



Research

Cite this article: Thuppil V, Coss RG. 2013 Wild Asian elephants distinguish aggressive tiger and leopard growls according to perceived danger. *Biol Lett* 9: 20130518. <http://dx.doi.org/10.1098/rsbl.2013.0518>

Received: 5 June 2013

Accepted: 16 August 2013

Subject Areas:

behaviour

Keywords:

antipredator behaviour, Asian elephant, sound playbacks, growls

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Electronic supplementary material is available at <http://dx.doi.org/10.1098/rsbl.2013.0518> or via <http://rsbl.royalsocietypublishing.org>.

Animal behaviour

Wild Asian elephants distinguish aggressive tiger and leopard growls according to perceived danger

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Prey species exhibit antipredator behaviours such as alertness, aggression and flight, among others, in response to predators. The nature of this response is variable, with animals reacting more strongly in situations of increased vulnerability. Our research described here is the first formal study to investigate night-time antipredator behaviour in any species of elephants, Asian or African. We examined the provocative effects of elephant-triggered tiger and leopard growls while elephants attempted to crop-raid. Tigers opportunistically prey on elephant calves, whereas leopards pose no threat; therefore, we predicted that the elephant response would be reflective of this difference. Elephants reacted similarly cautiously to the simulated presence of felids of both species by eventually moving away, but differed markedly in their more immediate behavioural responses. Elephants retreated silently to tiger-growl playbacks, whereas they responded with aggressive vocalizations, such as trumpets and grunts, to leopard-growl playbacks. Elephants also lingered in the area and displayed alert or investigative behaviours in response to leopard growls when compared with tiger growls. We anticipate that the methods outlined here will promote further study of elephant antipredator behaviour in a naturalistic context, with applications for conservation efforts as well.

1. Introduction

Antipredator behaviour refers to a suite of behaviours that prey species exhibit in response to predators including alertness, aggression, flight and vocalizing, among others [1–3]. This antipredator response is reflective of the degree of predatory threat; animals respond more strongly to a more dangerous predatory species or to situations of increased vulnerability [4]. While these behaviours have been documented extensively in many mammals, they are virtually unexplored in Asian elephants (*Elephas maximus*).

Comparatively, more antipredator behaviour research has been conducted on African elephants (*Loxodonta africana*). McComb *et al.* [5] showed that, in African elephants, female family groups hearing lion-roar playbacks were able to identify situations that represented the greatest danger and those with older matriarchs were particularly adept at recognizing the specific danger presented by male (as opposed to female) lions. Other research on elephant risk assessment has shown that African elephants retreat and alarm call in response to playbacks of threatening African bees [6]. In contrast to these daytime playback studies, our research is the first empirical investigation of night-time elephant antipredator behaviour and the first to examine elephant differentiation of growls from two sympatric felid species posing differential predatory threats.

We investigated whether wild elephants could discriminate the aggressive growls of tigers and leopards. Tigers are known to opportunistically prey on elephant calves, whereas there is no mention, either in the literature or anecdotally, of elephants being a part of leopards' diets [7–9]. Elephants themselves produce

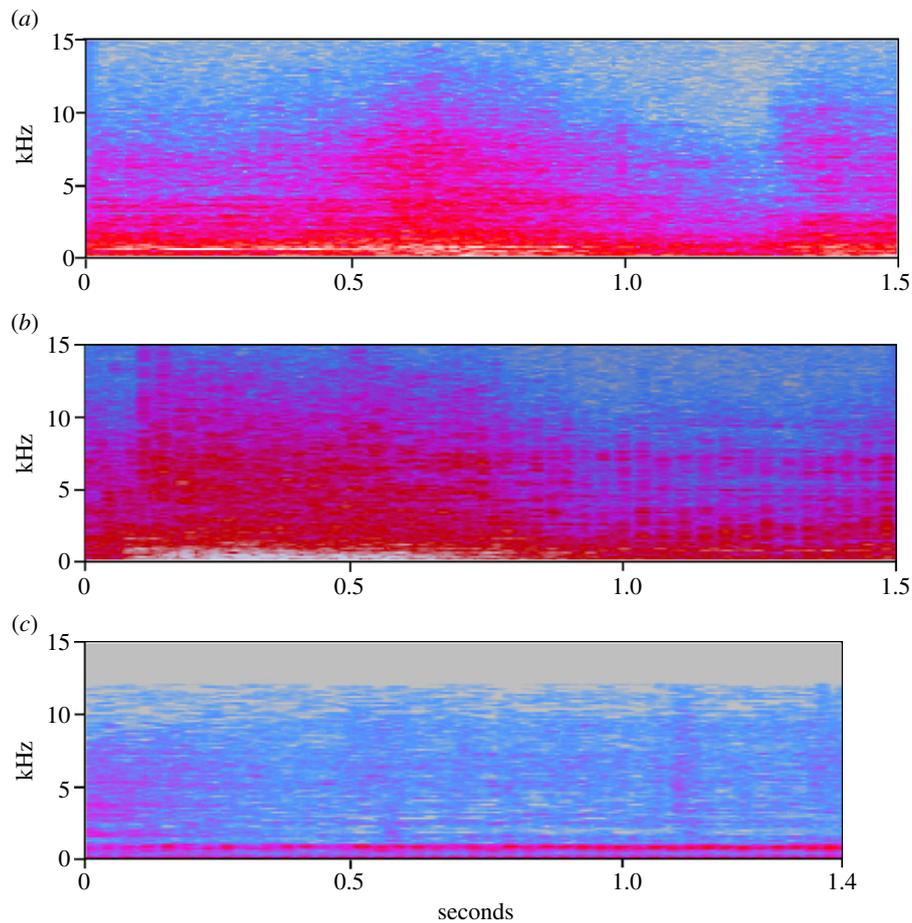


Figure 1. Spectrograms of the onset of (a) tiger, (b) leopard and (c) elephant growls. The leopard growl exhibits a greater energy distribution at higher frequencies than the tiger growl, yielding a raspier sound. The guttural pulse rate of the elephant growl approximates that of the leopard growl, a property that might facilitate growl discrimination. (Online version in colour.)

guttural growls while communicating with conspecifics [10,11] and may possess a broad, low-frequency acoustical-assessment ability useful for differentiating similar growls of other species. Therefore, we predicted that elephants would discriminate the acoustically distinct growls of tigers and leopards and would display stronger antipredator behaviour to the more dangerous tiger-growl playbacks.

2. Material and methods

From previous research, we had recordings of aggressive growls of a single tiger and leopard at the Bannerghatta Zoological Park, Bangalore, obtained using a Sennheiser ME 80 directional microphone coupled to a Sony TC-D5 PROII analogue recorder. To engender growling, both cats were agitated similarly when the keeper entered their cages and banged a stick repeatedly. We did not repeat this procedure with other individuals owing to the potential danger involved. The natural pauses in growling were used to split the growl playbacks into two exemplars each, with durations of 9 and 17 s and 21 and 35 s for the leopard and tiger, respectively. We digitized these growl recordings in 16-bit mode and 48 kHz sampling frequency for random playback by Blue Point Engineering 10-channel mp3 players. We used AUDACITY software to generate spectrograms of the onset of felid growls (figure 1).

We conducted field research near villages around Bandipur Tiger Reserve and Wayanad Wildlife Sanctuary in southern India. Playback growls were amplified by battery-powered 200 W PylePro speaker systems in water-proof enclosures positioned approximately 50 m ahead of where elephants triggered

the playbacks. Playback growls were produced at an intensity of 105 dB sound pressure level (SPL) at a distance of 1 m from the source. At a distance of 50 m, elephants heard these growls at intensities of 58–62 dB SPL. Elephants triggered these playbacks by tripping a Takex PB-60 TK active infrared beam positioned at a height of 1.85 m. Elephants encountered these playback systems along paths leading to crop fields and we assume that these elephants were similarly motivated to crop-raid.

We deployed this set-up simultaneously in three study sites from August 2010 to February 2011 and recorded a total of 26 incidents of elephants activating leopard- and tiger-growl playbacks. For the purposes of our analyses here, we have only included distinct individuals in their first encounter of the playback system, without any repeated playbacks. This corresponds to seven instances where elephants encountered tiger-growl playbacks and eight instances where elephants encountered leopard-growl playbacks.

We logged post-playback elephant movement paths on a Garmin eTrex device by tracking their footprints on the morning following a beam trip. From the point of beam trip, the difference of the compass bearing of the elephant's position at 25 m away and the compass bearing of the speaker provided a movement angle relative to the speaker. Elephant movements were categorized as toward, lateral and away, corresponding to movement angle ranges of 0–60°, 60–120° and 120°–180°, respectively. We used a 1-factor analysis of variance (ANOVA) test to determine whether there was a significant difference in movement trajectory between the two felid-growl categories. Upon discovering that the means were nearly identical, we used the inverse *F*-ratio (with reversed d.f.) statistic to determine whether the means were reliably similar.

Using high-definition infrared video cameras equipped with microphones, we individually identified elephants using

Table 1. Demographic breakdown of elephants that encountered our felid-growl playbacks. For herds, the leading elephant's behavioural response was considered for our analyses. All elephant encounters shown in this table are distinct individuals with no repeated playbacks.

no. instances	single male elephant	single female elephant	herd led by male elephant	herd led by female elephant	per cent of herds that contained more than 1 adult elephant	per cent of herds that contained non-leading adult males	per cent of herds that contained at least one juvenile elephant
leopard-growl playbacks	0	0	0	8	25	12.5	100
tiger-growl playbacks	1	3	1	2	66.7	33.3	66.7

morphological attributes, such as ear or tusk shape, and herd composition, if any. We aged elephants into adult/sub-adult or juvenile categories based on height [12]. Our video cameras also captured tigers and leopards at our study sites, ensuring that these playbacks represented naturalistic threats.

Owing to the constraints of passively recording elephant behaviour at night, we restricted quantification of behaviour to frequencies of occurrence instead of rates of behaviour reported in daytime studies [6]. To compare the interactions of frequencies of occurrence, we used multinomial log-linear analyses with maximum-likelihood estimations. We observed both individual elephants and herds of elephants encountering our playbacks (table 1). In situations of herds encountering our playbacks, we analysed the behaviour of the elephant leading the herd, usually an adult female, whose response always characterized the overall herd behaviour captured on video.

We used ANOVA to compare elephant reaction times, quantified in milliseconds (ms), from frame-by-frame mpeg4 video in increments of 33 ms. Elephant vocalizations that were recorded on video were categorized as trumpets and grunts (see electronic supplementary material) based on previous literature showing spectrograms and descriptions of dominant frequencies and durations [10,11]. Elephant grunts [13] have also been characterized as 'roars' [11]. In some instances where a herd of elephants triggered felid-growl playbacks, elephants also produced growls, which were captured by our video cameras. Using AUDACITY software, we have provided a spectrogram of an elephant growl for comparison purposes (figure 1).

3. Results

Initial elephant responses to all playbacks were nearly instantaneous (mean reaction time = 575 ms, range = 393–820 ms, $n = 11$). Similarly, elephants vocalized shortly after growl-playback onset (mean latency = 4.3 s, range = 2–10 s, $n = 7$), rendering natural differences in growl duration as unimportant because elephants vocalized prior to growl termination.

We recorded seven instances where elephants encountered tiger-growl playbacks and eight instances where elephants encountered leopard-growl playbacks. Elephants exhibited reliably similar movement angles away from both tiger- and leopard-growl playbacks ($1/F_{13,1} = 378.39$; $p < 0.05$). However, a comparison of more immediate elephant responses provides different insight into elephant antipredator behaviour.

Elephants vocalized in a reliably different manner to playbacks of tiger and leopard growls (likelihood ratio $\chi^2_1 = 15.90$; $p < 0.001$). They silently retreated in response to tiger growls and vocalized in all but one instance to the

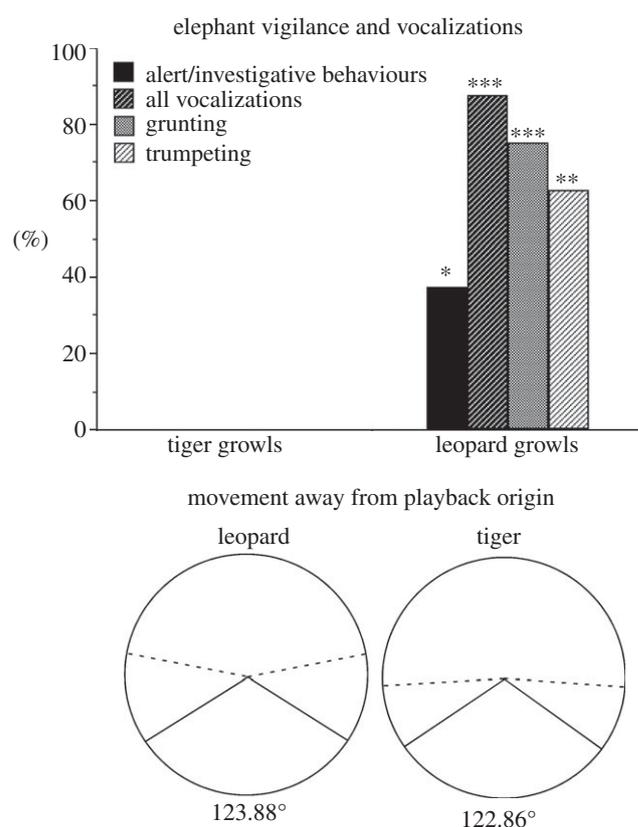


Figure 2. Elephant discrimination of felid-growl playbacks: $*p \leq 0.05$; $**p \leq 0.01$; $***p \leq 0.001$. Frequency comparisons of elephants displaying nearly immediate alert or investigative behaviours and vocalizing; delayed elephant movement trajectories away from the felid-growl playbacks are shown as means (solid lines) and standard deviations (dashed lines).

leopard growls (figure 2). Elephants were expected to linger less, and thus display a lower likelihood of alert or investigative behaviours to growls posing a greater threat. Indeed, a greater frequency of elephants displayed alert or investigative behaviours (likelihood ratio $\chi^2_1 = 4.43$; $p = 0.035$) to leopard-growl playbacks than to tiger-growl playbacks (figure 2). These behaviours included instances of elephants remaining stationary, searching for acoustic and olfactory cues, as well as elephants walking around and actively investigating the area.

The dominant vocalizations in response to leopard growls (figure 2), compared with the absence of vocalizing to tiger growls, were trumpets (likelihood ratio $\chi^2_1 = 8.51$; $p = 0.004$)

and grunts (likelihood ratio $\chi^2_1 = 11.193$; $p < 0.001$). Both trumpets and grunts are used by elephants in instances of alarm, disturbance and interspecific aggression [11]. After hearing an angry leopard maintaining its position rather than fleeing, some elephants exhibited conflicted behaviour as evidenced by their investigative circling, kicking dirt and even kicking a battery box powering the playback-trigger device. Such displays of redirected aggression are typical following adversarial encounters [14].

4. Discussion

While both felid-growl playback categories eventually evoked similarly cautious retreat away from the speaker systems, there were interesting differences in the more immediate elephant responses, indicating that elephants were able to discriminate tiger and leopard growls and perceived differing levels of threat from these two playback categories.

Elephants retreated stealthily from dangerous tigers, yet announced their presence by vocalizing, particularly through aggressive vocalizations, for instance trumpets, in the majority of leopard-growl playback situations. Elephants also did not linger in the area by displaying alert or investigative behaviours to tiger-growl playbacks. While there were some demographic differences in exposure to the two playback categories (table 1), we do not believe that this impacted our results. Both herds and lone elephants encountering tiger-growl playbacks responded identically by retreating quickly and silently.

Our results are consistent with findings that African elephants retreat significantly more quickly from clothes associated with dangerous Maasai hunters compared with ethnic groups that present lower levels of perceived threat [15]. Elephants did display aggressive behaviours when dangerous Maasai hunter clothes were displayed visually, but Maasai olfactory cues were absent. Bates *et al.* [15] concluded that the presence of clothes without accompanying olfactory cues indicated that the humans were no longer present in the area. Thus, a reduced level of threat perception allowed elephants to react more aggressively, as we propose happened when our elephants perceived lesser threat from leopard growls.

Research on elephant threat assessment can have other applications as well. For example, fences incorporating hives of dangerous African bees deterred crop-raiding attempting elephants from breaking through them [16]. Similarly, we implemented our research in a manner that mitigated nighttime crop-raiding [17]. Thus, we anticipate that future elephant antipredator behaviour research will generate useful applications for elephant conservation in addition to providing insights into how the world's largest terrestrial animals assess threats across their myriad habitats.

Acknowledgements. We thank A. Pittet, R. Johnson and S. Joshi for providing electronics assistance and R. Sukumar for hosting our research at his field research station. We thank D. Thiwary for logistical support and our assistants Arun, Madhan, Rajesh, Sudhakar and Sunil. We thank the Karnataka and Kerala forest departments for research permissions.

Funding statement. This research was financially supported by the U.S. Fish and Wildlife Service Asian Elephant Conservation Fund, the Rufford Small Grants Foundation and the University of California, Davis.

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