



Calls for concern: Matching alarm response levels to threat intensities in three Neotropical primates

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ABSTRACT

Various species of animals maximise energy gained through foraging by minimising excessive energy spent on nonessential activities. Avoiding predation is key for maximising an individual's lifespan, as well as that of its kin; however, anti-predation behaviours can be energetically costly. We investigated the relationship between the potential threat levels by predators, pseudo-predators, and non-predators, and the subsequent energetic cost of behavioural reactions to these threats, in the white-bellied spider monkey (*Ateles belzebuth*), golden-backed uacari (*Cacajao ouakary*), and red-nosed cuxiú (*Chiropotes albinasus*). We analyzed a total of 270 interactions across three independent field studies of the three primate species. Our results revealed significant differences in the behavioural response to predators and non-predators for both *C. ouakary* and *C. albinasus*, but not for *A. belzebuth*. In terms of risk-categorized behaviours, response to predators differed from response to non-predators (being much more intense and energy intensive), while there was no difference in response to predators versus pseudo-predators. Thus, response to potential predators represents an integral part of the time-management and defence strategies of two of the three studied species, and should be integrated into future studies of primate responses to varying levels of predation threat.

1. Introduction

Primates often have to travel substantial daily distances to find appropriate food (Wrangham et al., 1993; Norconk and Kinzey, 1994; Di Fiore, 2003; Boyle et al., 2009; Shaffer, 2013), often at great energetic cost (Grove, 2012; Markham and Gesquiere, 2017). It is widely thought that species with extensive daily ranges should minimize wasteful temporal or energetic expenditures, to optimize their time and energy budgets (Barton et al., 1992; Pontzer et al., 2014). While it is unlikely that a group of primates will be subject to frequent events of successful predation (Treves, 1999a; Ferrari, 2009; Barnett et al., 2017), predation attempts are quite common, as are encounters with pseudo-predators, which are species that look sufficiently similar to actual predators to elicit anti-predator reactions in potential prey (Mourthé and Barnett, 2014). Indeed, frequency of pseudo-predator encounters may far exceed those with true predators (Barnett et al., 2018). The responses of primates to predators vary, and can include reactive (e.g., alarm calling, chasing, mobbing, attacking or flight: Barnett et al., 2011; Ferrari, 2009;

de Luna et al., 2010; di Fiore, 2002; Miller and Treves, 2007; Mourthé, 2011; Mourthé and Barnett, 2014) and crypsis-related behaviours (e.g., concealing, freezing: Guilford and Dawkins, 1991; Miller and Treves, 2007; Zuberbühler et al., 1997). Given that such predation-avoidance behaviours expend resources, both in terms of energy spent conducting them, and feeding opportunities lost while they are in process, it is expected that primates should optimize the time and energy they invest in responses based on the level of predation risk (Brown et al., 1999; Blanchard et al., 2011; Isbell, 1994). Doing so avoids unnecessary energy expenditure.

Primates give alarm calls that distinguish between predator types, thereby eliciting behaviours appropriate for avoiding predation (e.g., ground-hunting felid, tree-based snake, aerial raptor: Zuberbühler, 2000, 2001; Fichtel and Kappeler, 2002; Crockford and Boesch, 2003; Arnold and Zuberbühler, 2006). In addition, individuals that optimally manage their energy budgets might be expected to respond appropriately to the level of threat that a potential predator represents, in terms of proximity and apparent hunting intent (Creel and Christianson, 2008;

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Embar et al., 2011). Thus, the energetic costs of different antipredator reactions should match the level of threat. Alarm calls are expected to be used against low-level threats (to communicate to the predator that it has been seen: Zuberbühler et al., 1999), hiding against mid-level threats, and fleeing and mobbing against more intense threats (Ydenberg and Dill, 1986). Such analyses should also include the possibility that brief-but-intense actions (e.g., branch thrashing), might be energetically equal to repeated low-cost actions (e.g., head turning when tracking a potential assailant).

However, matching energetic investment in reactions to threat intensities has been less frequently tested than predictions relating to threat types (Stankowich and Blumstein, 2005; Embar et al., 2011). In addition, it is possible that specific sex-age classes might engage more frequently in predation reactions. For example, in a study of red-nosed cuxiús (*Chiropotes albinasus*), Barnett et al. (2018) found that adult males engage in defensive actions against predation threats more than adult females. One of the factors complicating thorough investigations of such phenomena is that both predation and predation attempts are rarely observed, even in long-term field studies of wild animals (Goodman et al., 1993; Isbell, 1994; Hill and Dunbar, 1998; Stanford, 2002; Ferrari, 2009; Gursky-Doyen and Nekaris, 2007). Therefore, sample sizes are often small.

To overcome sample-size and rarity effects, we pooled data from independent field studies (Mourthé and Barnett, 2014; Barnett, 2010; Barnett et al., 2017, 2018) to investigate whether the intensity levels of antipredator responses of three Neotropical primate species (white-bellied spider monkey, *Ateles belzebuth*; golden-backed uacari, *Cacajao*

ouakary; and red-nosed cuxiú, *Chiropotes albinasus*) matched predator-threat levels. All three species are large- (*Ateles*: 8 kg on average; Smith and Jungers, 1997) or medium-bodied (*Cacajao*: 2.9 kg; *Chiropotes*: 2.8 kg) species that exhibit fission-fusion social ecology (Aureli et al., 2008) and range widely in the upper canopy of Amazonian forests (Barnett, 2010; Barnett et al., 2017, 2018; Mourthé, 2014). Moreover, these three species share the same suite of arboreal and aerial predators (e.g., *Panthera onca*, *Harpia harpyja*, *Spizaetus tyrannus*, and *Boa constrictor*: Martins et al., 2005; Barnett et al., 2011, 2017, 2018; Mourthé and Barnett, 2014) and see tables 1A, 1B, 1C. Given that individuals of the primates have extensive daily ranges (and thus a high daily energetic output), we expected that these species would be extremely sensitive to means of optimizing overall energetic expenditure. As energy spent on predator avoidance forms part of the general energy budget (Grove, 2012; Markham and Gesquiere, 2017), we hypothesized that the energy investment spent by individuals is proportional to the intensity of the threat level imposed by potential predators. Using a combined data set that consisted of reactions of the primates to varying intensities of threat level, we tested the following predictions: (i) reactions of primates will vary with threat risks; and (ii) energetic expenditure will vary with threat risks. Because risk of predation is often lower in larger-bodied primates (Cheney and Wrangham, 1987; Stanford, 2002; Zuberbühler and Jenny, 2002), we expected a lower rate of reaction to potential predators by *Ateles* than by *Cacajao* and *Chiropotes* (Mourthé and Barnett, 2014).

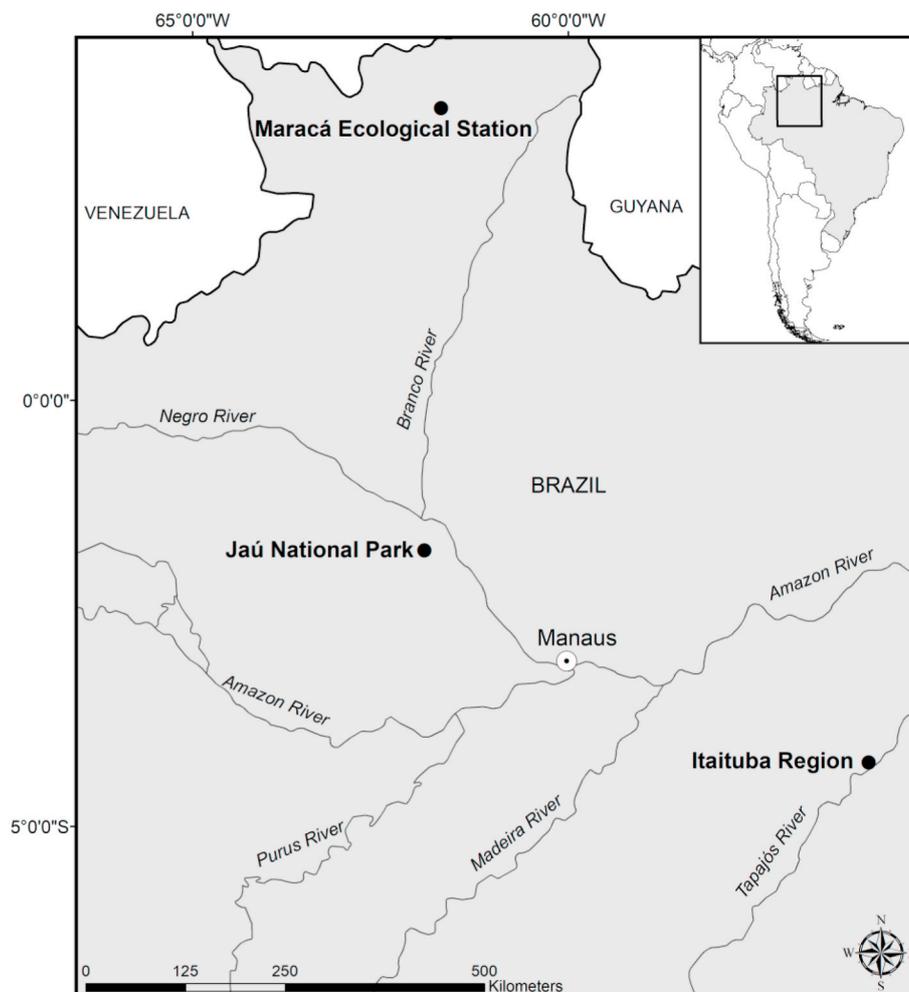


Fig. 1. Map of the Brazilian Amazon, showing the study area locations.

2. Methods

We compiled data from field studies of *Ateles belzebuth* at Maracá Ecological Station, Roraima State, Brazil (Mourthé, 2014; Mourthé and Barnett, 2014); *Cacajao ouakary* at Jaú National Park, Amazonas State, Brazil (Barnett, 2010); and *Chiropotes albinasus* in the region of Itaituba, on the mid-Tapajós river, Pará State, Brazil (Barnett et al., 2017, 2018, Fig. 1). All studies were conducted under license from the appropriate Brazilian environmental authorities (IBAMA and ICMBio), and obeyed the strictures therein. Field-methods were non-invasive, and no animals were harmed, handled, or manipulated during the course of the studies.

We used the primate's point-of-view approach (Barnett, 1995) when ranking levels of primate reactions to predators. We divided levels of reaction into four risk categories: low, medium, high, and extreme (Supplementary Material - Table 1), based on the likelihood that the actions would summon the attention of a predator to any individual primate, or the likelihood of that animal getting hurt or killed. We operationalized the limit for "close" as 15 m, the distance that previous studies estimated that predators induced alarm reactions in these three primate species (Mourthé and Barnett, 2014; Barnett et al., 2018).

We considered energetic expenditure from the point of the animal's energy budget, so that activities resulting in an immediate expenditure of large amounts of energy, such as fleeing, were placed in the high-energy category. Concealment by individuals was also considered a high-energy response, since remaining still yet vigilant means an individual is unable to feed or rest (Supplementary Table 1). We divided threats into four levels, based on the following criteria: extreme (predator attack), high (predator or pseudo-predator close), medium (predator or pseudo-predator distant-but-approaching) and low (predator or pseudo-predator distant, non-predator in any position; Supplementary Table 1).

2.1. Statistical analysis

We analyzed the probability of the primate responses towards different potential predators using a cumulative logistic model (Montopoli and Anderson, 1991), with the class variable "species" (*Ateles*, *Cacajao*, *Chiropotes*) and its interaction with the variable "type of predator" (predator/non-predator/pseudo-predator). We added modeled probabilities over the lower ordered values (lower than the observational mean). We evaluated the models using Akaike information criterion (AIC). Then, we computed least-mean squares for the class variable "species", to compare behavioural reactions among the three species.

A Chi square test was used to evaluate significance of response. We then used an odds ratio score test to estimate the proportional odds assumption. This estimation quantifies how strongly the presence/absence of property A is associated with the presence/absence of property B in a given population (e.g., Morris and Gardner, 1988). We used an analysis of maximum likelihood estimate (AMLE) with an

association of predicted probabilities and observed responses (APPOR) to classify behavioural reactions according to three threat-intensity categories (low, medium, and high). The fourth category (extreme: fatal attack) was not included because the number of recorded events ($n = 3$) was too small for statistical analysis. We then used odds ratio estimates and profile-likelihood confidence intervals (Chen, 1994) to estimate the effect of "predator/non-predator/pseudo-predator" species encounters. We used SAS, version 9.4 (SAS Inst. Inc. Cary, NC), with 95% confidence limits, for all analyses.

3. Results

We recorded 270 events (*Ateles*, $n = 12$; *Cacajao*, $n = 155$; *Chiropotes*, $n = 103$). All three species encountered non-predators more frequently than actual predators (Table 1).

Behavioural reaction intensity was influenced by predator type ($p < 0.001$). *Cacajao* and *Chiropotes* showed significant reactions in their response to predators (*Cacajao*: $p < 0.001$, mean intensities = 0.50; *Chiropotes*: $p < 0.001$, mean intensities = 0.40) versus non-predators (*Cacajao*: $p < 0.001$, mean intensities = 0.099; *Chiropotes*: $p < 0.001$, mean intensities = 0.20). In contrast, *Ateles* demonstrated no significant difference in response to predators versus non-predators (Fig. 2).

In terms of risk-categorized behaviours, reactions were riskier (i.e., high probability that the animal is hurt or killed) when directed towards predators than non-predators ($p = 0.031$), while the behavioural response to predators and pseudo-predators was not significant ($p = 0.052$). We found that there was a predator effect (the extent of the likely threat) on the energetic cost of a reactive response ($p < 0.001$). The energetic cost of such a response to a predator differed significantly from a response to a non-predator ($p = 0.044$). However, there was no significant difference in the energetic costs of responses to predators and pseudo-predators ($p = 0.073$).

The most frequent reaction to a non-predator species was a low-level threat response (Fig. 3), which is in accordance with the low-medium level of threat such species represent. Low-medium and high-level threat responses were most often aimed at predator species (Fig. 3). For pseudo-predators, the frequency of responses to medium-level threats was moderately elevated in comparison to non-predators, and high threat response frequencies were slightly elevated (Fig. 3).

4. Discussion

Primates adjust their behavioural reactions to predator threat levels in two ways. First, primates assess whether or not the species in proximity is a predator. Second, if the species is considered a predator, primates assess the apparent threat level the potential predator appears to pose, and then respond accordingly. Although we recorded examples of the most extreme threat level (fatal attack), as well as the reactions of the survivors of the attacks (Barnett et al., 2011), the number of such events observed ($N = 3$) was too small for statistical analysis. However,

Table 1

Primate encounters categorized by threat level to the encountering animal. Percentages are within parenthesis.

Primate species	Number of encounters by threat type (%) [*]				
	Non-predators (low threat)	Pseudo-predators: distant (medium threat)	Pseudo-predators: close (medium threat)	Predators: distant (medium threat)	Predators: close or attempting predation (high threat)
<i>Ateles belzebuth</i> (N = 12) [†]	4 (33.3)	1 (8.3)	1 (8.3)	5 (41.8)	1 (8.3)
<i>Cacajao ouakary</i> (N = 155) ^{††}	117 (75.6)	20 (12.9)	12 (7.7)	5 (3.2)	1 (0.6)
<i>Chiropotes albinasus</i> (N = 103) ^{†††}	49 (47.6)	20 (19.4)	22 (21.4)	1 (1)	11 (10.6)
Total = 270	170 (62.9)	41 (15.2)	35 (12.9)	11 (4.2)	13 (4.8)

NOTES:^{*}Pseudo-predators classified as predators due to primate reaction, not due to actual threat represented, following Mourthé and Barnett (2014); [†]All records reported in Mourthé and Barnett (2014); ^{††}154 interactions reported in Mourthé and Barnett (2014), and one in Barnett et al. (2011); ^{†††}94 interactions reported in Barnett et al. (2018), of which two were potential attacks, and nine reported by Barnett et al. (2017) that were all predation attempts.

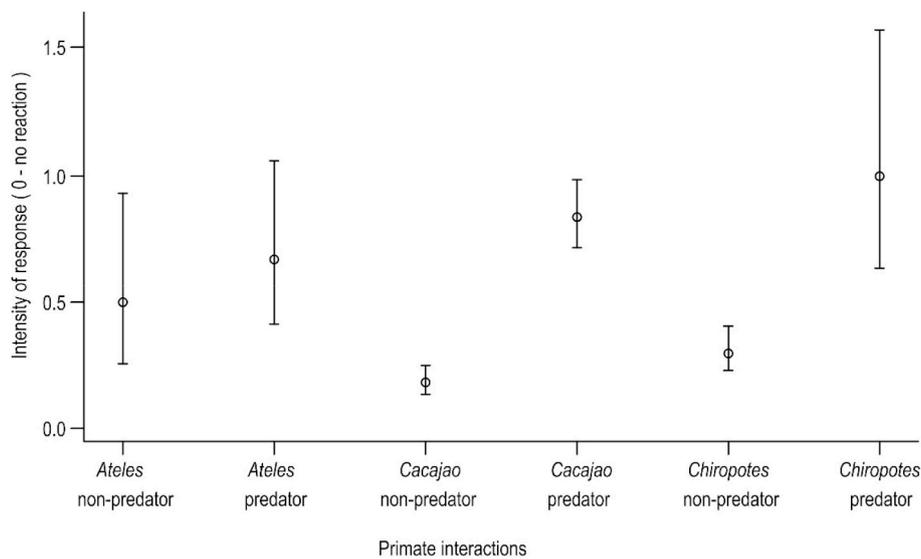


Fig. 2. Least square means for intensity of response to predator and non-predator species, with 95% confidence limits represented by vertical bars.

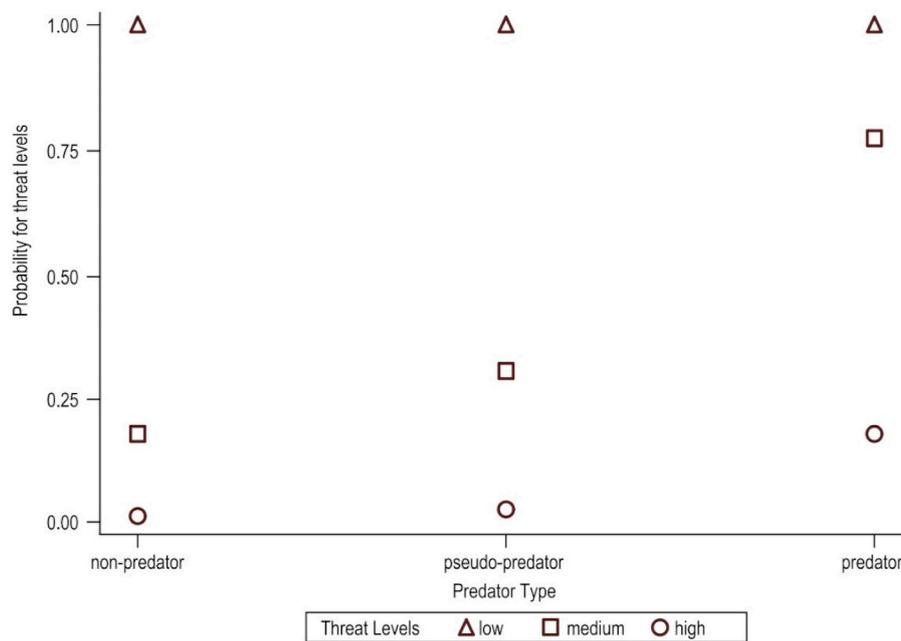


Fig. 3. Predicted cumulative probabilities for behavioural reactions to various threat levels (no, low-medium and high) for different predator types (non-predator, predator, and pseudo-predator).

the behaviours recorded under such extreme circumstances did fit the predicted trends: following the fatal attack, the survivors grouped closer together and continued to give alarm calls, often for an extended period (e.g. Barnett et al., 2011). Overall, we found that the behavioural reactions to pseudo-predators were similar to those reactions to predators; however, after the concrete identification of the attacker, the final phase of the reaction was less intense.

No matter if distant or close, in our study pseudo-predators (e.g., vultures, large hawks, toucans and large ducks) were consistently considered by the primates as medium-level threats. Inherent in the concept of pseudo-predators is that these animals do not truly pose a danger, but the primates treat such pseudo-predators as threats because they are evolutionary adapted to respond to a series of stimuli which most often denote a predator. Providing that encounters with pseudo-predators do not consistently compromise individual energy budgets,

such behavioural responses to non-predators presenting some of these stimuli can be adaptive responses (Dawkins and Krebs, 1979) since there are times when the risks are real. For example, neither tapirs (*Tapirus* spp.) nor vultures (Cathartidae) are predators of the three primate species we studied, but primates have been recorded responding to these animals as if they were threats (Mourthé and Barnett, 2014). From the perspective of the primates, responding to non-dangerous animals with energy-expending avoidance behaviours is more likely to enhance survival, compared with putting oneself at risk with an unanticipated encounter with a real predator. There is also an ontogenetic component: juvenile capuchin monkeys (*Cebus capucinus*) respond broadly to several potential predators, including harmless species, while they learn to make appropriate categorizations (Meno et al., 2013a).

The capacity to match the behavioural response to threat level may not depend solely on the individual assessment of the situation, but also

be mediated by communication between group members, previous history of contact with predators (Lima and Dill, 1990), and the size of predator and prey species (Mourthé and Barnett, 2014; Libório and Martins, 2013). Such matching may have a visual component (Tomasello et al., 1998), or occur because many species have graded calls that reflect threat intensity, often via an alteration of volume, pitch, or repetition rate (Fedurek and Slocombe, 2011; Ducheminsky et al., 2014). Both *Ateles* and *Cacajao* produce louder calls when responding to high-level threats, compared to low-level threats (Matsuda and Izawa, 2008; Mourthé, 2011; Mourthé and Barnett, 2014). In *C. ouakary*, threat escalation is communicated by the transition from "chok" to "cheng" alarm call. The former accompanies all events of low-level concern, while the latter is only heard in situations that are highly threatening (Barnett, 2010; Bezerra et al., 2011). Similar results have been reported for baboons (Fischer et al., 2001), lemurs (Fichtel and Kappeler, 2002), and chimpanzees (Crockford and Boesch, 2003).

Other variables may also influence the match between behavioural reactions and threat levels, such as social learning (e.g., previous contact with predators, presence of conspecifics), and size of species involved (Griffin, 2004; Mourthé and Barnett, 2014; Libório and Martins, 2013; Meno et al., 2013a, b). Although reactions to predators can be innate (Herzog and Hopf, 1984), both social (e.g., witnessing predation) and individual (e.g., being the subject of an attack) experiences can influence individual learning processes relating to predation risk (Griffin, 2004). Moreover, large species are attacked less often than smaller ones. To cope with a wider range of predators, smaller species show more sensitive, fine-tuned reactions to potential predators. Consequently, *Ateles* have fewer potential predators and respond less often to them than do smaller species (Di Fiore, 2002), including the *Cacajao* and *Chiropotes* in the current study (Mourthé and Barnett, 2014).

Field studies on behavioural reactions to predators are important in furthering the general understanding of the biological significance of species' behavioural responses to predation (Griffin, 2004). We acknowledge that the categories for threat, risk, and energy expenditure used in the current study were subjective, as was our allocation of each of the behavioural events to these categories. However, studying predation in the wild is not an easy task because predation events, or even predation attempts, are rare and unpredictable, and their effects may be difficult to detect in social animals such as primates (Ferrari, 2009).

In order to achieve sufficient sample sizes for analysis, we pooled our data from independent studies of three primate species, and then summed the reactions across time and space. Yet, levels of predation (and predation risk) may differ depending on the habitats used by the animals (Colishaw, 1997), influencing the resultant behaviours in each, since animals can adjust threat-sensitive anti-predator behaviour to the background level of predation risk (Helfman, 1989; Di Fiore, 2002; Helfman 1989; Brown et al., 2006). This difficulty can be overcome with studies that take into consideration predation-risk variables, such as differential vegetation density, and hence both prey and predator detectability (Embar et al., 2011).

Primates appear to be risk-sensitive animals, fine-tuning their reactions to potential predation events in a way that minimises unnecessary energy expenditure. Moreover, risk and threat assessment vary depending on size, so larger primates react in a generalized way, while smaller species react more selectively and spend more energy on behaviours with medium to high levels of risk. Low-risk threats, however, result in generalized low-energy reactions.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper. We wish to confirm that there are no known conflicts of interest associated with this publication and there has been no significant financial support for this work that could have influenced its outcome. The data used were taken partly from previously

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.actao.2020.103646>.

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Ethical approval

We confirm that we have given due consideration to the protection of intellectual property associated with this work and that there are no impediments to publication, including the timing of publication, with respect to intellectual property. In so doing we confirm that we have followed the regulations of our institutions concerning intellectual property.

Data evaluated in this study are based only on observation of three primate species. We neither physically manipulated any of the animals, nor ever interrupted their behaviour during the course of the fieldwork observations.

Informed consent

We confirm that the manuscript has been read and approved by all named authors and that there are no other persons who satisfied the criteria for authorship but are not listed. We further confirm that the order of authors listed in the manuscript has been approved by all of us.

We understand that the Corresponding Author is the sole contact for the Editorial process (including Editorial Manager and direct communications with the office). He is responsible for communicating with the other authors about progress, submissions of revisions and final approval of proofs. We confirm that we have provided a current, correct email address which is accessible by the Corresponding Author and which has been configured to accept email from: tomanekpa@seznam.cz.

Author contribution

Pavel Tománek wrote the text and conducted the statistical analysis; Italo Mourte collected field data on *Ateles* and commented on the text; Sarah Boyle edited the text and made statistic suggestions; Adrian Barnett collected field data on *Cacajao*, helped form the initial idea, and edited text.

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