Primate-predator interactions: is there a mismatch between laboratory and ecological evidence?

Biases in primate-predator studies

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Author Contributions

Original idea: XB. Conceptualization and writing of first version of the manuscript: KZ. Data collection, data management and statistical analyses: KZ. All authors contributed to the elaboration of the research questions and to the methodology. All authors contributed to writing, improvements and approved the submitted version.

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Conflict of Interest

The authors declare that they have no conflict of interest.

Abstract

Abundant empirical and theoretical studies indicate that predation is a key driver of primate evolution. The Snake Detection Theory (SDT) posits that snakes have been the main predators of primates since the late Cretaceous, and that they influenced the diversification and evolution of primates. Laboratory research focusing on the innate ability of primates to detect snakes amid complex visual stimuli has provided strong support for key tenets of the SDT. While this theory has greatly contributed to our knowledge of primate evolution, supporting experimental studies may have overly focused on snakes and disregarded other important predators. This potential sampling bias weakens the conclusion that primates respond with a specific (high) intensity to snakes compared to other predators. We reviewed the literature about primate-predator interactions under natural and experimental conditions. We listed the primate and predator species involved in natural versus experimental studies. Predation events on primates recorded in the field mainly involved other primates, then raptors and carnivorans. SDT-related experimental studies heavily focused on snakes as predator stimuli and did not include raptors. Other experimental studies largely used snakes and primates, and to a lesser extent carnivorans. Apes were the most often tested primates in experimental studies, other primate taxa were neglected. Moreover, predators used as stimuli in experimental studies were inaccurately identified, notably snakes. Altogether, our results show that SDT-related studies neglected most of the major natural predators of primates. SDT studies also focused on a handful of primate species, while the theory relies on comparisons among taxa. Finally, poor taxonomic information on snakes used as stimuli blurs the interpretation of their relationship with primates. We suggest that future studies test the SDT by presenting a wide range of predators to different primate species to improve our understanding of the complexity of predator-prey interactions.

Keywords: Snake Detection Theory; predation; primate evolution; visual cues

Introduction

The selective pressures exerted by predators rank amongst the most powerful evolutionary forces and are capable of rapidly transforming phenotypes (Darimont et al., 2009). There is a broad consensus that predators are one of the most important drivers of primate evolution (Cartmill, 1992; Gursky-Doyen & Nekaris, 2007; Mcgraw & Berger, 2013). Using extensive ecological, genetic, physiological, neuroanatomical, behavioural, and paleontological information, Isbell (2006) developed a comprehensive theory focused on predator-prey interaction. The Snake Detection Theory (SDT) posits that for the past 100 million years (My), snakes were the principal predators of mammals, including early primates, and exerted strong selective pressures on primates. The SDT proposes that besides high predation rates exerted by constrictor snakes, venomous snakes introduced an additional major risk in a broad Afro-Eurasian context. This risk is thought to have promoted an arm race between snakes and primates, and was "*ultimately responsible for the emergence of anthropoids*" (Isbell, 2006: p.12). More precisely, the SDT proposes that primates evolved an outstanding ability to detect concealed, motionless snakes before their fatal strike, and that primates acquired specific traits such as stereoscopic trichromatic colour vision and an enlarged brain to quickly process the massive amount of information generated (Isbell, 2006). Formalized in 2006, the SDT was extended to other human traits in 2009, including social and cultural traits (Isbell, 2009). A central tenet of the SDT, the capacity to detect snake stimuli more rapidly than other stimuli, has been validated experimentally in human and non-human primates (Le et al., 2014; Soares et al., 2014; Van Strien & Isbell, 2017; Weiss et al., 2015). Further research suggested that the remarkable capacity of primates and most notably humans to detect snakes, along with the sophisticated dedicated underlying neuronal structures, is innate and results from strong selection (Kawai, 2019).

Recently, however, the SDT has been challenged (Silcox & López-Torres, 2017; Wheeler, 2010). For example, a study using pupil dilation (mydriasis) in infants which suggested an innate fear of snakes (Hoehl et al., 2017) was questioned because this physiological response does not necessarily correlate with fear or negative stimuli (Denzer, 2018). Studies suggesting that the strong reactions elicited by snake stimuli are specific and hard-wired (Gomes et al., 2018) were also challenged when similar strong reactions were obtained using bicycles and cars instead of snakes (Gayet et al., 2019). Moreover, a lack of relationship between the degree of orbital convergence in primates and the duration of shared history with venomous snakes does not fit well with the hypothesized coevolution trajectory where dangerous snakes favoured different visual ability among primate taxa (Wheeler et al., 2011). Other authors have argued that the human visual detection and withdrawal reflex following snake detection are too slow to prevent bites in natural settings (Coelho et al., 2019).

A central assumption of the SDT is that snakes were the first predators of early primates, and that other classes of predators did not affect the evolution of early primates due to their late emergence (Isbell, 2006, 2009; Kawai, 2019). This assumption is not supported by any paleontologically established facts and is thus debatable. It is likely that various groups of carnivorous mammals and birds were major predators of primates from their emergence (Brusatte et al., 2015; Choiniere et al., 2021; Wilson et al., 2016) until recent times (Berger & Mcgraw, 2007; Camarós et al., 2015; McGraw et al., 2006; Zuberbühler & Jenny, 2002). Moreover, if primates emerged in the late Cretaceous, as genetic data suggest, then it seems likely that they would have been preyed on by various theropods that ruled terrestrial ecosystems. Carnivorans and raptors may, therefore, have deeply influenced primate evolution, as hypothesized by a study that found better detection of carnivores in trichromatic human subjects than in dichromatic ones (de Moraes et al., 2021). Therefore, besides snakes, it is important to include other major predators of primates, such as carnivorans, raptors and crocodilians (that evolved long before early primates: Grigg & Kirshner, 2015), in experimental studies. Moreover, encompassing the diversity of primate predators is essential to assess the extent to which snakes elicit specific antipredator responses, ranging from detection to behaviours; otherwise we cannot distinguish the SDT from a more general predator detection theory.

It is equally critical to test a phylogenetic and taxonomic diversity of primates in experimental studies. There are 79 genera and approximately 500 species of extant primates (Estrada et al., 2017; Mittermeier et al., 2013). Strepsirrhines comprise 27% of primate species; Pan-American monkeys 35%, Afro-Eurasian monkeys (excluding great apes) 37%, and great apes just 1%. The distinction and characterization of these groups is central to the SDT as it holds that the divergent evolutionary routes among these primate species were caused by different assemblages of snakes (especially venomous snakes) across biogeographical areas (Isbell, 2006).

Finally, it is important to consider the taxonomic accuracy used by experimenters within and among studies, and to use the most precise taxonomic level to describe the predatory stimuli presented to the primates tested. Most primate predators can be easily identified. Few carnivores are large enough to regularly feed on primates. Few raptors specialize on primates. Most dangerous snakes are recognizable and the low diversity of crocodiles greatly simplifies identification. In experimental studies, each species should therefore be named to the species or subspecies level without technical difficulty. For a large primate, the risk and threat of encountering a small cat *versus* a leopard are very different, rendering accurate identification of predators during experimental tests an important parameter. Taxonomic inaccuracy makes it impossible to account for the differential reactions of primates facing different types of predators.

To address these issues, we scrutinized the scientific literature on primate-predator interactions. For each study, we recorded which stimulus and subjects (primates) were observed in natural conditions (observational studies) or used in experimental settings (experimental studies). For experimental studies, we considered whether the authors aimed to test the SDT (SDT studies) or had other objectives (Non-SDT studies). First, we assessed if the stimuli presented in SDT and Non-SDT experimental studies differed and whether they matched the types of predators encountered by primates in natural conditions (Q1). Second, we compared the range of primates tested in SDT and Non-SDT experimental studies (Q2). Third, we assessed the taxonomic accuracy used to describe the predators observed in the wild or used as stimuli and presented to primates during experiments in SDT and Non-SDT studies (Q3). Observations of predation recorded in the wild are essential to evaluate the ecological relevance of the stimuli used and of the primate species tested in experimental studies (Non-SDT and SDT). Moreover, comparing Non-SDT studies and studies based on primate-predator interactions recorded in the wild provides an opportunity to examine the methodological choices that characterize SDT publications.

Methods

Selection of publications

We used the PRISMA method to perform a systematic and reproducible literature survey (Page, McKenzie, et al., 2021; Page, Moher, et al., 2021). We used different combinations of keywords and adopted automatic procedures to extract scientific articles from JSTOR, ScienceDirect, Springer, Web of Science Core Collection, Wiley Online Library and Google Scholar databases (Table 1). From the total number of articles extracted (N=18,153,145), automatic and manual procedures enabled us to discard out-of-focus publications and to retain N=201 studies that we could allocate to experimental versus observational categories. We examined the selected articles and retained those that evaluated the ability of primates to detect a specific stimulus (e.g. predator, dangerous/harmless animal or neutral), measured the fear level elicited by a stimulus, examined antipredator behaviour(s) in laboratory, captivity or the wild, or that reported clear predation cases. We only included original experimental or observational studies and discarded reviews except one (see below). For experimental studies, we narrowed our focus to visual stimuli because vision is central to SDT, and more generally to hypotheses for primate evolution (Cartmill, 1992; Pessoa et al., 2014; Sussman, 2017). We excluded studies that considered the response of primates to auditory or chemical stimuli. Although these stimuli play important roles in primates to inform congeners about predatory threats for example (Fichtel & Kappeler, 2002), and their exclusion may influence the prevalence of specific stimulus types, they were out of the scope of the current investigation. We also used a comprehensive list of references from a book chapter that provided a review of predation events in primates, including reports that were not detected with our automated procedures (Miller & Treves, 2011). Further details of the search procedure are provided in the supplementary material (Online Resource 1 Figures 5 and 6).

For observational studies, we searched for publications reporting direct observations of attempted predation events (successful or not) on primates in natural settings and indirect events with sufficient evidence to disregard scavenging. After screening, we retained 76 publications. We categorized these publications into the Predation group.

For experimental studies, we retained 125 articles that we subsequently allocated into two groups. SDT studies included publications explicitly framed around the SDT, or where the results were interpreted in this context (Isbell, 2006 or Isbell, 2009 had to be referenced in the bibliography). Non-SDT studies included publications that did not make explicit reference to the SDT. To precisely compare Non-SDT and SDT studies, we limited our search to the time period 2006-2022, after the first SDT publication (Isbell, 2006).

Overall, we selected N=201 articles (Predation N=76, SDT N=59, Non-SDT N=66).

Table 1.

Search words employed for the selection of experimental studies and publications reporting predation attempts upon primates in the wild and number of publications selected for each bibliographic database and a book chapter (Miller & Treves, 2011). We limited searching to the first 100 articles per search words for each bibliographic database. Note that the total number of selected publications displayed in this table (N=367) does not correspond to the final total number of publications analysed (N=201) because several publications appeared repeatedly through different combinations.

Search session	Search words	JSTOR	Science Direct	Springer	Web of Science	Wiley	Google Scholar	Miller & Treves
Experimental studies	Primates Fear Predators	5	14	14	18	7	12	-
	Primates Detection Predators	7	13	8	14	8	13	-
	Primates Antipredator Behaviors OR Behaviours	7	4	7	9	5	8	-
	Snake Detection Theory	5	19	9	20	7	32	-
Predation studies	Predation on Primates	5	2	13	10	6	10	47
	Animals Attack Humans	1	0	0	6	1	1	-

Data extraction and categorization of variables

In all groups, we considered each encounter between a primate or a group of primates and a stimulus as an interaction (I). We retained only unambiguous interactions where both the stimulus and the subject(s) were described. As SDT is strictly based on visual signals and taxidermized animals may also carry strong odors triggering antipredator response and acting as confounding factors, we decided to exclude this type of stimulus, as well as auditory stimulus. This choice resulted in the exclusion of only 12 interactions and four “Non-SDT” studies which is unlikely to change the results. The number of “Non-SDT” studies considered was thus 62 and the total number of publications analysed was 197. The mean number of interaction(s) per article was 50 (SD = 122.31; SEM = 8.71; range: 1-1,254); the total number of interactions recorded was higher than the total number of articles scrutinized (N=9,816 interactions in 197 articles). For brevity, we pooled non-animal stimuli like plants, fungi, and objects into a single category named “items”. Items were generally used as controls. The accuracy in describing animal stimuli provided in the methods section of the articles varied greatly: for example, some studies gave scientific names while others gave only very crude information. We assigned each animal stimulus to the most precise possible taxonomic level, typically ranging from species to order. We considered the ecological prey-predator context rather than phylogenetic relationships to pool stimuli into categories. For example, we treated crocodiles, which are more closely related to birds than to squamates, as a distinct group because they represent a unique threat to primates. We summarized the resulting categorization in Online Resources 1 (Table S1) and 2. Depending on the question examined, we used ecological groups, taxonomic groups, or the most precise taxonomic information available. The distinction between strepsirrhines, Pan-American monkeys (platyrrhines), Afro-Eurasian monkeys and apes (catarrhines), is central to the SDT; we therefore categorized primate species accordingly.

Study questions

<u>Q1: Do stimuli used in experimental studies include the main predators encountered by primates in the wild?</u> Some interactions (notably predation events) might be difficult to observe (Isbell, 1994) and observational biases affect which predation events can be witnessed. In addition, it is not always easy to combine scientific, anecdotal and non-scientific predation

reports. Nonetheless, the choice of predator stimuli used in experimental studies should be based on prey-predator interactions documented in the field or inferred from indirect evidence of predation (discarding scavenging). Therefore, we used predation events in the wild (Predation studies) as a crude ecological baseline. Although such reports do not provide accurate predation rates because observation biases cannot be controlled for, they provide direct and reliable information that can be easily quantified. For example, abundant reports of leopards hunting monkeys show that this large felid represents a strong predatory threat to primates; and such reports can be counted. We conducted two complementary analyses: a) we compared the main types of predators reported in Predation studies *versus* those used in Non-SDT and SDT studies; b) we assessed and compared the diversity of visual stimuli used in Non-SDT and SDT studies, notably the variety of predators, non-predator animals and various items (e.g. objects, plants). Because experimental studies testing the SDT are likely to compare primate responses to snakes, it is likely that snakes will be the most commonly used predators in SDT studies compared to Non-SDT studies. However, other animals, especially predators (e.g., carnivorans, raptors), should be used to test the extent to which reactions are snake-specific, which is key for evaluating the validity of the SDT.

<u>Q2: Are the main taxa of primates represented in experimental studies?</u> Experiments are constrained by the availability of the primate species kept in captivity or that can be easily observed in the field. We compared the primates involved in Non-SDT and SDT studies with the primates involved in Predation studies, but also compared Non-SDT and SDT studies separately. Since humans are the most easily available primate species, it is likely that SDT and Non-SDT studies will rely primarily on human subjects.

Q3: Does taxonomic accuracy differ among predator types? There is no practical reason for a difference in taxonomic accuracy between SDT, Non-SDT and Predation studies. We thus quantified the taxonomic accuracy of the predators of primates in the three groups. We defined the taxonomic accuracy as the accuracy of the taxonomic allocation used to describe an animal and divided it into two groups (i.e. two taxonomic levels) to ensure a sufficient number of interactions in each group for statistical comparisons: 1) Species or Family; 2) Suborder or Order.

Statistical analysis

For most analyses, we compared the occurrence of animals or items belonging to different categories across studies and within studies using contingency tables. Each experimental study (SDT and Non-SDT) can use a great variety of visual stimuli (e.g. snakes, flowers, objects) to examine the responses of different primate species while testing variable numbers of individuals. Some Predation studies can describe multiple predation events on primates, especially during long term monitoring of a group of primates. Consequently, the number of interactions (Ni) provides an accurate measurement to quantify and compare, using robust statistical tests: 1) the distributions of primates tested *versus* observed, and 2) the stimuli used *versus* predators observed across the three groups of study. Thus, we decided to consider all interactions in the statistical analyses and to focus on Ni. Nonetheless, we also performed analyses using the number of publications (Np; Online Resource 1, Figures 7-9). Since an experimental study could be included more than once when the experimenter(s) used different types of stimuli to test primate's reaction (generating pseudo-replicates), statistical tests were not conducted (selecting which type of stimulus per publication should be retained would have been arbitrary). Yet, we provided detailed information on the number of publications. We used Pearson's chi-square tests of independence to compare the distributions associated with each question under focus. For example, we only considered predator stimuli to compare the frequency of the main predators recorded in Predation studies *versus* the frequency of those used as picture or model stimuli in Non-SDT and SDT studies (Q1a). By contrast, we considered predator, non-predator animals and items to compare the distribution of stimuli used in Non-SDT and SDT studies (Q1b).

In addition to independence tests, we conducted chi-square tests of homogeneity to compare the distribution of stimuli used with a uniform distribution and pairwise chi-square comparisons using Bonferroni correction to adjust p-values for multiple comparisons to evaluate whether some types of stimuli were used preferentially. With the number of interactions per group and all statistical comparisons, we ranked stimuli groups from the most often to the least used, and indicated the statistical differences with letters in the tables. Sample sizes varied depending on the question and the variable or category selected, so we indicated the number of interactions taken into account for each group in each test.

In independence tests, if the test was not applicable due to insufficient occurrences (less than 5 expected observations, Cochran, 1954), we excluded the group with the smallest expected frequencies from the contingency table. Consequently, the number of publications and interactions often differ slightly between those indicated in the statistical tests and those in the graphs. We performed post-hoc analyses based on residuals of Pearson's chi-squared test using Bonferroni correction to identify whether the observed frequency was significantly higher or lower than the expected frequency for each group.

For brevity, we presented only the main figures and summary tables. We performed all analyses using R (R Core Team, 2022) in the integrated development environment Rstudio (RStudio Team, 2022). We provide the database (Online Resource 3), publications reviewed (Online Resource 1; Table S2), bibliographic analysis grid (Online Resource 1; Table S3), details of the statistical analyses (Online Resource 1, Tables S4-S11), additional analyses with the number of publications as measurement (Online Resource 1, Figures 7, 8, 9), and R script (Online Resource 4) in the electronic supplementary materials.

Ethical note

No original data were collected for this study; thus, the matter of ethical approval does not arise.

Data availability statement

Data and code are freely available in the electronic supplementary materials.

Results

Q1: Do stimuli used in experimental studies include the main predators encountered by primates in the wild?

<u>a) Presence of the main predators of primates in the literature.</u> The proportions of the main types of predators of primates observed in Predation studies, those used as stimuli in Non-SDT studies and those used as stimuli in SDT studies differed significantly (independence test: $\mathrm{Ni} = 4491;\ \mathrm{T} = 2634.9 \sim \chi^2_6, \mathrm{p} < 0.001$; Table 2). In Predation studies, most reported predation events involved primates, while interactions with raptors and carnivorans were observed less often, and those involving snakes and crocodilians were rare (Figure 1). In Non-SDT studies, experimenters mostly presented primate and snake stimuli to primates, then carnivorans stimuli and rarely raptor and crocodilian stimuli (Figure 1). In SDT studies, snakes were overwhelmingly common, raptors were not used, and few tests (i.e. interactions) involved a primate, a carnivoran or a crocodile stimulus (Figure 1). Raptors and primates were involved significantly more often in predation events (Predation studies) than used as predator stimuli in SDT and Non-SDT studies (Table 2). Carnivorans were used significantly more often in

Non-SDT studies than in predation reports and SDT studies (Table 2). Snakes were used significantly more often in SDT studies than in Non-SDT studies and predation reports (Table 2). Crocodiles were rare in Predation, SDT and Non-SDT studies (Figure 1, Table 2). We found similar graphical results using Np as measurement (Online Resource 1, Figure 7).

The considerable proportion of primate-on-primate predation events recorded (Figure 1, Table 2, Online Resource 1, Figures 10 and 11) was mainly due to abundant predation cases by chimpanzees (*Pan troglodytes*) reported notably in two publications (Stanford et al., 1994; Watts & Amsler, 2013). Chimpanzees accounted for 98% of the primate-on-primate predation events with N=1358 interactions over a total of N=1,381. Removing these outliers from the analyses drastically reduced the proportion of primate-on-primate predation events (5%), increased the prevalence of raptors (61%) and carnivorans (29%), and slightly changed the proportion of snake (3%) and crocodile predations (2%, Online Resource 1, Figure 11). However, the main outcomes of pairwise comparisons did not change, showing that snakes were significantly more represented in SDT studies than in Predation studies and Non-SDT studies (Table 2, Online Resource 1, Tables S4 and S5). In practice, removing these outliers revealed that raptors and carnivorans are the main predators of primates in the wild.

Table 2.

Simplified results of Pearson's chi-square tests of independence and associated post-hoc tests comparing the main predators of primates in three types of study. "Predation" studies: predation events observed in natural conditions. "Non-SDT" studies: predator stimuli used in experimental studies that do not refer to the Snake Detection Theory (SDT). "SDT" studies: predator stimuli used in experimental studies framed around the SDT (Isbell, 2006).

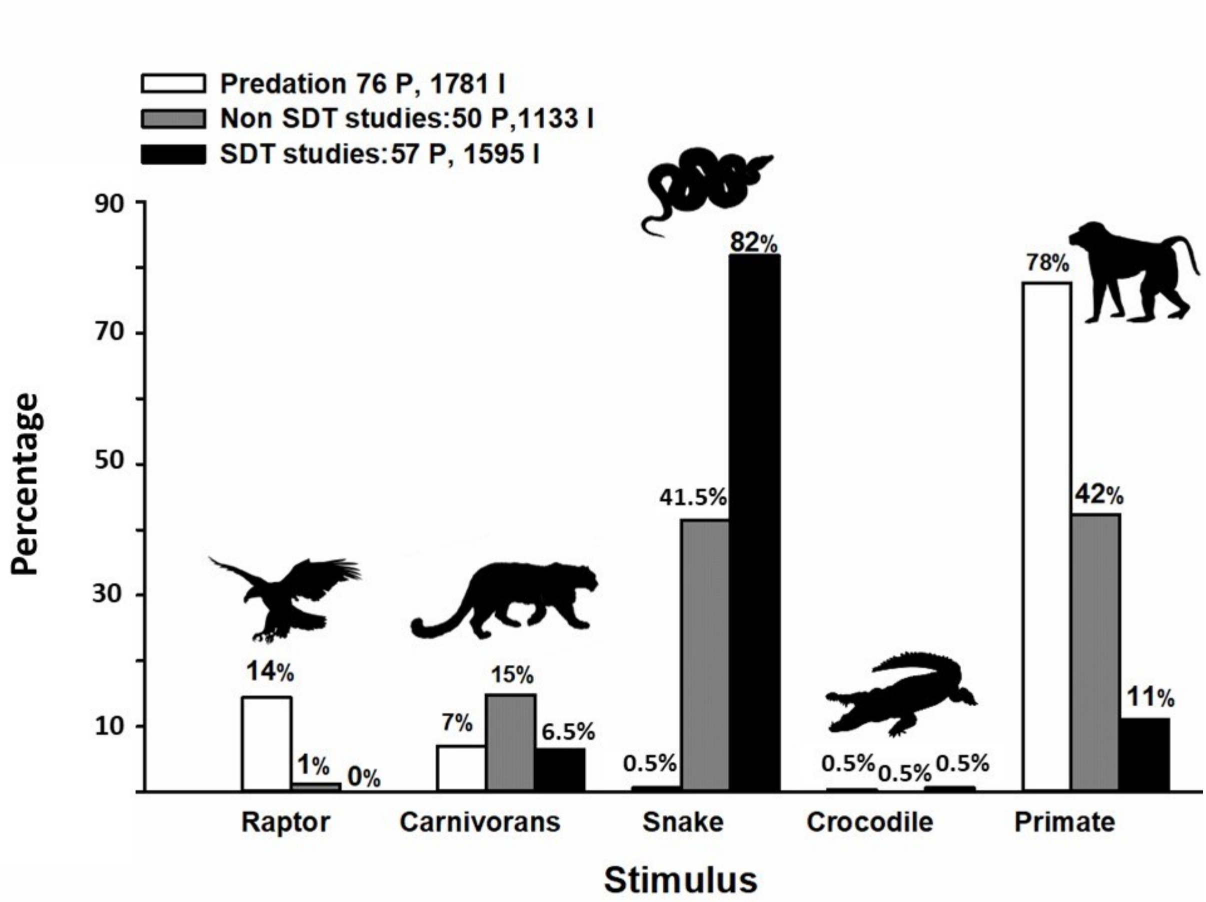
Threat	Predation	Non-SDT	SDT
Raptor	+	-	-
Carnivorans	-	+	-

Snake	-	=	+
Primate	+	-	-
Crocodile	E	E	E

"+" and "-" indicate the sign of the difference between the observed frequency and the expected frequency (z-score), positive or negative signs indicate a statistically significant difference ($p < 0.05$) and "=" indicates a non-statistically significant difference ($p > 0.05$). "E" indicates a stimulus group excluded from Pearson's chi-squared test of independence.

Figure 1.

Relative representation (% of interactions) of the main predators of primates in three types of studies. "Predation" studies: predation events observed in natural conditions. "Non-SDT" studies: predator stimuli used in experimental studies that do not refer to the Snake Detection Theory (SDT). "SDT" studies: predator stimuli used in experimental studies framed around the SDT (Isbell, 2006). "P" indicates the number of publications and "I" the number of interactions.



<u>b) Diversity of stimuli used in Non-SDT and SDT studies.</u> The visual stimuli presented to primates during experiments diverged markedly between Non-SDT and SDT studies (independence test, $\mathrm{Ni} = 7991;\ \mathrm{T} = 762.9 \sim \chi^2_{14}, \mathrm{p} < 0.001$). Primates, carnivorans, fish and raptors were used more often as animal stimuli in Non-SDT studies than in SDT studies and snakes (although abundantly used) were not predominant (Figure 2, Table 3). The proportion of items was high both in SDT and Non-SDT studies; objects and plants were used as controls and thus were used significantly more frequently than other stimuli (Table 3). The difference of item frequency between SDT (39%) and Non-SDT (43%) might appear marginal in Figure 2, but it was significant (Table 3). In SDT studies, snakes were the most often used animal stimuli, all other taxa were poorly or not represented (Figure 2, Table 3). Regardless of the experimental study type, some stimuli were used preferentially in experimental studies (homogeneity test, $\mathrm{Ni} = 8035;\ \mathrm{T} = 31062.0 \sim \chi^2_{20}, \mathrm{p} < 0.001$), with snakes being the most

often used animal stimuli due to their strong representation in SDT studies (Figure 2, Table 3). We found similar trends using Np instead of Ni (Online Resource 1, Figure 8).

Table 3.

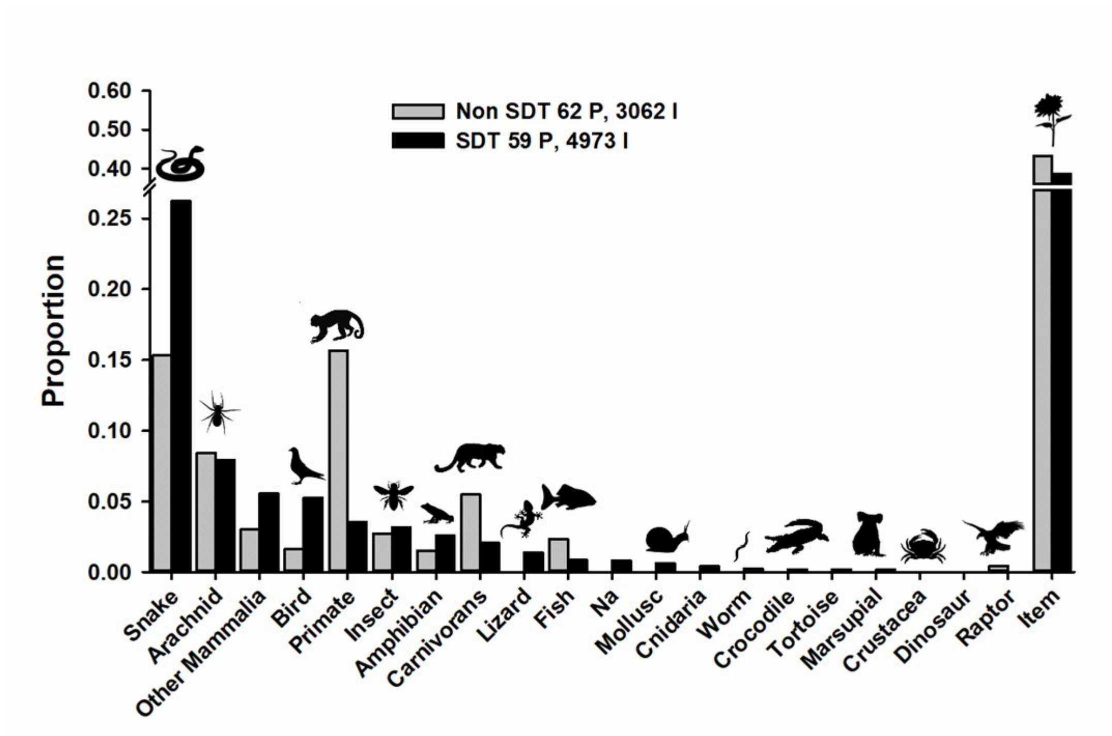
Simplified results of Pearson's chi-square tests of independence and associated post-hoc tests comparing the stimuli used in experimental studies. "Non-SDT" studies: predator stimuli used in experimental studies that do not refer to the Snake Detection Theory (SDT). "SDT" studies: predator stimuli used in experimental studies framed around the SDT (Isbell, 2006).

Animal stimuli	Non-SDT	SDT	Statistical significance
Item	+	-	a
Snake	-	+	b
Primate	+	-	c
Arachnid	=	=	c
Other Mammalia	-	+	d
Bird	-	+	d,e
Carnivorans	+	-	e,f
Insect	=	=	f
Amphibian	-	+	g
Fish	+	-	h
Lizard	-	+	i
Na	-	+	i,j
Mollusc	-	+	j,k
Cnidaria	-	+	j,k,l
Raptor	+	-	k,l
Worm	E	E	l
Crocodile	E	E	l,m
Tortoise	E	E	l,m
Marsupial	E	E	l,m
Dinosaur	E	E	m
Crustacea	E	E	m

"+" and "-" indicate the sign of the difference between the observed frequency and the expected frequency (z-score), positive or negative signs indicate a statistically significant difference (p < 0.05) and “=” indicates a non-statistically significant difference (p > 0.05). Stimulus groups sharing the same letter in the ‘Statistical significance’ column are not statistically different from each other (p > 0.05), based on pairwise chi-square comparisons. “E” indicates a stimulus group excluded from the Pearson's chi-squared test of independence.

Figure 2.

Relative representation of the stimuli in experimental studies. “Non-SDT” studies: predator stimuli used in experimental studies that do not refer to the Snake Detection Theory (SDT). “SDT” studies: predator stimuli used in experimental studies framed within the SDT (Isbell, 2006). “P” indicates the number of publications and “I” the number of interactions.



Q2: Are the main taxa of primates represented in experimental studies?

We found a significant difference between the preyed-on primate taxa in Predation studies and those tested in Non-SDT and SDT studies (independence test: $\mathrm{Ni} = 9816$; $T = 5893.6 \sim \chi^2_6$, $p < 0.001$, Table 4). Most field observations of predation events concerned Afro-Eurasian monkeys (Figure 3). By contrast, Non-SDT and SDT studies were highly biased toward apes (homogeneity test, Ni = 8035; $T = 17875.4 \sim \chi^2_3, p < 0.001$; Table 4, Online Resource 1, Figure 12). We found similar trends using Np instead of Ni (Online Resource 1, Figure 9). In experimental studies, the ape category was essentially represented by human subjects: 81% in SDT (N = 4,311) and more than 99% in Non-SDT studies (N = 2,863). Removing interactions with humans in experimental studies from the analyses drastically reduced the proportion of apes in Non-SDT studies (4%) and in SDT studies (56%), increased the prevalence of Afro-Eurasian monkeys in Non-SDT studies (72%) and in SDT studies (40%), and slightly changed the proportion of Pan-American monkeys in Non-SDT studies (21%, Online Resource 1, Figure 13). However, the main outcomes of pairwise comparisons did not change. Apes were significantly more represented in SDT than in Predation studies and Non-SDT studies. This difference was due to one SDT study using pictures of snakes to test the disruptive effect of negative stimuli on the cognitive abilities of chimpanzees, gorillas and Japanese macaques (Hopper et al., 2021; Table 4, Online Resource 1, Table S8). More importantly, whatever the case, in experimental studies, Pan-American monkeys were under represented (especially in SDT studies) while Strepsirrhines and Tarsiiformes were absent.

Table 4.

Simplified results of Pearson's chi-square tests of independence and associated post-hoc tests comparing the primate taxa represented in the three types of study. Simplified results of the chi-square test of homogeneity and associated post-hoc tests comparing the primate taxa represented in SDT and Non-SDT studies. "Predation" studies: predation events observed in natural conditions. "Non-SDT" studies: predator stimuli used in experimental studies that do not refer to the Snake Detection Theory (SDT). "SDT" studies: predator stimuli used in experimental studies framed around the SDT (Isbell, 2006).

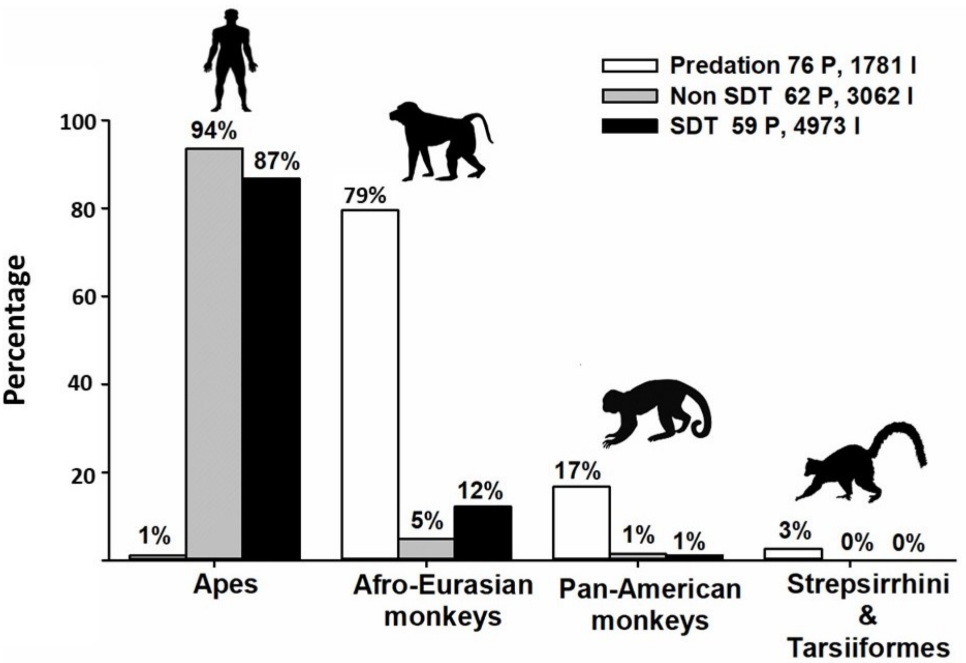
Broad taxon	Predation	Non-SDT	SDT	Statistical significance

Apes	-	+	+	a
Afro-Eurasian monkeys	+	-	-	b
Pan-American monkeys	+	-	-	c
Strepsirrhines & Tarsiiformes	+	-	-	d

"+" and "-" indicate the sign of the difference between the observed frequency and the expected frequency (z-score), positive or negative signs indicate a statistically significant difference ($p < 0.05$). Stimulus groups sharing the same letter in the 'Statistical significance' column are not statistically different from each other ($p > 0.05$), based on pairwise chi-square comparisons and chi-square test of homogeneity for SDT and Non-SDT studies only.

Figure 3.

Relative representation (% of interactions) of the primate taxa in three types of studies. "Predation" studies: predation events observed in natural conditions. "Non-SDT" studies: predator stimuli used in experimental studies that do not refer to the Snake Detection Theory (SDT). "SDT" studies: predator stimuli used in experimental studies framed around the SDT (Isbell, 2006). "P" indicates the number of publications and "I" the number of interactions.



Q3: Does taxonomic accuracy differ among predator types?

Predators in SDT and Non-SDT studies were not identified as accurately as in Predation studies (independence test: $\mathrm{Ni} = 4509$; $\mathrm{T} = 1689.3 \sim \chi^2_2$, $\mathrm{p} < 0.001$, Figure 4, Table 5). In SDT and Non-SDT studies, snakes were often crudely identified compared to other predators (independence test: $\mathrm{Ni} = 2728$; $\mathrm{T} = 1496.8 \sim \chi^2_4$, $\mathrm{p} < 0.001$, Table 6). Snake stimuli were named more accurately in Non-SDT studies than in SDT studies (independence test: $\mathrm{Ni} = 1774$; $\mathrm{T} = 12.9 \sim \chi^2_1$, $\mathrm{p} < 0.001$, Table 7).

Table 5.

Simplified results of Pearson's chi-square tests of independence and associated post-hoc tests comparing the taxonomic accuracy of predators between groups of study. "Predation" studies: predation events observed in natural conditions. "Non-SDT" studies: predator stimuli used in experimental studies that do not refer to the Snake Detection Theory (SDT). "SDT" studies: predator stimuli used in experimental studies framed around the SDT (Isbell, 2006).

Taxonomic accuracy	Predation	Non-SDT	SDT
Species or Family	+	=	-
Suborder or Order	-	=	+

"+" and "-" indicate the sign of the difference between the observed frequency and the expected frequency (z-score), positive or negative signs indicate a statistically significant difference (p < 0.05) and "=" indicates a non-statistically significant difference (p > 0.05).

Table 6.

Simplified results of Pearson's chi-square tests of independence and associated post-hoc tests comparing the taxonomic accuracy between predators used in experimental studies.

Taxonomic accuracy	Species or Family	Suborder or Order
Raptor	+	-
Carnivorans	+	-
Snake	-	+
Crocodile	=	=
Primate	+	-

"+" and "-" indicate the sign of the difference between the observed frequency and the expected frequency (z-score), positive or negative signs indicate a statistically significant difference ($p < 0.05$) and "=" indicates a non-statistically significant difference ($p > 0.05$).

Table 7.

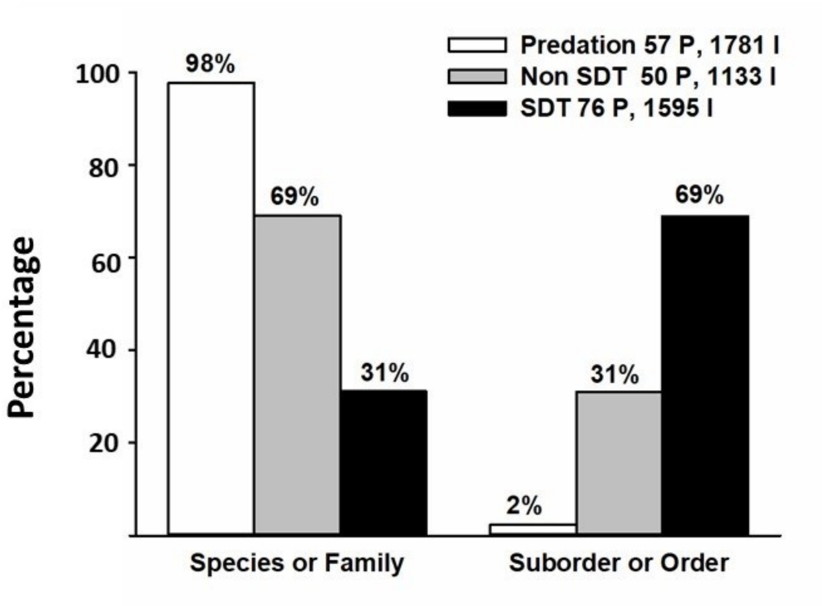
Simplified results of Pearson's chi-square tests of independence and associated post-hoc tests comparing the taxonomic accuracy of snake stimuli in experimental studies. "Non-SDT" studies: predator stimuli used in experimental studies that do not refer to the Snake Detection Theory (SDT). "SDT" studies: predator stimuli used in experimental studies framed around the SDT (Isbell, 2006).

Taxonomic accuracy	Non-SDT	SDT
Species or Family	+	-
Suborder or Order	-	+

"+" and "-" indicate the sign of the difference between the observed frequency and the expected frequency (z-score), positive or negative signs indicate a statistically significant difference ($p < 0.05$).

Figure 4.

Relative representation (% of interactions) of predators identified to species or family *versus* suborder or order in three types of study. "Predation" studies: predation events observed in natural conditions. "Non-SDT" studies: predator stimuli used in experimental studies that do not refer to the Snake Detection Theory (SDT). "SDT" studies: predator stimuli used in experimental studies framed within the SDT (Isbell, 2006). "P" indicates the number of publications and "I" the number of interactions.



Discussion

Comparisons among publications related to predation events recorded in the wild, Non-SDT and SDT experimental studies highlighted strong biases. The primate species tested in experimental studies and the predator stimuli used to elicit responses did not coincide with the range of primate-predator interactions observed in the wild. This mismatch was strong and key stimuli and primate species were lacking in the experimental SDT studies. Moreover, both the stimuli and the primate species selected in SDT studies markedly differed from those used in Non-SDT studies.

Predator diversity bias

Analyses indicated that reports of predation events on primates observed in the wild failed to support the assumption that snakes are major predators of modern primates. Instead, raptors, carnivorans and to a lesser extent other primates (when chimpanzee studies are discarded, Online Resource 1, Figure 11) exert strong predatory pressures on primates, a result supported by extensive reviews of primate ecology (Ferrari, 2009; Fichtel, 2012; Goodman et al., 1993;

Mittermeier et al., 2013). Although the conclusions that can be drawn are limited due to the difficulty of witnessing predation events on primates in the wild and restricted access to specific literature about predation on primates, it still seems unlikely that the low observed predation rate by snakes compared to other predator types might result from an underestimation.

Raptors were involved in numerous predation events on primates observed in the field, but were strongly under-represented or absent in experimental studies. Carnivorans also provided many cases of predation; they were slightly over-represented in Non-SDT studies and strongly under-represented in SDT studies. Snakes were very rarely involved in wild predation events, but were frequently used in Non-SDT studies and overwhelmingly used in SDT studies. This rarity of observed predation attempts cannot be explained by the secretiveness of snakes. While raptors kill their prey and take away their catch rapidly, snakes swallow their prey slowly, just after the catch, especially large items, increasing the observation probability. Raptors are used as audio stimuli in primate anti-predator experimental studies (Fichtel, 2007; Fichtel & Kappeler, 2002). The inclusion of audio stimuli in our data would have likely increased the number of raptors used in experimental studies. However, primates use both acoustic and visual clues in search of raptorial threats (Gil-da-Costa et al., 2003; Westoll et al., 2003). There was even less reason for their absence as visual stimuli in SDT studies (Mcgraw & Berger, 2013).

Surprisingly, primate-on-primate predation provided more than three quarters of the predation events recorded in the field, surpassing raptors and carnivorans. Most cases involved chimpanzees predating monkeys (76%, N=1,358 among 1,781 events), especially red colobus monkeys (*Piliocolobus sp.*). This over-representation was due to very large samples (N > 300 events) provided by few field studies where groups of habituated chimpanzees were closely monitored during specialized hunting, with a huge amount of data amassed over time (Stanford et al., 1994; Watts & Amsler, 2013). In contrast, in most reports of predation on primates (other predators than chimpanzees), sample sizes were small and often limited to a single observation (e.g. one monkey killed by a felid). By excluding chimpanzee predation studies, 5% of the total predation events involved another primate (N=23), then raptors and carnivorans are the main predators of primates, representing respectively 61% and 29% of the total number of predation events recorded in the field (Online Resource 1, Figure 11). Chimpanzees are certainly a predatory threat to smaller primates (Boesch & Boesch, 1989; Gašperšič & Pruetz, 2004; Newton-Fisher et al., 2002; Wrangham & Riss, 1990), but field evidences show that primates in general are predators of primates (Butynski, 1982; Cheney et al., 1981; Hohmann & Fruth, 2007; Jolly et al., 2000; Utami & Van Hooff, 1997).

Crocodilians were poorly represented in our data. This result was unexpected because numerous reports show that crocodiles are a major threat to humans (Das & Jana, 2017; Fukuda et al., 2014; García-Grajales & Buenrostro-Silva, 2019; Wallace et al., 2012). They would have been well represented if our literature survey had included many non-scientific reports (e.g., many cases have been published in local newspapers) and had focused on predation of humans by large predators. Nonetheless, the low occurrence of crocodiles is not easy to explain. The extreme rapidity of crocodilian attacks may have reduced observation opportunities. Whatever the explanation, the low occurrence of crocodiles in experimental studies does not allow us to determine whether these large predators trigger a strong fear and antipredator response and this issue deserves further investigation.

Considering all types of stimuli used in experimental studies, including various animals (predators, herbivores, etc.), plants and objects used as control stimuli, Non-SDT studies mainly used primates and then carnivorans (Figure 2). Many domestic objects and a great variety of plants were used as visual control stimuli, making this group the largest type of stimuli used. This suggests that experimenters incorporated a wide variety of items as control stimuli in their tests but did not do the same with predators. Snakes were the most often used animal stimuli in SDT studies. Most SDT studies compared the reactions of humans facing snakes, various objects, or harmless animals such as spiders (Hauke & Herzig, 2017), but neglected other major predators. The discrepancy between the predators of primates observed in the wild and the stimuli used in SDT experiments makes it difficult to assess comprehensively the main predictions of the SDT. Our results question the legitimacy of focusing almost exclusively on snakes as evolutionary-relevant stimuli when studying the influence of predators on primate evolution. Instead, we believe that observed predation events should provide a baseline for the design of experimental studies.

Primate diversity bias

The diversity of primates facing predation in the wild did not coincide with the species involved in Non-SDT and SDT studies. Predation observations involved a wide range of primate species in the field, but experimental studies most often tested apes, almost exclusively humans, and to a lesser extent included Afro-Eurasian monkeys. Pan-American monkeys were largely neglected while Strepsirrhines and Tarsiiformes were totally overlooked. This may partly result from observational difficulties: arboreal and nocturnal primates are not easily observed. However, many primate taxa would make suitable subjects in captive conditions. Focusing on non-human primates inevitably reduced taxonomic diversity of the subjects tested in experimental studies (Online Resource 1, Figure 13). Despite a general taxonomic bias in primate cognition studies and in field primatology in general (Altschul et al., 2019; Bezanson & McNamara, 2019), the almost exclusive focus of experimental studies on humans and on a handful of macaques results from the choice of experimenters. This choice may echo the appealing idea that the SDT provides a straightforward explanation for snake phobia (e.g. National Geographic News, 2017), possibly prompting studies looking for the module for fear dedicated to snakes in the human brain (Kawai, 2019). According to the SDT, Pan-American monkeys, Strepsirrhines and Tarsiiformes should exhibit lower abilities to detect snakes compared to Afro-Eurasian monkeys and apes. Unfortunately, the rarity or absence of tests performed with representatives of these main taxa precludes comparison across primate species.

Taxonomic accuracy bias

The taxonomic status of the predators of primates was reported less accurately in experimental than in field studies. This bias resulted almost exclusively from the low taxonomic accuracy used to describe snake stimuli in experimental studies. Snakes were well described in field predation studies, and they were described more precisely in Non-SDT studies than in SDT studies. This dearth of taxonomic accuracy is not justified by technical difficulties because pictures and scientific names are available for almost all snake species.

The SDT distinguishes between rapid visual detection and slower visual-cognitive recognition; investigators focusing on the former may see no reason to consider specific snake species, as they presumably all share visual cues unique to snakes that allow for rapid detection and processing of emotionally significant information by primates (Isbell & Etting, 2017; Lobue & Deloache, 2011; Van Strien & Isbell, 2017). If a snake shape represents a serious threat, it is logical to assume that strong selection occurred for an innate general detection mechanism for all snake-like stimuli occurred (Bertels et al., 2020; Ohman & Mineka, 2001). However, whether for rapid detection or slower recognition experiments, the deficiency of tests with primates facing different snake species is regrettable because more than 3,900 species of snakes have been inventoried. Snakes exhibit an immense variety of body sizes, body shapes and colour patterns (Allen et al., 2013). Some primates can differentiate dangerous from harmless snakes (e.g. moor macaques, *Macaca maura*, Hernández Tienda et al., 2021) and behave accordingly (Falótico et al., 2018). Besides, an encounter may be risky for the primate (Adukauskienė et al., 2011; Foerster, 2008; Shine et al., 1998), but it may also be risky for the snake, including venomous species (Boinski, 1988; Da Silva et al., 2019; Lorenz, 1971). Large, potentially dangerous snakes have evolved an extended repertoire of warning signals to avoid confrontation and minimize the use of defensive strikes (Glaudas & Winne, 2007).

Primate-snake relationships are likely more complex than assumed in most experiments reviewed in this study. To demonstrate that snakes elicit particular responses in primates, irrespective of the snake's appearance, it is crucial to account for the diversity of snakes. Therefore, the taxonomic accuracy of the visual stimuli used in experiments should be improved and investigators should compare reactions of different primate species facing a wide range of snake species encompassing sizes, colour, body shapes and behaviours.

Limitations and caveats

Many limitations of our survey could not be considered, such as the difficulty of encompassing the diversity of predation reports. We performed a systematic search and adopted automatic procedures to select scientific articles that excluded numerous reports of predation events on primates published in non-scientific journals (i.e. newspaper articles). Another difficulty emerged from the lack of standardization in the methodology and approaches used in field and experimental studies. Some reports involved a single predator, a single prey, and a single event; other studies were based on a wide diversity of stimuli, including different primate subjects and a range of tests. Despite this disparity, results obtained using Np were similar to those using Ni, suggesting that our conclusions are robust

Other limitations could not be considered. For example, observational biases affect which predation events can be recorded in the field. Technical difficulties to present realistic stimuli to the primates tested also limit our ability to measure their responses in a relevant manner. In addition, the proxies used to assess the fear response of animals (including humans) are often indirect (e.g. pupil dilatation) and not easy to interpret.

Nonetheless, the strong methodological biases we found in experimental studies are based on a large data set and on different albeit complementary questions. All the results converge to highlight a mismatch between laboratory and ecological evidences. They cannot be explained by observational difficulties in the field or other limitations evoked above. Instead, they largely resulted from the choice of the experimenters.

Conclusions

Abundant ecological evidence shows that predation attempts on modern primates are largely exerted by other animals than snakes. Yet, by heavily focusing on snakes and neglecting the role of carnivorans and raptors in the evolution of primate traits (Isbell, 2006, 2009; Kawai, 2019), SDT-related studies are unable to determine whether fear responses are snake-specific or anti-predator more generally. The biases we show here suggest that studies focusing on predator detection might benefit from including a more comprehensive list of predators and primates and should focus on phylogenetic gaps in the primates tested.

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