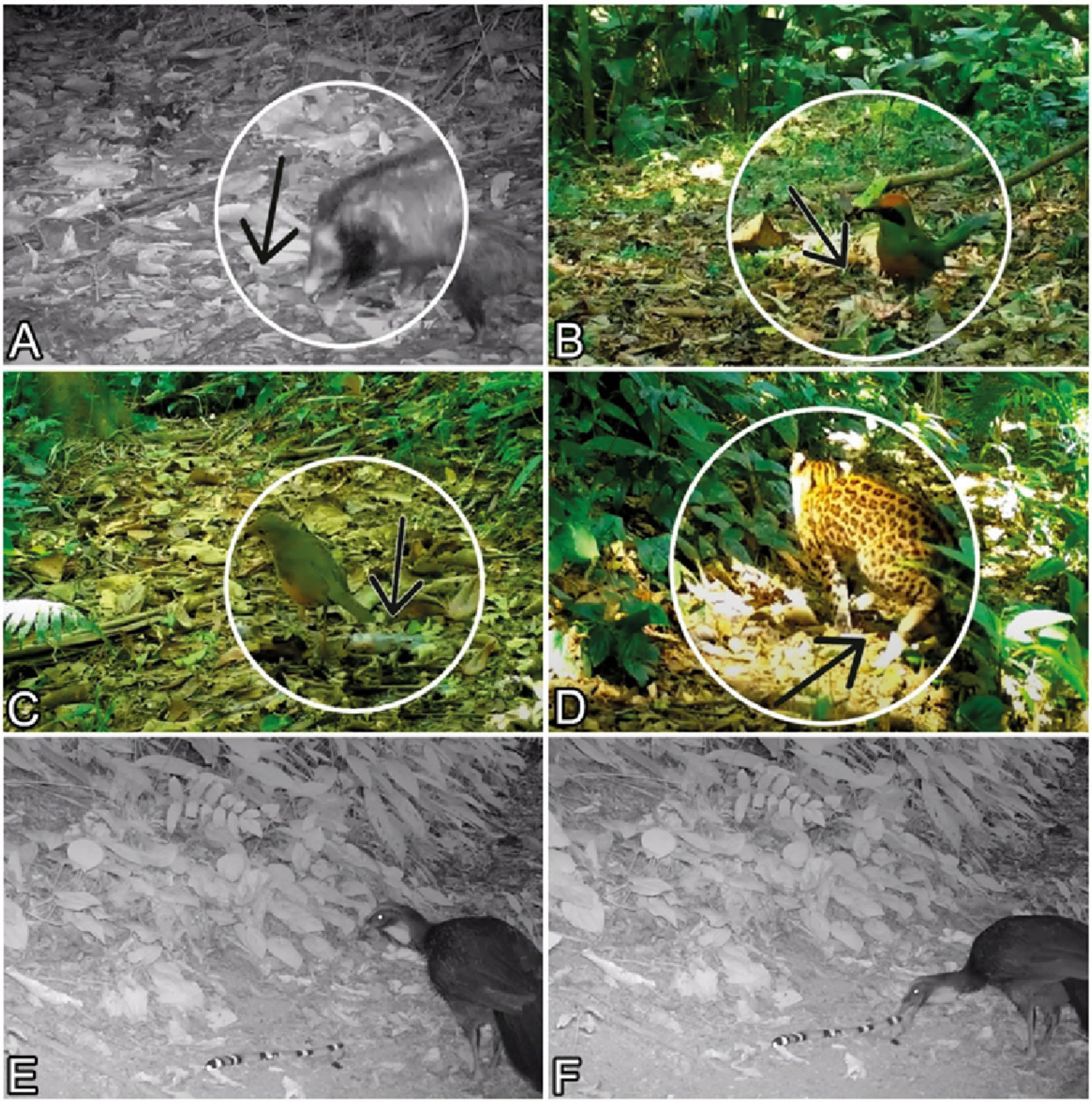

Figure 4. Images extracted from trail cameras depicting interaction with snake plasticine models.Within the white circles, the images enlarged. **(A)** Predation by the black-eared opossum *Didelphis aurita* on a model of the venomous pitviper *B. jararaca*; **(B)** rufous-capped motmot *Baryphthengus ruficapillus* examines and pecks at a *B. jararaca* model; **(C)** rufous-bellied thrush *Turdus rufiventris* lands over the same snake species model; **(D)** southern tiger cat *Leopardus guttulus* urinates on a *B. jararaca* model; **(E-F)** dusky-legged guan *Penelope obscura* examines and pecks at one of the aposematic models of the non-venomous *Erythrolamprus aesculapii*. Arrows indicate where models were placed.

not visualise the model. Only four interactions between mammals and the models occurred during the day, three with no contact (75%) and one with the individual not visualising the model. During the day we did not observe physical interaction between mammals and the models.

We detected six behaviours of potential predators: four "interaction" (chewing and/or eating, n = 72, 96%; urinating, n = 1, 1.3%; sniffing, n = 1, 1.3%; and landing on model/foraging in surroundings, n = 1, 1.3%) and two "not-interaction" behaviours, which were classified as "moving", when the potential predators passed by the model or were foraging in the surroundings, with no physical interaction with the model (n = 11, 32%), or did not display a clear signal of perception (n = 23, 68%).

In general, all models were "avoided" by predators (Fig. 3), but Ivlev's index showed difference among treatments: all values ranged from -0.13, for the *M. corallinus* model, to -0.24, for the generic green conspicuous model. When the two predator groups were considered individually, values for mammals remained close to 0 for all models, ranging from 0 for the *M. corallinus* model, to -0.16 for the generic brown cryptic model. For birds the indexes were lower, ranging from -0.5 for the *B. jararaca* model, to -0.71 for the *M. corallinus* model (Fig. 3). We observed no interaction with generic brown cryptic models by birds. Our results of the GLM analysis showed that none of the models influenced the predators' interactions (models: $\chi^2 = 2.906$, $p = 0.71$). However, we observed a significant difference between predator groups ($\chi^2 = 38.03$, $p < 0.001$), whereby interactions with plasticine models were greater in mammals than in birds (Table 2).

We recorded several predation events on all the snake models for mammal and bird species (Fig. 4). The black-eared opossum *Didelphis aurita*, for example attacked and ate parts of the *B. jararaca* model (Fig. 4A), whereas the rufous-capped motmot *Baryphtengus ruficapillus* examined and pecked at the model of the same venomous snake (Fig. 4B). One individual of the dusky-legged guan *Penelope obscura* examined and pecked a model (Fig. 4 E–F), but apparently lost interest after an initial peck and subsequently foraged in the proximity of the model. Similarly to *P. obscura*, an individual of rufous-bellied thrush *Turdus rufiventris* alighted over the *B. jararaca* model and foraged in close proximity to the model (Fig. 4C).

Camera trap videos indicate olfactory location of models by mammals. For example, this behaviour was observed for an individual of the southern tiger cat *Leopardus guttulus*, which urinated on a model of *B. jararaca* (Fig. 4D). An individual of the grey brocket deer *Mazama gouazoubira* was observed sniffing a generic green conspicuous model for some time. The water rat *Nectomys* sp. and the brown four-eyed opossum *Metachirus nudicaudatus*, which are part of the *B. jararaca* diet (Sazima, 1992), did not avoid the models and ate parts of them.

Table 2. Coefficients of Generalised Linear Model analysis. Significant value is in bold.

	Estimate	Std. Error	z value	p
Intercept	-0.73	0.62	-1.17	0.24
Models				
Micrurus corallinus	0.05	0.89	0.06	0.95
Erythrolamprus aesculapii	-0.79	0.95	0.83	0.41
Xenodon neuwiedii	0.44	1.01	0.43	0.65
Brown cryptic	-1.66	1.11	-1.49	0.14
Green conspicuous	-0.65	0.89	-0.73	0.47
Predators				
Mammals	3.31	0.63	5.28	**< 0.001**

DISCUSSION

Our results indicate that, although the use of plasticine models is readily available to test hypotheses, it is not entirely reliable for studies that aim to test the defensive colouration of snakes. We noted that the behaviour of potential predators toward the models differs from these relationships in natural encounters, as suggested by Beckers et al. (1996). While mammals clearly did not regard any models as a threat, birds appeared to avoid the interaction with the models. It was a clear pattern in our study, since we observed that most of the bird interactions occurred during the day, and with no physical contact, while interactions by mammals occurred during the night with physical contact. Since the defensive repertoire of a species against a predator is intrinsically related to its survival in the wild (Tozetti et al., 2009), the mechanisms of prey-predator interaction are important elements to be evaluated in experiments that aim to represent natural history of an interaction. Our study revealed potential caveats when using plasticine models to evaluate predation, especially in the context of snakes, and particularly when mammals are the predators.

Mammals commonly use olfaction for localisation, since odour is an important clue for this animal group for recognising potential prey (Apfelbach et al., 2005; Laska et al., 2005). The feeding on plasticine models by the marsupials and rodents is unsurprising, as both marsupials are omnivorous generalists and their diets range from fruits to vertebrates (Cáceres, 2004), which also applies to small rodents such as those from the genus *Nectomys* spp., excluding vertebrates as food (Lessa et al., 2019). However, we observed only a few interactions with plasticine models during the day, and consequently we cannot address if mammals tend to avoid the models in daylight. In relation to birds, it was expected that they would avoid snake models (Smith, 1976; Brodie, 1993), with exception of motmots (Brodie, 1993; present study) and some other bird species (Brodie, 1993). Our results suggest that most birds avoided the interaction with the snake models. However, our observations are not complete enough to highlight properly if birds avoid the contact by perceiving some danger signal, or if the activity predominantly during the day could improve their visualisation. Species that perceived the simulacra as a real snake would not approach the models, by the perception of some danger, and consequently would not be recorded by cameras. Those birds that approached the models but did not interact with models could (i) perceive that those were not real snakes; (ii) perceive the absence of movement, and consequently consider that the snake was dead, presenting no risk; or (iii) show no avoidance to snakes. Further studies with experimental approaches, such as experiments with multiple choice testing if birds could visualise the models during the night and mammals avoid during the day, and with recording of animal behaviour are necessary to evaluate these hypotheses.

Among the 18 recorded species, the only potential predators that include vertebrates in their diet are a bird and a mammal. The rufous-capped motmot *B. ruficapillus* preys on rodents (Pagotto et al., 2019) and the big-eared opossum *D. aurita* preys on snakes, including the venomous ones as the pitviper *B. jararaca* (Almeida-Santos et al., 2000; Jared et al., 1998; Oliveira & Santori, 1999; Sazima, 1992). Both the motmot and opossum species showed more interactions with the model of *B. jararaca*, a snake that displays a varied defensive repertoire ranging from immobility to retaliation (Sazima, 1992). No predator species engaged into the predation sequence described by Oliveira & Santori (1999), and attacked several places of the model apparently with no discrimination at which end the head could be. Using plasticine coral snake-like models, Brodie (1993) recognised a few bill marks due to motmot attacks on some models, which agrees with our observations. However, a comparison between handling live prey and immobile plasticine models could be unduly speculative, though motionless rattlesnakes were eaten alive by the opossum *D. aurita* (as *D. marsupialis*), which preferably targets the tail first (Almeida-Santos et al., 2000).

The use of plasticine models is based on assumptions such as confirmation of 'attacks', the ability to identify predators, and the accuracy of models in representing prey to draw conclusions about predation (Bateman et al., 2017). Apparently, these assumptions are limited if the behavioural interactions between potential predators and their prey models are not considered. Thus, we recommend that future studies must consider behavioural aspects in their research, such as defensive strategies of the modelled prey, and also strive to emulate their natural movements. Additionally, the odour of models may be another confounding and relevant factor for mammals. In this sense, caution is needed since robust statistics may obscure flaws in primary data collection.

Plasticine models have long been considered useful for testing shapes (Guimarães & Sawaya, 2011) and colours (Rebouças et al., 2019). However, our observations indicate that using only predation marks on the models can lead to biased conclusions that do not portray real encounters between predators and snake prey. We should not underestimate the ability of predators to detect and identify its prey. Thus, it is essential that the behavioural and innate characteristics of prey (e.g. movement, defensive repertoire, odour) are also considered, or at least considered in this type of experimental trail.

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DATA ACCESSIBILITY

Data are available in Museu de Diversidade Biológica (MDBio), Unicamp, under request.

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