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

3

4 Biases in primate-predator studies

5

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21

22 **Author Contributions**

23 Original idea: XB. Conceptualization and writing of first version of the manuscript: KZ. Data
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27

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39 **Conflict of Interest**

40 The authors declare that they have no conflict of interest.

41

42 **Abstract**

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

66

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

68

69 **Introduction**

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

91 sophisticated dedicated underlying neuronal structures, is innate and results from strong
92 selection (Kawai, 2019).

93 Recently, however, the SDT has been challenged (Silcox & López-Torres, 2017; Wheeler,
94 2010). For example, a study using pupil dilation (mydriasis) in infants which suggested an
95 innate fear of snakes (Hoehl et al., 2017) was questioned because this physiological response
96 does not necessarily correlate with fear or negative stimuli (Denzer, 2018). Studies suggesting
97 that the strong reactions elicited by snake stimuli are specific and hard-wired (Gomes et al.,
98 2018) were also challenged when similar strong reactions were obtained using bicycles and
99 cars instead of snakes (Gayet et al., 2019). Moreover, a lack of relationship between the degree
100 of orbital convergence in primates and the duration of shared history with venomous snakes
101 does not fit well with the hypothesized coevolution trajectory where dangerous snakes favoured
102 different visual ability among primate taxa (Wheeler et al., 2011). Other authors have argued
103 that the human visual detection and withdrawal reflex following snake detection are too slow
104 to prevent bites in natural settings (Coelho et al., 2019).

105 A central assumption of the SDT is that snakes were the first predators of early primates,
106 and that other classes of predators did not affect the evolution of early primates due to their late
107 emergence (Isbell, 2006, 2009; Kawai, 2019). This assumption is not supported by any
108 paleontologically established facts and is thus debatable. It is likely that various groups of
109 carnivorous mammals and birds were major predators of primates from their emergence
110 (Brusatte et al., 2015; Choiniere et al., 2021; Wilson et al., 2016) until recent times (Berger &
111 McGraw, 2007; Camarós et al., 2015; McGraw et al., 2006; Zuberbühler & Jenny, 2002).
112 Moreover, if primates emerged in the late Cretaceous, as genetic data suggest, then it seems
113 likely that they would have been preyed on by various theropods that ruled terrestrial
114 ecosystems. Carnivorans and raptors may, therefore, have deeply influenced primate evolution,
115 as hypothesized by a study that found better detection of carnivores in trichromatic human

116 subjects than in dichromatic ones (de Moraes et al., 2021). Therefore, besides snakes, it is
117 important to include other major predators of primates, such as carnivorans, raptors and
118 crocodylians (that evolved long before early primates: Grigg & Kirshner, 2015), in
119 experimental studies. Moreover, encompassing the diversity of primate predators is essential
120 to assess the extent to which snakes elicit specific antipredator responses, ranging from
121 detection to behaviours; otherwise we cannot distinguish the SDT from a more general predator
122 detection theory.

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

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

140 it impossible to account for the differential reactions of primates facing different types of
141 predators.

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

157

158 **Methods**

159 *Selection of publications*

160 We used the PRISMA method to perform a systematic and reproducible literature survey (Page,
161 McKenzie, et al., 2021; Page, Moher, et al., 2021). We used different combinations of
162 keywords and adopted automatic procedures to extract scientific articles from JSTOR,
163 ScienceDirect, Springer, Web of Science Core Collection, Wiley Online Library and Google
164 Scholar databases (Table 1). From the total number of articles extracted (N=18,153,145),

165 automatic and manual procedures enabled us to discard out-of-focus publications and to retain
166 N=201 studies that we could allocate to experimental versus observational categories. We
167 examined the selected articles and retained those that evaluated the ability of primates to detect
168 a specific stimulus (e.g. predator, dangerous/harmless animal or neutral), measured the fear
169 level elicited by a stimulus, examined antipredator behaviour(s) in laboratory, captivity or the
170 wild, or that reported clear predation cases. We only included original experimental or
171 observational studies and discarded reviews except one (see below). For experimental studies,
172 we narrowed our focus to visual stimuli because vision is central to SDT, and more generally
173 to hypotheses for primate evolution (Cartmill, 1992; Pessoa et al., 2014; Sussman, 2017). We
174 excluded studies that considered the response of primates to auditory or chemical stimuli.
175 Although these stimuli play important roles in primates to inform congeners about predatory
176 threats for example (Fichtel & Kappeler, 2002), and their exclusion may influence the
177 prevalence of specific stimulus types, they were out of the scope of the current investigation.
178 We also used a comprehensive list of references from a book chapter that provided a review of
179 predation events in primates, including reports that were not detected with our automated
180 procedures (Miller & Treves, 2011). Further details of the search procedure are provided in the
181 supplementary material (Online Resource 1 Figures 5 and 6).

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

186 For experimental studies, we retained 125 articles that we subsequently allocated into two
187 groups. SDT studies included publications explicitly framed around the SDT, or where the
188 results were interpreted in this context (Isbell, 2006 or Isbell, 2009 had to be referenced in the
189 bibliography). Non-SDT studies included publications that did not make explicit reference to

190 the SDT. To precisely compare Non-SDT and SDT studies, we limited our search to the time
 191 period 2006-2022, after the first SDT publication (Isbell, 2006).

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

193

194 **Table 1.**

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

202

203

204 *Data extraction and categorization of variables*

205 In all groups, we considered each encounter between a primate or a group of primates and a
 206 stimulus as an interaction (I). We retained only unambiguous interactions where both the
 207 stimulus and the subject(s) were described. As SDT is strictly based on visual signals and
 208 taxidermized animals may also carry strong odors triggering antipredator response and acting
 209 as confounding factors, we decided to exclude this type of stimulus, as well as auditory

210 stimulus. This choice resulted in the exclusion of only 12 interactions and four “Non-SDT”
211 studies which is unlikely to change the results. The number of “Non-SDT” studies considered
212 was thus 62 and the total number of publications analysed was 197. The mean number of
213 interaction(s) per article was 50 (SD = 122.31; SEM = 8.71; range: 1-1,254); the total number
214 of interactions recorded was higher than the total number of articles scrutinized (N=9,816
215 interactions in 197 articles). For brevity, we pooled non-animal stimuli like plants, fungi, and
216 objects into a single category named “items”. Items were generally used as controls. The
217 accuracy in describing animal stimuli provided in the methods section of the articles varied
218 greatly: for example, some studies gave scientific names while others gave only very crude
219 information. We assigned each animal stimulus to the most precise possible taxonomic level,
220 typically ranging from species to order. We considered the ecological prey-predator context
221 rather than phylogenetic relationships to pool stimuli into categories. For example, we treated
222 crocodiles, which are more closely related to birds than to squamates, as a distinct group
223 because they represent a unique threat to primates. We summarized the resulting categorization
224 in Online Resources 1 (Table S1) and 2. Depending on the question examined, we used
225 ecological groups, taxonomic groups, or the most precise taxonomic information available. The
226 distinction between strepsirrhines, Pan-American monkeys (platyrrhines), Afro-Eurasian
227 monkeys and apes (catarrhines), is central to the SDT; we therefore categorized primate species
228 accordingly.

229

230 *Study questions*

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

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

251

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

258

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

266

267 *Statistical analysis*

268 For most analyses, we compared the occurrence of animals or items belonging to different
269 categories across studies and within studies using contingency tables. Each experimental study
270 (SDT and Non-SDT) can use a great variety of visual stimuli (e.g. snakes, flowers, objects) to
271 examine the responses of different primate species while testing variable numbers of
272 individuals. Some Predation studies can describe multiple predation events on primates,
273 especially during long term monitoring of a group of primates. Consequently, the number of
274 interactions (N_i) provides an accurate measurement to quantify and compare, using robust
275 statistical tests: 1) the distributions of primates tested *versus* observed, and 2) the stimuli used
276 *versus* predators observed across the three groups of study. Thus, we decided to consider all
277 interactions in the statistical analyses and to focus on N_i . Nonetheless, we also performed
278 analyses using the number of publications (N_p ; Online Resource 1, Figures 7-9). Since an
279 experimental study could be included more than once when the experimenter(s) used different
280 types of stimuli to test primate's reaction (generating pseudo-replicates), statistical tests were
281 not conducted (selecting which type of stimulus per publication should be retained would have
282 been arbitrary). Yet, we provided detailed information on the number of publications. We used
283 Pearson's chi-square tests of independence to compare the distributions associated with each

284 question under focus. For example, we only considered predator stimuli to compare the
285 frequency of the main predators recorded in Predation studies *versus* the frequency of those
286 used as picture or model stimuli in Non-SDT and SDT studies (Q1a). By contrast, we
287 considered predator, non-predator animals and items to compare the distribution of stimuli used
288 in Non-SDT and SDT studies (Q1b).

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

297 In independence tests, if the test was not applicable due to insufficient occurrences (less than
298 5 expected observations, Cochran, 1954), we excluded the group with the smallest expected
299 frequencies from the contingency table. Consequently, the number of publications and
300 interactions often differ slightly between those indicated in the statistical tests and those in the
301 graphs. We performed post-hoc analyses based on residuals of Pearson's chi-squared test using
302 Bonferroni correction to identify whether the observed frequency was significantly higher or
303 lower than the expected frequency for each group.

304 For brevity, we presented only the main figures and summary tables. We performed all
305 analyses using R (R Core Team, 2022) in the integrated development environment Rstudio
306 (RStudio Team, 2022). We provide the database (Online Resource 3), publications reviewed
307 (Online Resource 1; Table S2), bibliographic analysis grid (Online Resource 1; Table S3),
308 details of the statistical analyses (Online Resource 1, Tables S4-S11), additional analyses with

309 the number of publications as measurement (Online Resource 1, Figures 7, 8, 9), and R script
310 (Online Resource 4) in the electronic supplementary materials.

311

312 *Ethical note*

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

315

316 *Data availability statement*

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

318

319 **Results**

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

322 a) Presence of the main predators of primates in the literature. The proportions of the main
323 types of predators of primates observed in Predation studies, those used as stimuli in Non-SDT
324 studies and those used as stimuli in SDT studies differed significantly (independence test: $N_i =$
325 4491 ; $T = 2634.9 \sim \chi_6^2$, $p < 0.001$; Table 2). In Predation studies, most reported predation
326 events involved primates, while interactions with raptors and carnivorans were observed less
327 often, and those involving snakes and crocodilians were rare (Figure 1). In Non-SDT studies,
328 experimenters mostly presented primate and snake stimuli to primates, then carnivorans stimuli
329 and rarely raptor and crocodilian stimuli (Figure 1). In SDT studies, snakes were
330 overwhelmingly common, raptors were not used, and few tests (i.e. interactions) involved a
331 primate, a carnivoran or a crocodile stimulus (Figure 1). Raptors and primates were involved
332 significantly more often in predation events (Predation studies) than used as predator stimuli
333 in SDT and Non-SDT studies (Table 2). Carnivorans were used significantly more often in

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

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

350

351 **Table 2.**

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

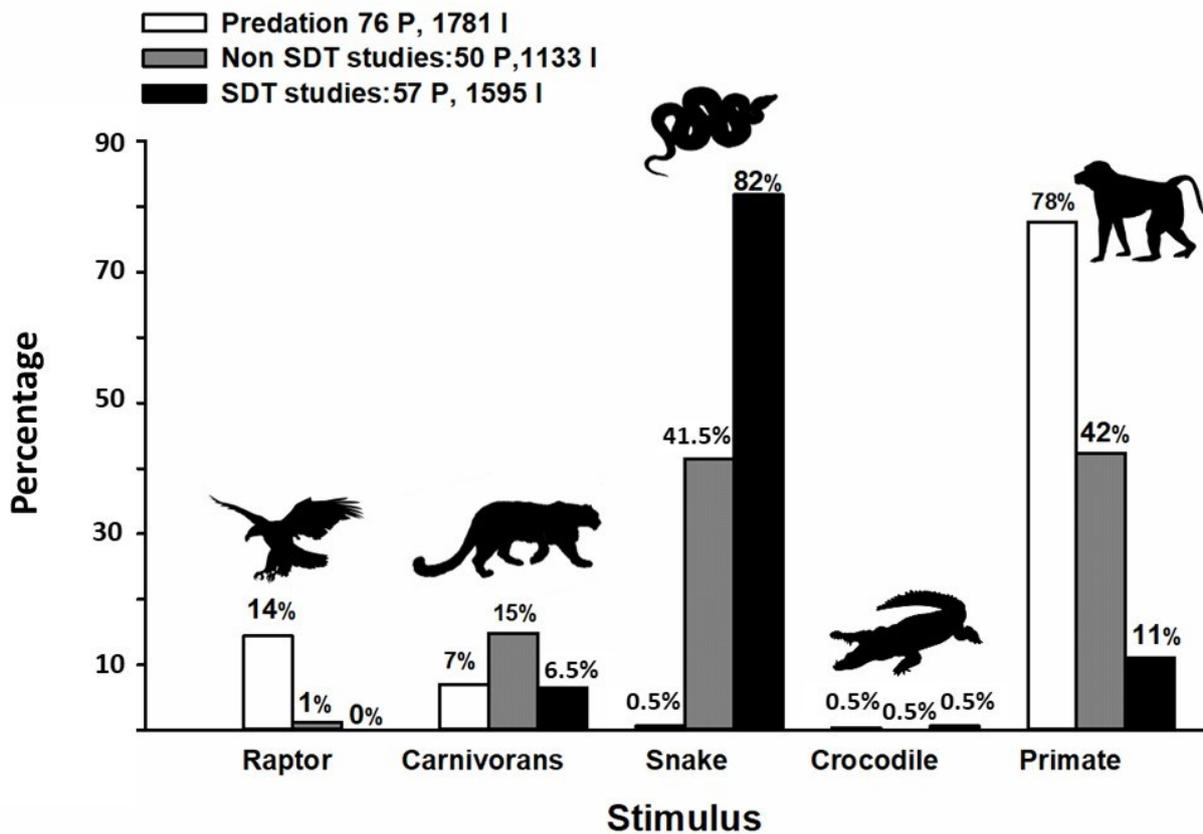
Threat	Predation	Non-SDT	SDT
Raptor	+	-	-
Carnivorans	-	+	-

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

357 “+” and “-” indicate the sign of the difference between the
358 observed frequency and the expected frequency (z-score),
359 positive or negative signs indicate a statistically significant
360 difference ($p < 0.05$) and “=” indicates a non-statistically
361 significant difference ($p > 0.05$). “E” indicates a stimulus group
362 excluded from Pearson's chi-squared test of independence.
363

364 **Figure 1.**

365 Relative representation (% of interactions) of the main predators of primates in three types of
366 studies. “Predation” studies: predation events observed in natural conditions. “Non-SDT”
367 studies: predator stimuli used in experimental studies that do not refer to the Snake Detection
368 Theory (SDT). “SDT” studies: predator stimuli used in experimental studies framed around
369 the SDT (Isbell, 2006). “P” indicates the number of publications and “I” the number of
370 interactions.
371



372

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

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

387

388 **Table 3.**

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

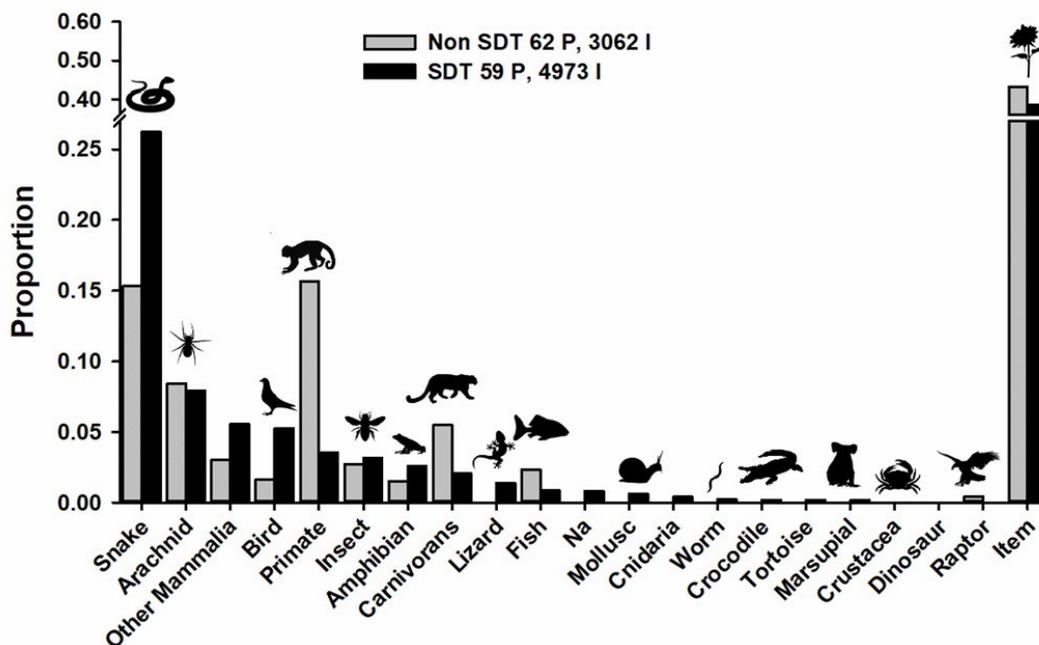
Animal stimuli	Non-SDT	SDT	Statistical significance
Item	+	-	a
Snake	-	+	b
Primate	+	-	c
Arachnid	=	=	c
Other Mammalia	-	+	d
Bird	-	+	d,e
Carnivorans	+	-	e,f
Insect	=	=	f
Amphibian	-	+	g
Fish	+	-	h
Lizard	-	+	i
Na	-	+	i,j
Mollusc	-	+	j,k
Cnidaria	-	+	j,k,l
Raptor	+	-	k,l
Worm	E	E	l
Crocodile	E	E	l,m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

393 “+” and “-” indicate the sign of the difference between the
 394 observed frequency and the expected frequency (z-score),
 395 positive or negative signs indicate a statistically significant

396 difference ($p < 0.05$) and “=” indicates a non-statistically
 397 significant difference ($p > 0.05$). Stimulus groups sharing
 398 the same letter in the ‘Statistical significance’ column are
 399 not statistically different from each other ($p > 0.05$), based
 400 on pairwise chi-square comparisons. “E” indicates a
 401 stimulus group excluded from the Pearson's chi-squared test
 402 of independence.
 403

404 **Figure 2.**

405 Relative representation of the stimuli in experimental studies. “Non-SDT” studies: predator
 406 stimuli used in experimental studies that do not refer to the Snake Detection Theory (SDT).
 407 “SDT” studies: predator stimuli used in experimental studies framed within the SDT (Isbell,
 408 2006). “P” indicates the number of publications and “I” the number of interactions.



409

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

411 We found a significant difference between the preyed-on primate taxa in Predation studies and
 412 those tested in Non-SDT and SDT studies (independence test: $N_i = 9816$; $T =$
 413 $5893.6 \sim \chi^2_6, p < 0.001$, Table 4). Most field observations of predation events concerned
 414 Afro-Eurasian monkeys (Figure 3). By contrast, Non-SDT and SDT studies were highly biased

415 toward apes (homogeneity test, $N_i = 8035$; $T = 17875.4 \sim \chi^2_3, p < 0.001$; Table 4, Online
416 Resource 1, Figure 12). We found similar trends using N_p instead of N_i (Online Resource 1,
417 Figure 9). In experimental studies, the ape category was essentially represented by human
418 subjects: 81% in SDT ($N = 4,311$) and more than 99% in Non-SDT studies ($N = 2,863$).
419 Removing interactions with humans in experimental studies from the analyses drastically
420 reduced the proportion of apes in Non-SDT studies (4%) and in SDT studies (56%), increased
421 the prevalence of Afro-Eurasian monkeys in Non-SDT studies (72%) and in SDT studies
422 (40%), and slightly changed the proportion of Pan-American monkeys in Non-SDT studies
423 (21%, Online Resource 1, Figure 13). However, the main outcomes of pairwise comparisons
424 did not change. Apes were significantly more represented in SDT than in Predation studies and
425 Non-SDT studies. This difference was due to one SDT study using pictures of snakes to test
426 the disruptive effect of negative stimuli on the cognitive abilities of chimpanzees, gorillas and
427 Japanese macaques (Hopper et al., 2021; Table 4, Online Resource 1, Table S8). More
428 importantly, whatever the case, in experimental studies, Pan-American monkeys were under
429 represented (especially in SDT studies) while Strepsirrhines and Tarsiiformes were absent.

430

431 **Table 4.**

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

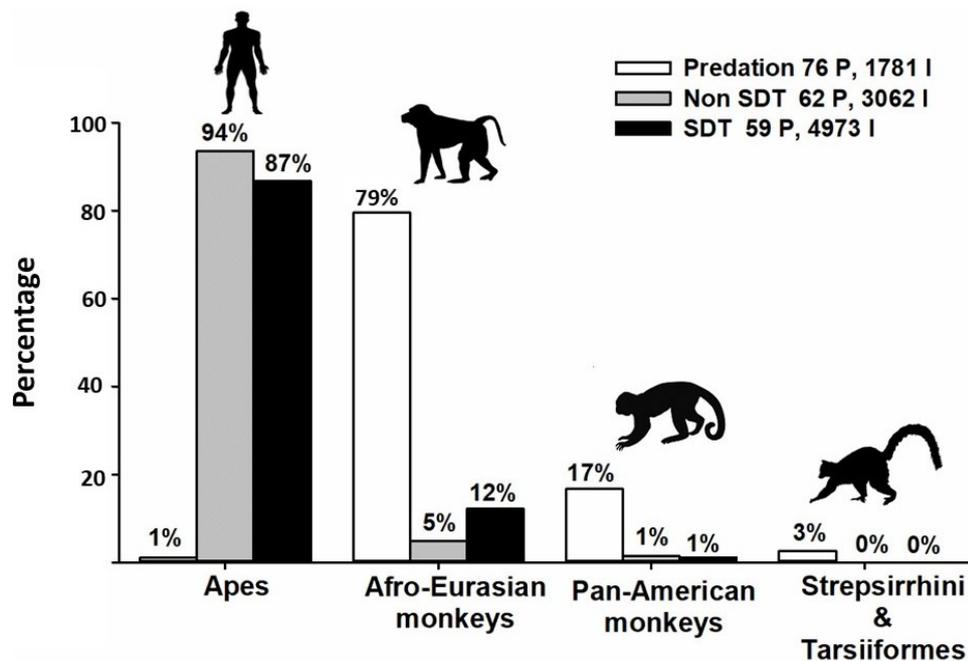
Broad taxon	Predation	Non-SDT	SDT	Statistical significance
-------------	-----------	---------	-----	--------------------------

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

439 “+” and “-” indicate the sign of the difference between the observed frequency
440 and the expected frequency (z-score), positive or negative signs indicate a
441 statistically significant difference ($p < 0.05$). Stimulus groups sharing the same
442 letter in the ‘Statistical significance’ column are not statistically different from
443 each other ($p > 0.05$), based on pairwise chi-square comparisons and chi-square
444 test of homogeneity for SDT and Non-SDT studies only.
445

446 **Figure 3.**

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



452

453

454 *Q3: Does taxonomic accuracy differ among predator types?*

455 Predators in SDT and Non-SDT studies were not identified as accurately as in Predation studies
 456 (independence test: $N_i = 4509$; $T = 1689.3 \sim \chi_2^2$, $p < 0.001$, Figure 4, Table 5). In SDT
 457 and Non-SDT studies, snakes were often crudely identified compared to other predators
 458 (independence test: $N_i = 2728$; $T = 1496.8 \sim \chi_4^2$, $p < 0.001$, Table 6). Snake stimuli were
 459 named more accurately in Non-SDT studies than in SDT studies (independence test: $N_i =$
 460 1774 ; $T = 12.9 \sim \chi_1^2$, $p < 0.001$, Table 7).

461

462 **Table 5.**

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

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

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

472

473 **Table 6.**

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

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

476 “+” and “-” indicate the sign of the difference between the observed
 477 frequency and the expected frequency (z-score), positive or negative
 478 signs indicate a statistically significant difference ($p < 0.05$) and “=”
 479 indicates a non-statistically significant difference ($p > 0.05$).
 480

481 **Table 7.**

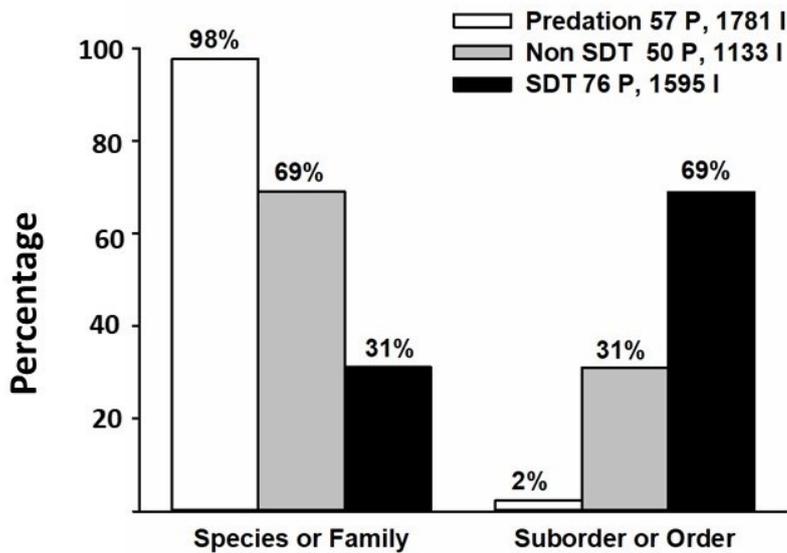
482 Simplified results of Pearson’s chi-square tests of independence and associated post-hoc tests
 483 comparing the taxonomic accuracy of snake stimuli in experimental studies. “Non-SDT”
 484 studies: predator stimuli used in experimental studies that do not refer to the Snake Detection
 485 Theory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

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

487 “+” and “-” indicate the sign of the difference between
 488 the observed frequency and the expected frequency (z-
 489 score), positive or negative signs indicate a statistically
 490 significant difference ($p < 0.05$).
 491

492 **Figure 4.**

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



499

500

501 **Discussion**

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

509

510 *Predator diversity bias*

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

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

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

533 Surprisingly, primate-on-primate predation provided more than three quarters of the
534 predation events recorded in the field, surpassing raptors and carnivorans. Most cases involved
535 chimpanzees predating monkeys (76%, N=1,358 among 1,781 events), especially red colobus
536 monkeys (*Piliocolobus sp.*). This over-representation was due to very large samples (N > 300
537 events) provided by few field studies where groups of habituated chimpanzees were closely
538 monitored during specialized hunting, with a huge amount of data amassed over time (Stanford
539 et al., 1994; Watts & Amsler, 2013). In contrast, in most reports of predation on primates (other
540 predators than chimpanzees), sample sizes were small and often limited to a single observation

541 (e.g. one monkey killed by a felid). By excluding chimpanzee predation studies, 5% of the total
542 predation events involved another primate (N=23), then raptors and carnivorans are the main
543 predators of primates, representing respectively 61% and 29% of the total number of predation
544 events recorded in the field (Online Resource 1, Figure 11). Chimpanzees are certainly a
545 predatory threat to smaller primates (Boesch & Boesch, 1989; Gašperšič & Pruetz, 2004;
546 Newton-Fisher et al., 2002; Wrangham & Riss, 1990), but field evidences show that primates
547 in general are predators of primates (Butynski, 1982; Cheney et al., 1981; Hohmann & Fruth,
548 2007; Jolly et al., 2000; Utami & Van Hooff, 1997).

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

559 Considering all types of stimuli used in experimental studies, including various animals
560 (predators, herbivores, etc.), plants and objects used as control stimuli, Non-SDT studies
561 mainly used primates and then carnivorans (Figure 2). Many domestic objects and a great
562 variety of plants were used as visual control stimuli, making this group the largest type of
563 stimuli used. This suggests that experimenters incorporated a wide variety of items as control
564 stimuli in their tests but did not do the same with predators. Snakes were the most often used
565 animal stimuli in SDT studies. Most SDT studies compared the reactions of humans facing

566 snakes, various objects, or harmless animals such as spiders (Hauke & Herzig, 2017), but
567 neglected other major predators. The discrepancy between the predators of primates observed
568 in the wild and the stimuli used in SDT experiments makes it difficult to assess
569 comprehensively the main predictions of the SDT. Our results question the legitimacy of
570 focusing almost exclusively on snakes as evolutionary-relevant stimuli when studying the
571 influence of predators on primate evolution. Instead, we believe that observed predation events
572 should provide a baseline for the design of experimental studies.

573

574 *Primate diversity bias*

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

591 compared to Afro-Eurasian monkeys and apes. Unfortunately, the rarity or absence of tests
592 performed with representatives of these main taxa precludes comparison across primate
593 species.

594

595 *Taxonomic accuracy bias*

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

602 The SDT distinguishes between rapid visual detection and slower visual-cognitive
603 recognition; investigators focusing on the former may see no reason to consider specific snake
604 species, as they presumably all share visual cues unique to snakes that allow for rapid detection
605 and processing of emotionally significant information by primates (Isbell & Etting, 2017;
606 Lobue & Deloache, 2011; Van Strien & Isbell, 2017). If a snake shape represents a serious
607 threat, it is logical to assume that strong selection occurred for an innate general detection
608 mechanism for all snake-like stimuli occurred (Bertels et al., 2020; Ohman & Mineka, 2001).
609 However, whether for rapid detection or slower recognition experiments, the deficiency of tests
610 with primates facing different snake species is regrettable because more than 3,900 species of
611 snakes have been inventoried. Snakes exhibit an immense variety of body sizes, body shapes
612 and colour patterns (Allen et al., 2013). Some primates can differentiate dangerous from
613 harmless snakes (e.g. moor macaques, *Macaca maura*, Hernández Tienda et al., 2021) and
614 behave accordingly (Falótico et al., 2018). Besides, an encounter may be risky for the primate
615 (Adukauskiene et al., 2011; Foerster, 2008; Shine et al., 1998), but it may also be risky for the

616 snake, including venomous species (Boinski, 1988; Da Silva et al., 2019; Lorenz, 1971). Large,
617 potentially dangerous snakes have evolved an extended repertoire of warning signals to avoid
618 confrontation and minimize the use of defensive strikes (Glaudas & Winne, 2007).

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

625

626 *Limitations and caveats*

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

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

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

646

647 **Conclusions**

648 Abundant ecological evidence shows that predation attempts on modern primates are largely
649 exerted by other animals than snakes. Yet, by heavily focusing on snakes and neglecting the
650 role of carnivorans and raptors in the evolution of primate traits (Isbell, 2006, 2009; Kawai,
651 2019), SDT-related studies are unable to determine whether fear responses are snake-specific
652 or anti-predator more generally. The biases we show here suggest that studies focusing on
653 predator detection might benefit from including a more comprehensive list of predators and
654 primates and should focus on phylogenetic gaps in the primates tested.

655

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