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ORIGINAL ARTICLE

Snakes and forbidden fruits: non-consumptive effects of snakes on the behaviors of frugivorous birds

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Abstract

Usually, incited by fear, prey try to detect stimuli that announce the presence of predators, which, in turn, must develop strategies to remain imperceptible. Although this relationship traditionally involves the consumption of prey, predators can also affect their prey through predator-induced alterations in foraging, habitat use, or morphology. These alterations in prey traits, resulting from non-consumptive effects, were investigated through different stimuli induced by artificial snakes on the anti-predator behavior of birds when foraging upon *Morus nigra* trees. Experiments were developed for each type of snakes static position reflected different states of foraging behavior adopted by snakes (i.e., sit-and-wait, coiled, and active foraging) using three treatments: artificial snake, snake-shaped mimicry, and control (i.e., no stimulus). Regardless of the behavior adopted by snakes, the models caused drastic changes to the behaviors of birds. The other treatments did not trigger behavioral changes, except for the snake-shaped mimicry treatment, which simulated a coiled snake. This study demonstrates how birds perceive and respond to different predator-like stimuli, highlighting the cognitive and behavioral abilities of vertebrates.

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Significance statement

Predators control prey populations through a combination of consumptive and non-consumptive effects. We investigated the effects of non-consumptive effects induced by different stimuli emitted by tree snakes on the anti-predatory behaviors of neotropical frugivorous birds when foraging upon *M. nigra*. Our results revealed that they react to predation risk by identifying conspicuous visual signals of their predators and therefore alter their foraging behavior, resulting in a decreased fruit-collecting rate. In addition, we presented a new perspective on the cognitive and learning capacities of neotropical frugivorous birds, investigating some attributes they use to locate and identify their predators.

Keywords Bird anti-predatory behavior · Cognitive and behavioral abilities · Predator cues · Foraging behavior · Vertebrates

Introduction

In animals, fear is measurable and can trigger anti-predator responses in prey facing predation risk (Brown et al. 1999, 2001; Laundré et al. 2010; Romero et al. 2011). Anti-predator responses can initiate through the detection of visual (Valeix et al. 2009), auditory (Brinkerhoff et al. 2005) or chemical stimuli (Petranka et al. 1987), which then motivate the actions by the predator (Brown et al. 1999). These actions trigger different prey anti-predatory strategies (Bernot and Turner 2001) that can vary depending on predator identity (Breviglieri et al. 2013), or even through behavioral signs that denounce the intention of predators (see Jones 1980; Burger et al. 1991; Davidson et al. 2014).

In regard to the prey, the most common responses of prey facing predation risk are changes in group size (Valeix et al. 2009), activity patterns (Sih and McCarthy 2002), vigilance patterns (Hunter and Skinner 1998) and foraging patterns (Lima and Bednekoff 1999; Breviglieri et al. 2013). Stereotyped avoidance behaviors, e.g., *mobbing*, which are described for birds, bats and fishes (Altmann 1956; Dominey 1983; Lučan and Šálek 2013), and landscape movement patterns (Hernández and Laundré 2005; Ripple and Beschta 2006; Laundré et al. 2010) are also common anti-predator behaviors among the vertebrates. These strategies, when assessed, can influence the magnitude of the non-consumptive effects of predators on prey fitness (e.g., Lima 1998) and, consequently, on the abundance, biomass, dispersion, and fitness of organisms from lower trophic levels (Abrams 1995).

The present study investigated the effects of predation risk induced by different stimuli emitted by tree snakes (e.g., *Chironius bicarinatus* or *Philodryas olfersii*, Colubridae) on the anti-predatory behaviors of neotropical frugivorous birds when foraging upon *Morus nigra* (Moraceae). Artificial models of snakes were manipulated on tree branches, simulating different behaviors adopted by these animals. Tree snakes occur in the Atlantic Rainforest biome, exhibit diurnal habits, eat several groups of small vertebrate, and are considered to be the main predators of birds in the neotropical region (Skutch 1985; Hartmann and Marques 2005; Marques et al. 2005; Koenig et al. 2007). Therefore, tree snakes are suitable to test the influence of non-consumptive effects on frugivorous birds, which are considered efficient seed dispersers (Jordano et al. 2007). We predicted that the birds reduce their visitation rates (i.e., collection of drupes) upon *M. nigra* in response to the presence of artificial snake models. This behavioral response might differ depending on different stimuli emitted by predators (i.e., different hunting strategies). For example, we would expect a more intense response under the influence of attributes that offer higher predation risk, such as active foraging strategy, in which the predators are more exposed, compared to sit-and-wait strategy, which could draw less attention of prey because the predator is more cryptic (Romero and Koricheva 2011). Finally, we expected that coiled posture could indicate low predation risk, since this behavior denotes that snakes are resting.

Material and methods

Area and study system

The study area is located in the northeast region of the state of São Paulo, in the city of Ubatuba, specifically in the surroundings of the Núcleo Picinguaba (23° 22 S, 44° 52 W), which is part of the Serra do Mar State Park (Parque Estadual da Serra do Mar—PESM). The region is composed exclusively by the Atlantic Rainforest biome, showing "Af" type climate characteristic (i.e., humid tropical climate, without dry season), according to Köppen's classification (see Rolim et al. 2007).

M. nigra is an exotic species, native to China and Japan, but highly cultivated in the south and southwest regions of Brazil. This species begins the development of its inflorescences between June and August, which then mature during the spring (Lorenzi et al. 2006). The fruits are composite, cylindrical drupes with a tuberculate surface and are red when unripe and then black when mature (Lorenzi et al. 2003). Each drupe has an average of 56.8 ($\pm$15.7 SE) seeds (Barnea et al. 1992). In Brazil, they are consumed and dispersed by mammals, birds, and reptiles (Lorenzi et al. 2003).

As prey models, we used several species of frugivorous birds of the family Thraupidae that visited *M. nigra* in search of its drupes and that were usually observed in the study area (Appendix S1 in Electronic supplementary material (ESM). As a predator model, we used green artificial rubber snakes (i.e., length and weight of 110 cm and 60 g, respectively), simulating the presence of arboreal species such as *C. bicarinatus* (Wied, 1820), the two-headed sipo, and *P. olfersii* Lichtenstein, 1823, the Lichtenstein's green racer (Colubridae). These snake species occur in the Atlantic Rainforest biome, exhibit diurnal habits, and are predators of several groups of small vertebrates, including frogs, birds, and mammals (Hartmann and Marques 2005; Marques et al. 2005).

Experimental design

To investigate whether birds decrease the rate of drupes collected upon plants of *M. nigra* in response to the presence of snakes, and whether the snakes induce behavioral changes in birds, we manipulated the presence of artificial models of snakes using a randomized-block design.

The snake models were manipulated in three different ways, simulating different behaviors adopted by snakes on the branches of trees in the field, namely, sit-and-wait (Fig. 1a), coiled (Fig. 1d), and active foraging (Fig. 1g). Thus, the manipulated artificial models were exposed on the branches in the following manner: (i) sit-and-wait—the artificial snake was placed in the ambush position, hanging, in front of the drupes (Fig. 1b); (ii) coiled—the artificial snake was placed in a coiled position on the branches, in front of the drupes (Fig. 1e); and (iii) active foraging—the artificial snake was exposed along the branches, among the drupes and the leaves (Fig. 1h).

An experiment was independently conducted for each of the behaviors adopted by the snakes, totalizing tree independent experiments. Each plant represented a block ($N=12$). The tree canopy was divided into four equal parts, and each part was randomly designed to receive one of the following treatments run concomitantly: (i) one artificial snake model exposed on one of the *M. nigra* branches, adopting one of

Fig. 1 Real snakes adopting different behaviors (**a**, **d**, **g**), artificial snake models (**b**, **e**, **h**) and vines to simulate snake-shaped mimicry (**c**, **f**, **i**). Sit-and-wait behavior adopted by *Oxybelis fulgidus* (**a**) in response to an artificial snake (**b**) and a vine (snake-mimicking shape) (**c**). Coiled behavior adopted by *P. boulengeri* (**d**) in response to an artificial snake (**e**) and a vine (snake-mimicking shape) (**f**). Active foraging behavior adopted by *P. olfersii* (**g**) in response to an artificial snake (**h**) and a vine (snake-mimicking shape) (**i**). (Photo credits: **a** and **d**: Paulo Sérgio Bernarde; **g**: Guilherme Amaral; **b**, **c**, **e**, **f**, **h**, **i**: Crasso Breviglieri)

the three behaviors described above (Fig. 1b, e, h), (ii) a fragment of vine with the same dimensions as the artificial models (i.e., snake-shaped mimicry treatment, Fig. 1c, f, i), and (iii) control, i.e., the absence of any object on the branches of plants. Each treatment was developed in different branches of large trees so that the birds could not see all the treatments at the same time, thus maintaining independence among treatments. The experiments lasted for 5 days, during the second half of October 2014.

Prior to the beginning of the experiments, two groups of *M. nigra* trees from distinct regions were delimited. The first group consisted of three fruiting individuals, and the second of nine, with the trees placed at least 30 m from each other in each of the groups. The groups were 4 km apart from each other. To avoid a possible behavioral change of birds caused by previous experiences induced by prior treatments, the experimental blocks were randomly replicated during the 5 days, alternating both the groups of trees and the treatments used in the experiment, so that none of the trees received blocks containing the same types of treatments.

It was previously observed that each bird removed only one drupe per visit. Therefore, the rate of fruits collected by the birds is related to the number of visits during the recording. In this way, we can identify how many fruit the birds fail to consume in response to different treatments (i.e., artificial snake model, snake-shaped mimicry, and control).

In each replicate (i.e., block), we filmed the treatments upon *M. nigra* trees over 40 min using Sony camcorders (model DCR-DVD 610). The cameras were placed on tripods (1.5 m height), 2 m from the branches where the treatments were placed, which allowed the capture of images over an area of 1 m^2, the equivalent of a tridimensional space of 2 m^3 between the camera and the treatments. The filmings were done in the morning (i.e., after sunrise until 12:00 h) and between 15:00 and 18:30 pm. Since all the treatments within each block occurred concomitantly, the random effects of block controlled temporal variations over the entire sampling period. The recording area was standardized based on the strike distance of snakes, which can usually reach one-third of their body's length (Fraga et al. 2013). Thus, the effects of predator models on the rate of drupes collected by birds upon *M. nigra* would be restricted to a reach radius of 36.6 cm from the point where each model was placed. Each model was manually exposed on the branches of the trees, and apparently

no effect of the observer was detected on the birds' activity during the handling of these models. To minimize observer bias, blinded methods were use when all behavioral data were recorded and/or analyzed.

Statistical analyses

To test the effects of the presence of snakes on the rate of drupes collected by the frugivorous birds to *M. nigra* (i.e., response variable), randomized-block analyses of covariance (ANCOVAs) were performed for each independent experiment (i.e., behavior: sit-and-wait, coiled, and active foraging). The artificial snake model, the snake-shaped mimicry, and control treatments (three levels) were considered as fixed effects, and the blocks were considered as random effects. The total number of ripe drupes distributed within the image captured area was recorded prior to each filming and was then used as a covariate in the analyses.

After a priori observations, each visit of a frugivorous bird to *M. nigra* refers to the removal of a drupe. Thus, we could quantify how many drupes were collected according to each treatment.

All analyses were performed using R statistical language and software, version 3.1.2 (R Development Core Team 2015), and the significance level was set at $\alpha = 0.05$. Heterogeneity of variances, normality and outliers were verified by means of graphic inspections (e.g., qq-plots, Cook's d, influence) and statistical tests (e.g., Levene's test). The data were log transformed as needed, and the data were back-transformed for the construction of the figures.

Results

Organisms

Seven species of birds were observed, all representatives of the Thraupidae family, visiting *M. nigra* during the experiment (Appendix S1 in ESM). Of these species, *Tangara seledon* represented 89 % of visits, followed by *Tangara sayaca* (6 %). The remaining five species (*Tangara cyanocephala*, *Ramphocelus bresilius*, *Tangara palmarum*, *Tangara ornata*, and *Tachyphonus coronatus*) each represented only 1 % of the total visits.

Bird visitation and drupes collected

Since *T. seledon* was the dominant species during the experiment, we focused on the behavioral analyses (below) of this species only. The ANCOVAs models detected a strong influence of the treatments (i.e., artificial snake, snake-shaped mimicry, and control) on the rate of

drupes collected by birds upon *M. nigra* (Table 1). After a posteriori analysis (Tukey's post hoc test), it was observed that the treatment using artificial snake models reduced the bird visitation rate to *M. nigra*, regardless of the behavior adopted by the snakes on the tree branches (Table 1; Fig. 2). The treatments simulating sit-and-wait, coiled, and active foraging behavior reduced the rates of drupes collected rates 17-, 21-, and 46-fold, respectively, compared to the control treatment (Fig. 2). However, after paired comparisons between the types of behaviors (i.e., artificial snake model) there were no differences in effect intensity (Tukey's post hoc test: sit-and-wait vs. active foraging, $P = 0.9805$; sit-and-wait vs. coiled, $P = 1.000$; and coiled vs. active foraging, $P = 0.9805$). Overall, snake-shaped mimicry treatments did not change the rates of drupes collected compared to controls, except for the snake-shaped mimicry treatment concerning the coiled behavior, which dramatically reduced the bird visitation rate 17-fold compared to the control treatment (Table 1; Fig. 2). The number of ripe drupes counted a priori (i.e., covariate) did not influence the collected drupes rates by birds in plants (Table 1).

Table 1 Analyses of covariance (ANCOVAs) examining the effects of treatments (artificial snake, snake-shaped mimicry, and control) for each type of behavioral mode adopted by the snakes on trees (i.e., sit-and-wait, coiled, and active foraging) and for the combination of behaviors (all behaviors) on the number of bird visiting *M. nigra*

| Sources of variation	df	MS	F	P
Sit-and-wait				
Block	11	0.023203	2.62	0.020
Treatment	2	1.489738	168.70	<0.001
Fruits (covariate)	1	0.002359	0.26	0.610
Error	21	0.008831		
Coiled				
Block	11	0.024585	1.41	0.239
Treatment	2	1.953587	112.09	<0.001
Fruits (covariate)	1	0.017674	1.01	0.325
Error	21	0.017427		
Active foraging				
Block	11	0.006558	0.5157	0.871
Treatment	2	1.643156	129.2095	<0.001
Fruits (covariate)	1	0.010246	0.8057	0.379
Error	21	0.012717		
All behaviors				
Block	11	0.021120	1.5196	0.139
Behavior (B)	2	0.307598	22.1311	<0.001
Treatment (T)	2	4.082742	293.7454	<0.001
B x T	4	0.531714	38.2558	<0.001
Fruits (covariate)	1	0.019107	1.3747	0.244205
Error	87	0.013899		
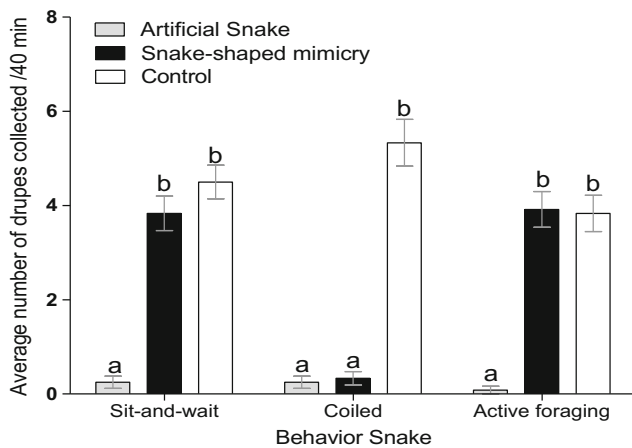
Fig. 2 Average number of drupes collected/40 min (±SE) by frugivorous birds to *M. nigra* in each of the applied treatments (i.e., artificial snake, snake-shaped mimicry, and control), according to the three different behaviors adopted by snakes on trees (see Fig. 1): sit-and-wait (i.e., model adopting an ambush position, in front of fruits), coiled (i.e., model adopting a coiled position on the branch, in front of fruits), and active foraging (i.e., model placed along the branch, among the ripe fruits). Different letters indicate significant differences between treatments ($P < 0.05$, ANCOVA/Tukey's post hoc test; $\alpha = 0.05$)

Anti-predatory behaviors

Tangara seledon was the only species that exhibited mobbing behavior in the presence of the snake models (Appendix S2, Fig. 1, and Appendix S3, video in ESM) and in response to the snake-shaped mimicry treatment replicating the coiled behavior (Appendix S4, video in ESM). This behavior was usually initiated when one of the individuals of the group (consisting of four or five birds on average) located one of the treatments (Appendix S2, Fig. 1a in ESM). At this point, the individual started to vocalize constantly and to flap its wings (Appendix S2, Fig. 1b in ESM) until all the other individuals of the group gathered around the treatments that simulated the different snake behaviors (Appendix S2, Fig. 1c in ESM) or the snake-shaped mimicry treatment for "coiled," in which the vine was coiled (Appendix S4, video in ESM). From this moment, all individuals started to vocalize and jump between *M. nigra* branches around the treatments; in a few minutes, one or two birds flew over the treatments (Appendix S2, Fig. 1d in ESM), vocalizing and apparently attacking the potential predators. This behavior lasted 1 or 2 min, and the birds then abandoned the *M. nigra* without carrying or consuming any drupes. In contrast, when *T. seledon* landed on *M. nigra* in pairs or alone, the birds just avoided the treatments, moving to nearby perches. In regard to the other species, when they identified the presence of artificial models and the presence of the snake-shaped mimicry treatment that simulated coiled behavior, they flew immediately toward the adjacent vegetation, apparently avoiding the risk.

Discussion

Our results show that frugivorous birds changed their foraging activities in response to predation risk on trees. However, aside from identifying and recognizing predators on the landscape (e.g., snake models), these animals also identified visual patterns that can indicate the risk of predation, i.e., they were able to detect risk when they found vines coiled on the plant (snake-shaped mimicry simulation of the coiled behavior of snakes, Fig. 1f). Consequently, the drupe rate collected decreased up to 46-fold in response to predation risk. These results offer new information regarding how the relationships between frugivorous birds and plants are molded by arboreal snakes and which attributes birds use to recognize their predators.

Birds decreased their visitation rates in response to artificial snake models. This reaction may be related to the cognitive and learning capacity of birds. In neotropical regions, snakes are known as the main predators of birds in nests (Skutch 1985; Koenig et al. 2007) compared to other predators, even with their combined effects (Weatherhead and Blouin-Demers 2004; Robinson et al. 2005). This predatory interaction between snakes and birds can even trigger defensive social behaviors among adult birds (e.g., mobbing) that, in turn, acquire and transmit information to young observers about the attributes of their aggressors, such as color, dimensions, location, and symmetry (Caro 2005; Templeton et al. 2005). Thus, we suggest that birds are able to identify artificial snakes as a predation risk based on their attributes, i.e., knowledge acquired during the learning process (see Caro 2005) and, consequently, to avoid them. These results add to a growing consensus that anti-predatory behaviors are widespread across many animal taxa (see Romero et al. 2011), including birds.

Contrary to the expectations, the snake-shaped mimicry treatment using coiled vine (coiled) also negatively affected the bird visitation rate on *M. nigra*, similar to the presence of a predator model. It is believed that this result is also related to the predator's attributes (e.g., symmetry) and the bird's learning processes. In the neotropical region, few liana species climb trunks and branches by circling them (Stevens 1987), with a tendency to grow in a spiral shape toward the canopy. Thereby, symmetrically coiled vine fragments are rare or scarce objects in nature. In contrast, diurnal (e.g., *Chironius* spp., *Oxybelis* spp. and *Pseustes* spp.) and nocturnal (e.g., *Dipsas catesbyi*, *Leptodeira annulata*, and *Tripanurgos compressus*) snakes are occasionally found coiled on tree branches (Martins 1993), representing a potential threat to birds (Hossie and Sherratt 2014), even during non-predatory attacks (e.g., defensive). Therefore, birds can apparently identify this type of snake-shaped mimicry treatment (i.e., symmetrically coiled vine) as a possible threat, contrary to the other snake-shaped mimicry treatments (e.g., sit-and-wait and active foraging) with vine patterns commonly observed

in nature. Thus, the birds' choice between risking themselves or not for a possible meal in front of a coiled vine can represent a trade-off, resulting in a lower collection rate of drupes by birds to *M. nigra*. Aversion behaviors of birds in response to visual stimuli that are similar to the predator's attributes have also been described by Janzen et al. (2010) and Hossie and Sherratt (2013). These authors noted that insectivorous birds show aversion to caterpillars that mimic snakes or even other vertebrate predators, even in the case of an effective food source, based only on their attributes (e.g., the presence of eyespots that mimic vertebrate's eyes).

The results of the present study indicate that neotropical frugivorous birds recognize predators on tree branches (e.g., artificial snake models) and also identify visual stimuli that may represent imminent predation risk (e.g., coiled vine). However, contrary to our predictions, *T. selodon* seemed to be unable to identify or discriminate among the different behaviors simulated by snake models representing different risk levels. Instead, these birds avoided all the snake behavior with similar intensity. Since venomous snakes may pose a threat, non-predatory attacks can also result in mortality, and even those snakes too small to consume an insect-eating bird could pose a considerable risk (Hossie and Sherratt 2014). This result suggests that the presence of a snake, regardless the behavior they adopt on the branches of a tree would be sufficient to inhibit the visitation of small fruit-eating birds.

The bird anti-predator behaviors recorded during the experiments varied with species identity and the treatments used. Most of the bird species simply avoided treatments with predation risk, whereas *T. selodon* frequently initiated mobbing. Mobbing behavior facing artificial snakes were also observed elsewhere for *Coereba flaveola* (GQR personal observations). Mobbing presents several social benefits, such as acquiring information (e.g., size or location) about the predator, teaching young birds about the risk and reducing the probability of predator return to the hunting place where it was found (Caro 2005; Templeton et al. 2005). However, this behavior can also present a high energetic cost and can minimize foraging time, presenting an injury risk in case of predator attack (Sordahl 1990) or even attracting other predators (Ostrow 2006). Here, we suggest that mobbing in *T. selodon* could intimidate tree-living predators in real situations, ensuring easier access to food for the group, compared to those bird species that display simple aversion.

In the presence of artificial snake models, the drupe collection rate was reduced. This suggests a possible reduction in the consumption of drupes as a result of predation risk (i.e., indirect, non-consumptive effects on plant fitness). However, these observations were done for only 40 min, and any interpretation on indirect effects should be viewed with caution in this system. Considering that snakes typically remain in the same place for several consecutive days (Fitzgerald et al. 2002) or even weeks (Durner and Gates 1989), and that *M. nigra* drupes are

exposed on the branches for only 2 or 3 days after maturation (CPBB personal observation), it is reasonable to suggest that snakes might decrease plant fitness via indirect interactions. This is a fruitful topic for further investigations.

We conclude that frugivorous birds modify their foraging activity in response to predation risk. Our results revealed that they react to predation risk by identifying conspicuous visual signals of their predators and therefore alter their foraging behavior, resulting in a decreased drupe collecting rate to *M. nigra*. In addition, we presented a new perspective on the cognitive and learning capacities of neotropical frugivorous birds, investigating some attributes they use to locate and identify their predators. Thus, these results bring forth new information on predatory effects and possible direct and indirect effects caused by the relationship between birds and snakes. Our results also add new information on the possible interactions between vertebrates that forage in the canopies of tropical forests.

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