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# Scars of human–elephant conflict: patterns inferred from field observations of Asian elephants in Sri Lanka

*Chase A. LaDue* [A,E], *Rajnish P. G. Vandercone* [B], *Wendy K. Kiso* [C] and *Elizabeth W. Freeman* [D]

[A]Department of Environmental Science and Policy, George Mason University, 4400 University Drive, MS 5F2, Fairfax, VA 22030, USA.
[B]Department of Biological Sciences, Faculty of Applied Sciences, Rajarata University of Sri Lanka, Mihintale 50300, Sri Lanka.
[C]White Oak Conservation Foundation, 581705 White Oak Road, Yulee, FL 32097, USA.
[D]School of Integrative Studies, George Mason University, 4400 University Drive, MS 5D3, Fairfax, VA 22030, USA.
[E]Corresponding author. Email: cladue@gmu.edu

## Abstract

***Context.*** Human–elephant conflict (HEC) is a major threat to Asian elephants as humans and elephants are forced to share common resources. In Sri Lanka, human-dominated landscapes adjacent to protected areas promote high rates of HEC, especially in the form of crop-foraging by elephants. Crop-foraging can be dangerous to both elephants and humans involved in the conflict. Gunfire is a common way for human communities to deter crop-foraging elephants, and gunshot wounds are commonly described in this elephant population on necropsy.

***Aims.*** We sought to quantify and describe unique scar patterns among Asian elephants in a protected area, Wasgamuwa National Park, attributed to HEC.

***Methods.*** We identified 38 adult female and 64 adult male elephants and recorded the age class and body condition of each with established standards. Using photographs, we counted the number, position, and relative size of all scars on each animal.

***Key results.*** Male elephants had significantly more scars than did females, and for males, the number of scars increased progressively with age. Additionally, male elephants with higher body conditions had more scars. Finally, males tended to have more scars towards the head, especially at older ages.

***Conclusions.*** Differences in total scar counts between the sexes in this population imply that male elephants in this area more frequently engage in HEC than do females, following observations previously described in the literature. Furthermore, the fact that male elephants acquired progressively more scars as they aged, and that fatter elephants had more scars, indicates that previous exposure to HEC may not have been a deterrent for future events among these males, and potentially, crops served as valuable food sources for these animals. Finally, the changing body locations of these scars with age in males possibly shows plastic behavioural responses during crop-foraging or lower tolerance by farmers towards habitual crop foragers.

***Implications.*** These results emphasise the need for animal-based approaches to HEC mitigation. Similarly, conservation managers in Sri Lanka and other elephant range countries should investigate similar methods that estimate patterns of HEC to develop effective management strategies directly targeting animals most likely to engage in conflict.

**Keywords:** Asian elephant, body condition, crop-foraging, gunshot, human–elephant conflict, Sri Lanka.

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## Introduction

Asian elephants (*Elephas maximus*) are endangered throughout their range, threatened primarily by habitat destruction and degradation (Choudhury *et al.* 2008; Riddle *et al.* 2010; Menon and Tiwari 2019). As these problems persist, so too does the issue of human–elephant conflict (HEC), encompassing any sort of negative interaction between people and elephants that occurs over shared resource(s) (Barua *et al.* 2013; Wilson *et al.* 2015; Anuradha *et al.* 2019). Commonly, HEC takes the form of crop-foraging (also known as 'crop-raiding'), when elephants encroach on agriculture to forage on crops, usually a consistent and nutritious food source (Webber *et al.* 2011). Many human communities in areas where Asian elephants exist depend on small, stakeholder farms for subsistence (Woodroffe *et al.* 2005;

 

Gunawardhana 2018). So, while HEC jeopardises the safety and livelihood of these people, it also threatens the existence of an endangered species that is critical to ecosystem functions where they live (Blake and Hedges 2004; Campos-Arceiz and Blake 2011; Tscharntke *et al.* 2012).

Sri Lanka is one of the last bastions for Asian elephants. With between 6000 and 7000 elephants that comprise ~12–15% of the global population, it hosts among the highest concentrations of elephants in Asia despite the country's small size (Leimgruber *et al.* 2003; Choudhury *et al.* 2008; Fernando *et al.* 2011). Unfortunately, Sri Lanka is not immune to the HEC problem (Santiapillai *et al.* 2010; Fernando *et al.* 2011; Prakash *et al.* 2020); this issue is escalating only because humans occupy over 70% of elephant habitat on the island (Fernando *et al.* 2021), with 407 elephant and 122 human deaths occurring in 2019 owing to HEC, according to Sri Lanka's Department of Wildlife Conservation. Even in protected areas such as national parks, elephants are subject to the negative effects of HEC, as the barriers surrounding these areas are porous, if present at all. Currently, most elephant deterrents in Sri Lanka are short-term solutions, including electric fences, explosives and firecrackers and gunfire (Santiapillai *et al.* 2010; Fernando *et al.* 2011; Fernando 2015; Shaffer *et al.* 2019). Even though illegal hunting is thought to be rare throughout Sri Lanka, people have often used guns as elephant deterrents or for retaliation against crop foragers (Fernando *et al.* 2011). It is common for elephants in areas of intense HEC throughout Sri Lanka to die from these events, and injuries among elephants are routinely observed (LaDue *et al.* 2021). Long-term solutions and mitigation strategies for HEC are urgently needed in Sri Lanka and other Asian elephant range countries to address this growing problem.

Numerous short-term approaches to counteracting HEC exist. Perhaps the most obvious strategy is to sequester elephants into protected areas, or at least areas away from human activity, by using physical fences to prevent elephant movement (Fernando *et al.* 2008; Kioko *et al.* 2008; Wilson *et al.* 2015). These fences are often used in conjunction with other deterrents, such as chili peppers, lights, beehives, or metal strips that elicit negative sensory responses (Osborn 2002; Wiafe and Sam 2014; Ngama *et al.* 2016; King *et al.* 2017; Von Hagen *et al.* 2021), and these structures may also be applied separately as repellents (Fernando *et al.* 2008; Zimmermann *et al.* 2009; Santiapillai *et al.* 2010; Le Bel 2015). Relocation or culling of 'problem' elephants commonly involved in HEC has also been implemented in various locations with limited or no success (van Aarde *et al.* 1999; Fernando *et al.* 2012; Pinter-Wollman 2012). These strategies seek to separate elephant and human activity at a broad scale. However, all of these address only the symptoms of HEC and not the systemic issues associated with this complex problem (Mumby and Plotnik 2018). Instead, others have suggested animal-based approaches that integrate information about how known individual differences among elephants, including health (Evans and Harris 2012; Lynsdale *et al.* 2017), reproduction (Freeman *et al.* 2009; Crawley *et al.* 2017), behaviour (Poole 1989; Poole and Moss 1989; Freeman *et al.* 2010; McComb *et al.* 2011), cognition (Bates *et al.* 2008; Foerder *et al.* 2011; Plotnik *et al.* 2011) and personality (Lee and Moss 2012; Yasui *et al.* 2013; Seltmann *et al.* 2019), affect the propensity of these animals to engage in HEC.

Animal-based approaches to HEC show promise, as they focus on addressing the motivational states of elephants engaged in conflict (Shaffer *et al.* 2019). Long-term, evidence-based HEC solutions should also consider both the temporal and spatial variation of the habitats in which elephants live, and intrinsic properties of the crop-foraging elephants, because these factors influence the propensity for elephants to engage in HEC. For example, many studies have indicated that male elephants are more likely to feed on crops than are females (Sukumar and Gadgil 1988; Campos-Arceiz *et al.* 2009; Ekanayaka *et al.* 2011; Prakash *et al.* 2020; Fernando *et al.* 2021). Male elephants are unique because they undergo a periodic reproductive condition called 'musth' that reflects the nutritional status of the animal (Jainudeen *et al.* 1972; Dickerman *et al.* 1994). Musth is energetically costly to sustain, and males that remain in musth longer may earn more breeding opportunities with females (Hollister-Smith *et al.* 2007; Rasmussen *et al.* 2008). Therefore, there may be strong evolutionary motivation for males to turn to human crops as a reliable, nutritious food source while they are in musth or as they prepare to transition into musth. Males in musth often exhibit erratic behaviour more frequently, making them an even larger threat to the safety of people they live around (Sukumar 1989). Additionally, male elephants are plastic in their behaviour, adopting novel strategies to acquire resources critical for survival and reproductive success and making them exceptionally good crop foragers (Srinivasaiah *et al.* 2012; Chiyo *et al.* 2014; Srinivasaiah *et al.* 2019). Understanding how male elephants in particular navigate human-dominated landscapes should be a research priority for addressing HEC (AsERSM 2017). This process depends on understanding the extent to which various elephant demographics (e.g. those based on sex, age class, and/or group size) engage in HEC, often requiring the development of non-invasive means to characterise interindividual variation in crop-foraging behaviour.

While observing elephants in a protected area in Sri Lanka, Wasgamuwa National Park, we noted the common occurrence of circular scars on elephants, similar in appearance to scar tissue resulting from surface abrasions or lesions. The scars we observed each measured between 5 and 15 cm in diameter, and they were located in unique patterns over the bodies of each elephant, serving as reliable distinguishing features among elephants. We presumed that most of these scars were incurred through gunfire, a common HEC deterrent in the region, as bullets and/or pellets are found inside many of elephants with these scars on necropsy (C. Jayasinghe, Veterinary Services, Sri Lanka Department of Wildlife Conservation, pers. comm.). Other causes for these scars were cautiously excluded because of unique properties of the elephants in Sri Lanka. For instance, it is highly unlikely that even a few of these scars resulted from sparring incidents. Female Asian elephants do not have tusks, and although most male Asian elephants possess large tusks that can be used in male–male competition, male elephants in Sri Lanka are an exception; only about 5% of adult male elephants have visible tusks, owing to genetic drift and/or historical hunting pressures (Hendavirtharana *et al.* 1994; Kurt *et al.* 1995; Santiapillai *et al.* 1999; Santiapillai and Wijeyamohan 2013). Similarly, we assumed that vegetation could not have caused the scars, because no plants (e.g. those with large thorns) exist in Wasgamuwa that could leave behind lesions in the thick skin of elephants (Green *et al.* 2007). Finally, we did not suspect that these were pathological, because they were exceedingly common among adult elephants of both sexes. Therefore, it stands to reason that elephants that engage in HEC more often should have more scars. In Kenya, human-caused wounds and scars on elephants are more prevalent during economic hardships, when pressure to hunt or retaliate against elephants is high (Wittemyer 2011). We hypothesised that the scars in this population of Asian elephants may serve as permanent indicators of their experience with HEC, potentially aiding in the development of tailored HEC mitigation strategies towards the specific elephants that are most active in the conflict.

The objective of the study was to describe the prevalence and patterns of scars among male and female Asian elephants observed in a protected area in Sri Lanka. By testing predictions of inter-individual variation in HEC that would be expected on the basis of sex and age differences, we aimed to validate these scars as useful tools to monitor patterns of HEC. Presumably, the distribution of these scars within and among individuals is indicative of how often certain demographics of elephants engage in HEC and the strategies they use to forage on crops. We predicted that scars would be more common on male elephants, with older elephants having more scars than younger elephants. Additionally, we expected that elephants that had higher or fatter body conditions, perhaps as a result of a heavier reliance on human crops, also would exhibit more scars. Taken together, we hypothesised that the patterns of scars on the elephants in our study would also reflect predictions, and support other studies on the propensity of certain elephants (e.g. male elephants, older/larger elephants) to engage in HEC.

## Materials and methods

### *Study site*

We observed elephants at Wasgamuwa National Park, in the Central and North Central provinces in the dry zone of Sri Lanka (Fig. 1). Wasgamuwa is one of the largest national parks in Sri Lanka, comprising 370.62 $km^2$ of grasslands and dry evergreen forests. Fieldwork took place during the dry season in the region, between December 2018 and April 2019, with a mean $\pm$ s.d. daily temperature of 29.9°C $\pm$ 5.6°C during this period. The park is open daily to tourists from 0600 hours to 1800 hours, although tourism is generally low, with a mean $\pm$ s.d. daily tourist load of 18.0 $\pm$ 17.3 vehicles on the days included in the present study (data obtained from the Department of Wildlife Conservation, Sri Lanka). A simple electrified wire fence encloses the park, which is further surrounded primarily by crop-based agriculture (primarily rice).

### *Sampling methods*

We conducted 57 days of observations from an open-air vehicle on roads located throughout the park, rotating between days of morning (0600 hours to 1200 hours) or afternoon (1200 hours to 1800 hours) observations. This resulted in over 300 h of field effort. Our daily driving plan alternated among three possible routes, which covered all accessible areas in the park. Time and other logistics permitting, we repeated a complete circuit multiple times each day in the park.

We continued driving until coming to an elephant or a group of elephants. Then, we stopped the vehicle and surveyed all visible elephants. For each adult elephant encountered (here, estimated to be older than 10 years old), we took photographs of both sides of the body (when possible) and recorded the elephant's sex. For photography, we used a Nikon D60 DSLR camera fitted with an AF-S VR Zoom-Nikkor 70–300 mm f/4.5–5.6G IF-ED telephoto lens (Nikon USA). We also estimated the age and body condition of the elephant by using visual standards (Arivazhagan and Sukumar 2008; Varma *et al.* 2012; Morfeld *et al.* 2016; Pokharel *et al.* 2017). For this study, we sampled only adult elephants 10 years of age or older, with age categories defined as 10–15 years, 15–20 years, 20–30 years, 30–40 years, and older than 40 years (Table 1). Body condition scores (BCS), reflective of the amount of body fat and muscle an animal has (Burkholder 2000), of each elephant older than 10 years old were recorded using visible differences in the relative shape and size of body protrusions caused by the ribs, backbone and pelvis, as reported by Pokharel *et al.* (2017) in wild Asian elephants. BCS criteria are listed in Table 2, with lower values indicating thinner body conditions.

On reviewing photographs of each elephant, we recorded scars estimated to be greater than 5 cm in diameter. Together, these scars were categorised as minor (between 5 and 15 cm in diameter) or major ($>$15 cm), and they were visually assigned to the head, mid-section, or rear of the elephant on a standardised diagram (Fig. 2). The head included the trunk, face and ears; the mid-section included the region from the neck to just below the breast (including the forelegs); and the rear included any body part behind the breast. For elephants sighted repeatedly ($n = 46$), we used photographs from the first 3 days of sightings for each elephant to determine the number, type and position of scars.

Our research protocols were approved by the George Mason University Institutional Animal Care and Use Committee (Project 1168839-1, #0383). Additionally, we obtained permission from the Department of Wildlife Conservation of Sri Lanka to perform this research (Permit WL/3/2/57/18).

### *Data analysis*

Only animals that had at least one complete side of their bodies photographed were included in the dataset, encompassing 38 adult females and 64 adult males from all of the elephants we surveyed. Our sample population was biased towards males, because this study was conducted concomitantly with another larger study on the dynamics of musth in male elephants. Some animals had only one side of their body reliably photographed ($n = 8$ for males, $n = 25$ for females). To include these partially photographed animals in the dataset, we analysed lateral differences in elephants that had both sides completely photographed, comparing the side that had more scars with the side that had fewer scars via a non-parametric Wilcoxon rank sum test. There was no significant difference in the total number of scars on either side in these well photographed animals ($W = 2146.5$, $P = 0.32$). Therefore, for the elephants in which only one side was photographed, we estimated the total number of scars for each elephant by simply doubling the number of scars on the known side.

We conducted pairwise Spearman's rank correlation tests to compare the number of major, minor and total (minor + major)

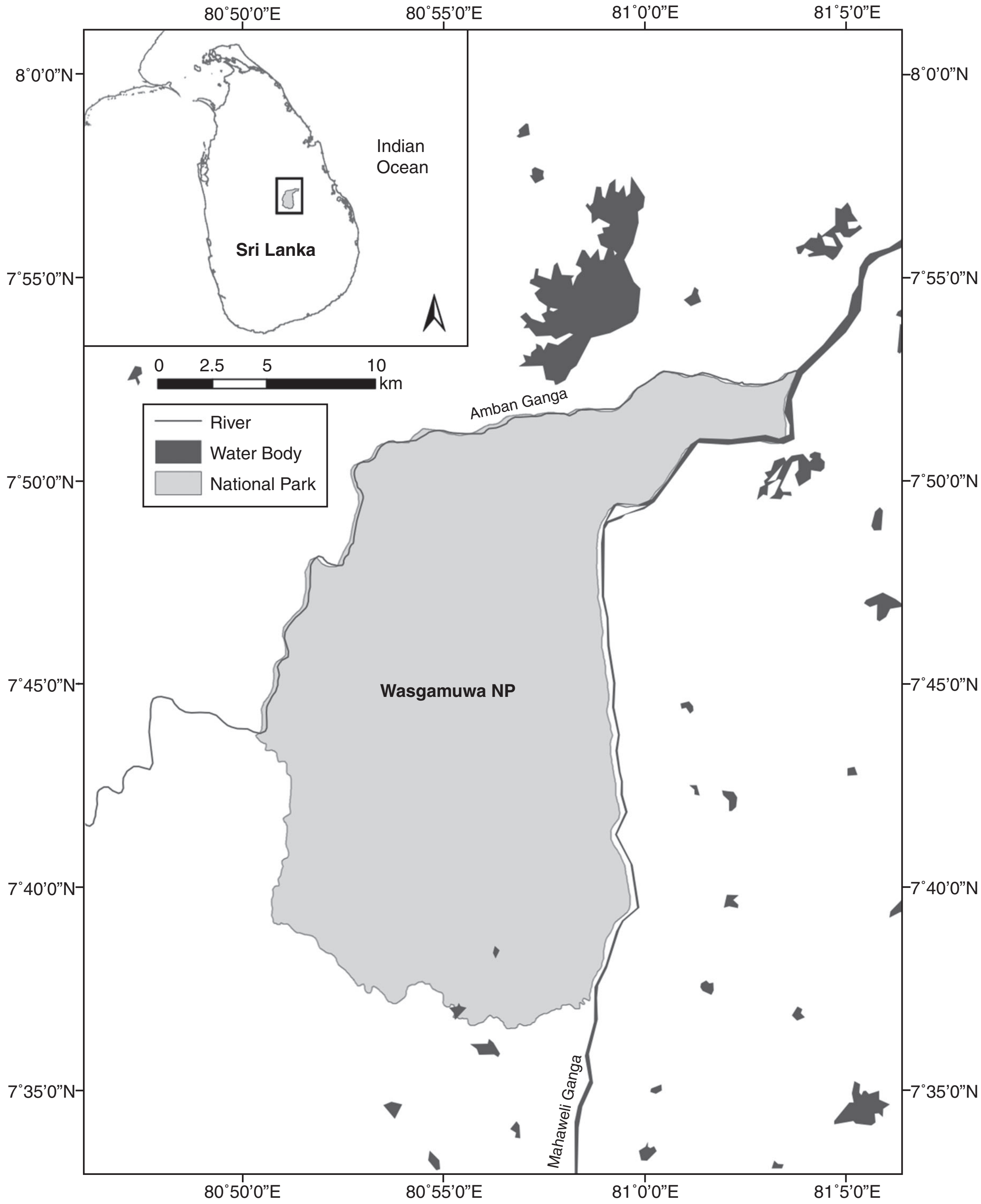


**Fig. 1.** Map of Wasgamuwa National Park, Sri Lanka.

scars for each elephant. All variable pairs were significantly correlated (major–minor: $S = 86910$, $P < 0.001$, $\rho = 0.509$; major–total: $S = 71578$, $P < 0.001$, $\rho = 0.595$; minor–total: $S = 1817$, $P < 0.001$, $\rho = 0.990$), so we simplified analyses by using the total number of scars as the response variable for each test described below. To identify relevant factors that influenced the number of scars, we conducted a factorial ANOVA, including age class, sex, BCS, and all of their interactions as possible explanatory variables. On discovering that any of these explanatory variables influenced the total number of scars, we analysed differences in each explanatory value with non-parametric Wilcoxon rank sum or Kruskal–Wallis tests, using pairwise

**Table 1. Standards used to estimate the age of elephants in the field, adapted from Arivazhagan and Sukumar (2008)**

| Age range | Height range (cm) | Other visual indicators |
|---|---|---|
| Females | | |
| 10–15 years | 197–213 | No depigmentation on ears/face |
| 15–20 years | 213–228 | Little or no depigmentation |
| 20–30 years | 228–238 | Light depigmentation; ears beginning to fold |
| 30–40 years | 238–240 | Apparent depigmentation; ear folds progresses from front to back of ear |
| >40 years | >240 | Prominent depigmentation; ear folds are complete and/or flattened |
| Males | | |
| 10–15 years | 217–235 | No depigmentation on ears/face; substantially shorter than other males |
| 15–20 years | 235–250 | Little or no depigmentation; beginning of accelerated growth |
| 20–30 years | 250–268 | Light depigmentation; prominent forehead |
| 30–40 years | 268–272 | Apparent depigmentation; some wear on ears |
| >40 years | >272 | Prominent depigmentation; obvious wear on ears |

**Table 2. Visual criteria used for body condition scores (BCS) for each elephant, adapted from Pokharel *et al.* (2017)**

| BCS | Ribs | Pelvis | Backbone |
|---|---|---|---|
| 1 | Individual ribs visible | Deep protrusion around pelvis | Backbone severely protruded |
| 2 | Three to four ribs visible | Pelvis clearly visible | Backbone obviously prominent |
| 3 | Rib(s) slightly visible | Slight depression in front of pelvis | Completely visible from head to tail |
| 4 | Not visible | Slightly flattened area in front of pelvis | Visible as ridge on back |
| 5 | Not visible | Not visible | Not visible |

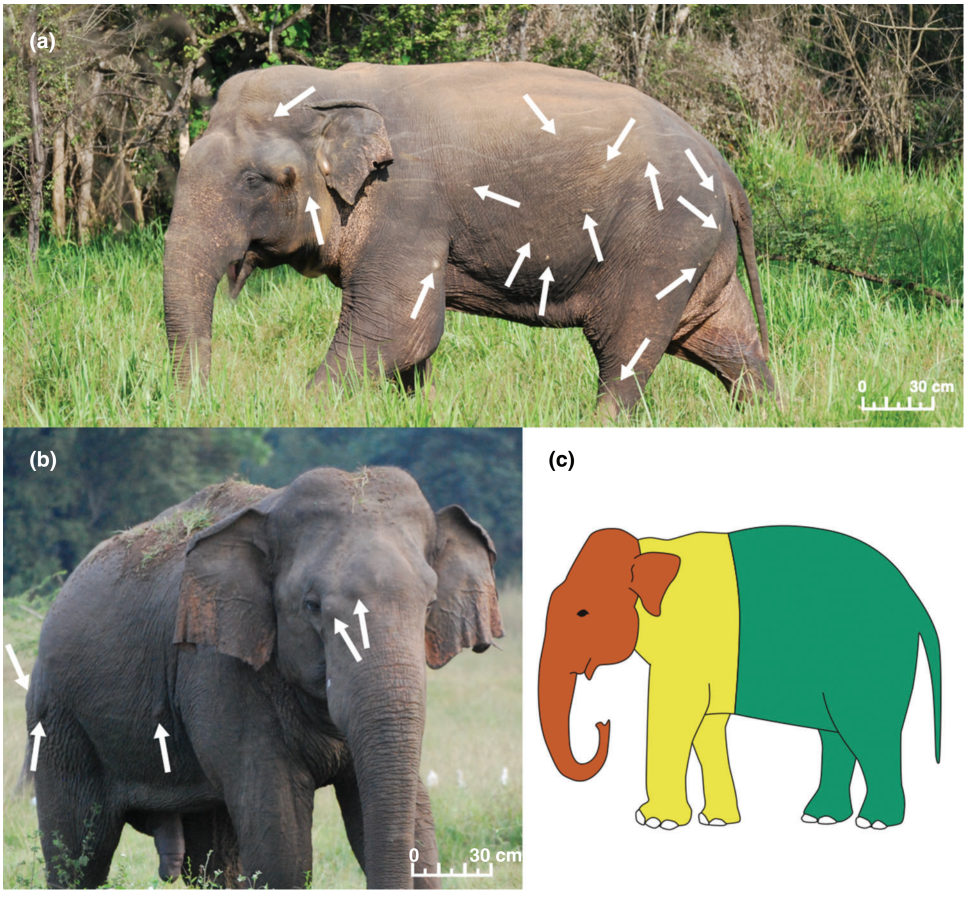


**Fig. 2.** (*a*) Arrows indicate positions of minor scars (between 5 and 15 cm) on a male Asian elephant. (*b*) Arrows indicate positions of major scars (>15 cm in diameter) on a male Asian elephant. (*c*) Scars were mapped into one of three regions on each elephant: head (red), midsection (yellow), or rear (green). Photographs by C. LaDue, scales are approximate.

**Table 3. Results of factorial ANOVA for differences in total number of visible scars, with age class (Age), sex, and body condition score (BCS), and their interactions, as potential explanatory variables**
Rows in bold indicate statistically significant factors ($P < 0.05$)

| Item | d.f. | Sum of squares | Mean squares | *F*-value | *P*-value |
|---|---|---|---|---|---|
| **Age** | **4** | **4564** | **1141** | **21.294** | **<0.001** |
| **Sex** | **1** | **3385** | **3385** | **63.171** | **<0.001** |
| **BCS** | **4** | **2526** | **631** | **11.784** | **<0.001** |
| **Age : Sex** | **4** | **1854** | **464** | **8.651** | **<0.001** |
| **Age : BCS** | **7** | **3920** | **560** | **10.450** | **<0.001** |
| Sex : BCS | 1 | 57 | 57 | 1.072 | 0.304 |
| Age : Sex : BCS | 2 | 13 | 6 | 0.118 | 0.888 |
| Residuals | 78 | 4179 | 54 | | |

Nemenyi tests when appropriate. Similarly, we analysed differences in the position of scars on the body on the basis of sex, and then on the basis of age class separately for males and females, with Kruskal–Wallis and Nemenyi tests. Statistical significance was set at $\alpha = 0.05$, with adjustments for multiple comparisons applied via Bonferroni corrections. We conducted statistical analyses and generated plots with R version 3.6.3 (R Core Team 2020), using the *tidyverse* package (Wickham *et al.* 2019).

## Results

Of the 38 adult female elephants in the study, 19 had visible scars (50.00%), and 53 of 64 males (82.81%) had scars. For the elephants that had scars, the average number of scars for females was 3.89 (90.54% of these were minor scars), and the average for males was 15.34 (92.50% minor). The maximum number of scars observed on a single elephant was 100 (on a male). Age, sex, and BCS, along with the interactions between age and sex, and age and BCS, significantly affected the number of scars visible on an elephant (Table 3).

Male elephants had significantly more scars than did females ($W = 510$, $P < 0.001$). Scars were apparent among adult males in the youngest ages categories, from 10 to 20 years, and males from older age groups had significantly more scars than did younger males ($\chi^2_4 = 36.795$, $P < 0.001$; Fig. 3). Significantly more scars appeared on female elephants between the ages of 20 and 30 years, but the number of scars did not increase with older age in these females ($\chi^2_4 = 9.611$, $P = 0.048$). Males of BCS 4 and BCS 5 (higher, fatter body condition) had more scars than did males of BCS 3 (lower, thinner body condition; $\chi^2_2 = 20.153$, $P < 0.001$); no male elephants were BCS 1 or BCS 2 (Fig. 4). However, no differences in the total number of scars were noted among female elephants of different BCS groups, although no females were observed with BCS 5 ($\chi^2_3 = 0.884$, $P = 0.829$).

For female elephants, very few scars were located in the head region (averaging 0.44% of all scars on each elephant) compared with the mid-section and rear ($\chi^2_2 = 17.276$, $P < 0.001$; Fig. 5). Males averaged proportionately more scars on their head (averaging 6.65% of scars) than females did, but for males, there were still proportionally more scars on the mid-section, and even more on the rear ($\chi^2_2 = 69.063$, $P < 0.001$). However, as male elephants aged, there were proportionally more scars located towards the anterior of the body than on the posterior part, and by age 40 years, there were proportionally more scars on the mid-section than on the rear (Fig. 6). No similar pattern was noted among females of different age classes, nor were any location relationships evident among different BCS categories for females or males.

## Discussion

The majority of adult elephants we sampled at Wasgamuwa National Park in north-central Sri Lanka had visible scars, with male elephants having significantly more scars than females. Scars were more numerous among older male elephants than among younger males; this pattern was not present in females. Additionally, male elephants with a higher BCS had more scars than did lower-BCS males; again, these BCS differences were not present in females. Finally, older male elephants tended to have more scars towards their head and chest, than did females and younger males, whose scars were located predominantly on the rear section of the body. The results of our study should be interpreted only in the context of the published literature on patterns of HEC, and we acknowledge that the implications of our dataset may be limited. We cannot be sure that all of the scars we observed were the result of HEC, but the unique aspects of our study site suggest that at least most of them were incurred from or around people. As mentioned earlier, most of elephants in Sri Lanka lack tusks that may cause injuries to conspecifics, and it is highly unlikely that the leafy vegetation in forested habitats around Wasgamuwa could have penetrated the skin of these elephants to leave behind a scar. Elephant skin can be up to 3.2 cm thick (Shoshani *et al.* 1982), and most scars we observed consisted of simple circular patterns inconsistent with injuries from conspecifics or vegetation, especially on the sides of the head and body. Even so, we should expect that both males and females would have similar scar patterns if they were caused by vegetation. Likewise, other skin pathologies similar to the scars we observed (e.g. lesions caused by bacterial or viral infections) would not be expected to be biased towards males, as indicated by the scars described here (Mikota 2006). We encourage readers to interpret these results with healthy caution, as future work is needed to confirm that the scars we observed were predominantly incurred during HEC (e.g. by observing elephant crop-foraging events directly, collecting more comprenehsive necropsy data on elephants in this population; C. Jayasinghe, pers. comm.; LaDue *et al.* 2021).

Taken together, our results support our initial hypotheses. First, male elephants had significantly more scars than females.

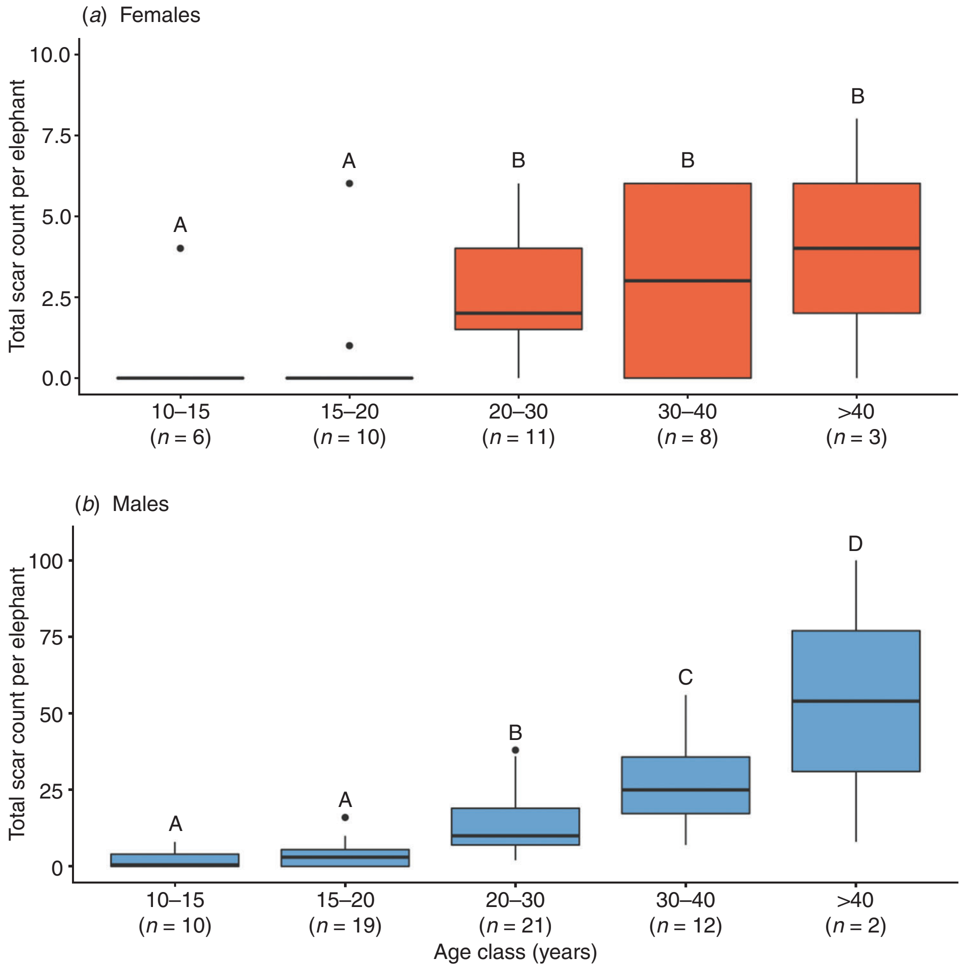


**Fig. 3.** Total scar count for (*a*) female and (*b*) male elephants of various age classes. Sample sizes (*n*) for each age class are given on the graph. Note different vertical axis scales for females and males. Female and male elephants were analysed separately, with letters indicating significantly ($P < 0.05$) different scar counts among age classes, as shown by Nemenyi tests. Thick lines inside the boxes indicate the median scar count for each age class, with boxes extending from the first to the third quartile; fences extend to 1.5 times the interquartile range. Circles show outliers beyond this range.

These results are not surprising, because they agree with other studies involving direct observations and accounts of crop-foraging elephants. For example, Campos-Arceiz *et al.* (2009) found that most HEC incidents in south-eastern Sri Lanka involved single or small groups of elephants, most of which were likely to be males. Further study in the same region of Sri Lanka indicated that 88% of crop-foraging incidents were instigated by male elephants (Ekanayaka *et al.* 2011). Surveys of Sri Lankan farmers throughout areas of high HEC indicated that male elephants are more apt to feed on crops, and that these incidents are common (Santiapillai *et al.* 2010). These sex-based patterns in elephant crop-foraging behaviour have been described by numerous other studies throughout Asia (Sukumar and Gadgil 1988; Sukumar 1989, 2003, 1990; Williams *et al.* 2001; Fernando *et al.* 2005) and Africa (Hoare 1999; Sitati *et al.* 2003; Osborn 2004; Chiyo *et al.* 2005; Ahlering *et al.* 2011; Kagwa 2011). In Sri Lanka, male elephants more frequently traverse areas of high human activity compared with females, so they may be more apt to engage in HEC, or perhaps they can be found in these areas because they are motivated to forage on crops (Fernando *et al.* 2021). Assuming the majority of scars recorded on the elephants were the results of HEC, our study offers indirect evidence of the propensity for male elephants to engage in crop-foraging. These incidents are often difficult to observe because they occur almost exclusively at night (Campos-Arceiz *et al.* 2009). Unfortunately, this also means that it can be impossible to accurately determine sex and/or age individuals in these settings, especially when male Asian elephants lack obvious distinguishing features such as tusks. Our results do not indicate that female elephants avoid crop-foraging (50% of adult females in this study had visible scars); instead we suggest that males may be the primary drivers of HEC in these instances. Further investigation will lend insight into whether these scars are prevalent among other elephant populations in Sri Lanka and elsewhere, and if so, this method may be useful in the process of identifying elephants most likely to be involved in persistent HEC.

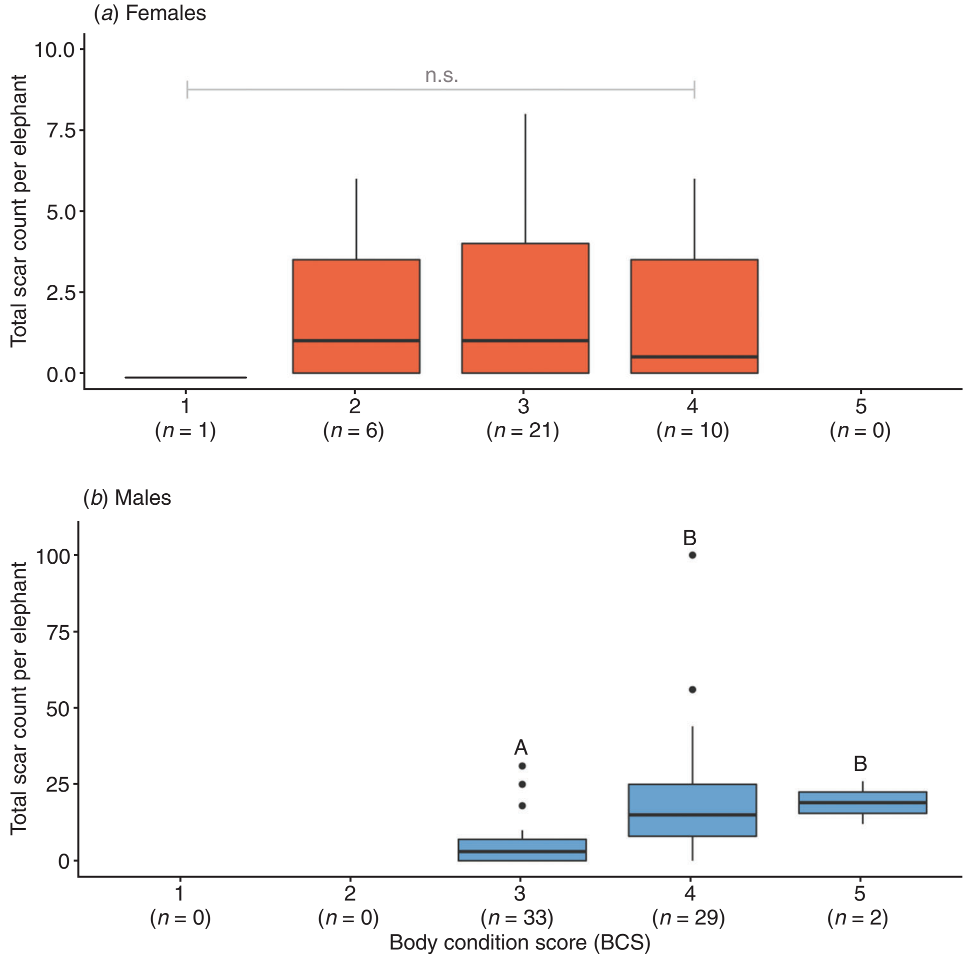


**Fig. 4.** Total scar count for (a) female and (*b*) male elephants of increasing body condition scores (BCS), with higher scores corresponding to fatter conditions. Sample sizes (*n*) for each BCS category are given on the graph. Note different vertical axis scales for females and males. Female and male elephants were analysed separately, with letters indicating significantly ($P < 0.05$) different scar counts between age classes, as shown by Nemenyi tests. n.s., no significant difference. Thick lines inside boxes indicate the median scar count for each age class, with boxes extending from the first to the third quartile; fences extend to 1.5 times the interquartile range. Circles show outliers beyond this range.

The fact that males acquired progressively more scars with age is also interesting, because it potentially indicates that previous negative encounters with people do not necessarily discourage future encounters. If gunfire was effective at deterring male elephants from foraging on crops, we would expect that one or a few exposures to gunfire would prevent further foraging events, and so, young males would have just as many scars as old males; this was not the case we observed. In contrast to males, females had few scars and did not appear to obtain more with age, potentially indicating that, compared with males, female elephants were deterred from agriculture by gunfire. Further longitudinal studies that track scars in this population will confirm or refute this conclusion, but this inference is supported by the social organisation of elephants (de Silva *et al.* 2011; de Silva and Wittemyer 2012). Mothers and other related females invest highly in offspring, with extensive parental care, low fecundity, and long interbirth intervals (Chelliah and Sukumar 2015; Lee and Moss 1986). On previous exposure to HEC, females may weigh the benefits gained through foraging on crops with the potential danger to their offspring. Alternatively, the dilution effect may put proportionally fewer females at risk during HEC incidents; because female elephants travel in groups, any single female is less likely to incur scars when foraging on crops, and this could explain why we observed fewer females with scars in this population. In contrat, males may be more likely to be hurt during HEC because they are solitary or part of much smaller groups (Campos-Arceiz *et al.* 2009). Perhaps both of these explanations are in effect, either of which is relevant for efforts to mitigate HEC. For instance, males may more readily habituate to non-lethal deterrents, challenging many of the current strategies implemented in Sri Lanka and elsewhere (Shaffer *et al.* 2019). Indeed, the cognitive complexity of elephants means that they easily habituate to novel stimuli,

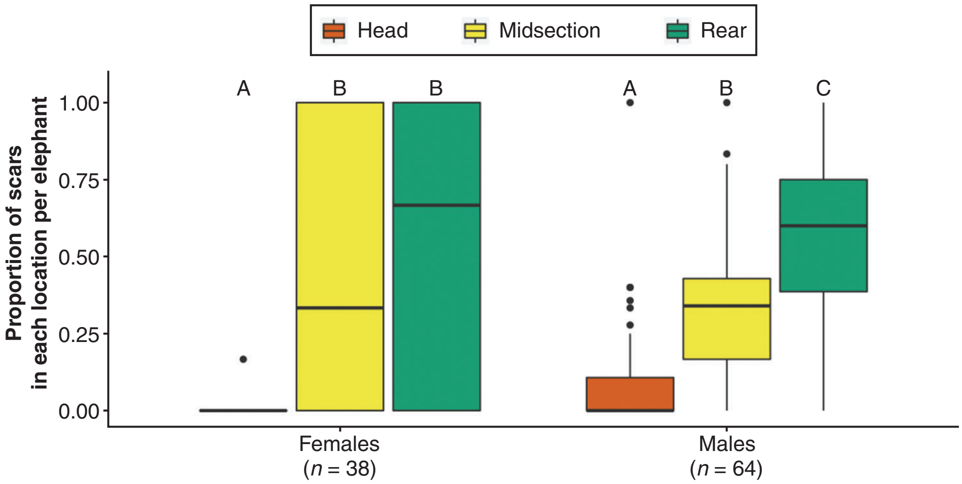


**Fig. 5.** Proportion of scars by body location for female and male elephants. Sample sizes (*n*) for each sex are given on the graph. Females and males were analysed separately, with letters indicating significantly ($P < 0.05$) different scar proportions between body locations, as shown by Nemenyi tests. Thick lines inside boxes indicate the median scar count for each age class, with boxes extending from the first to the third quartile; fences extend to 1.5 times the interquartile range. Circles show outliers beyond this range.

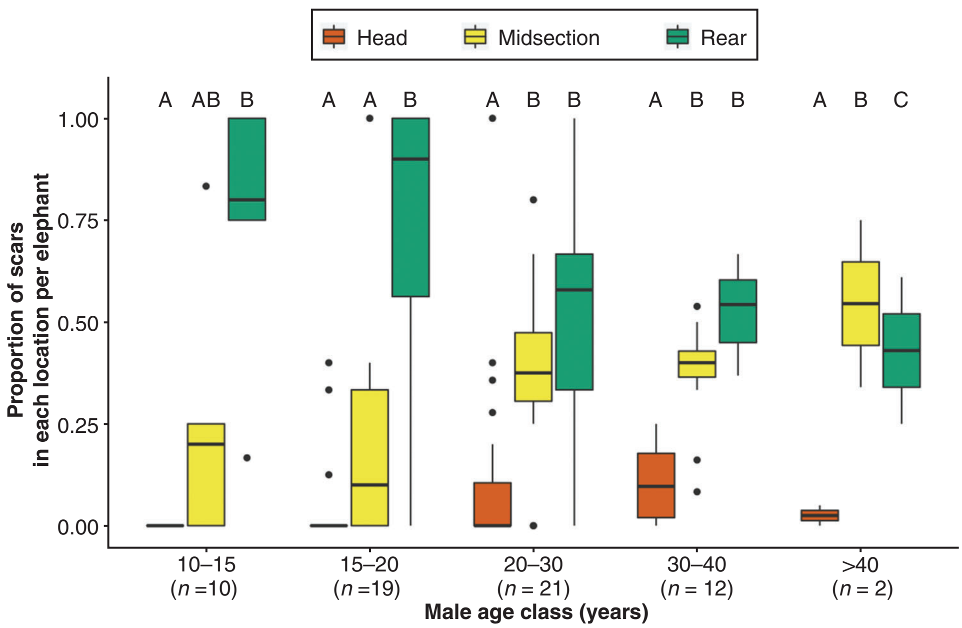


**Fig. 6.** Proportion of scars by body location for male elephants of various age classes. Age classes were analysed separately, with the sample size (*n*) of each age class given on the graph. Within each age class, letters indicate significantly ($P < 0.05$) different scar proportions between body locations, as shown by Nemenyi tests. Thick lines inside boxes indicate the median scar count for each age class, with boxes extending from the first to the third quartile; fences extend to 1.5 times the interquartile range. Circles show outliers beyond this range.

exacerbating the HEC problem (Goodyear and Schulte 2015; Mumby and Plotnik 2018; Barrett *et al.* 2019).

Male elephants, but not females, with a higher BCS also had more scars. Although we cannot causally link high BCS with increased crop-foraging behaviour, taken together with other studies, this suggests that males may rely on human crops to sustain their body condition. Elephants move between landscapes (including those dominated by human activity) to meet their nutritional needs (Sach *et al.* 2019; Sach *et al.* 2020). Additionally, even accounting for body size when young, male elephants that feed on crops can attain larger body sizes than those that do not (Chiyo *et al.* 2011). As described previously, one potential explanation for why male elephants benefit from an increased body condition, including those that engage in crop-foraging, is that it allows them to sustain musth and enhance their reproductive fitness with increased access to females (Chandrasekharan *et al.* 1992). This explanation would also account for the pattern of BCS-dependent scar counts that we observed in males but not females, justifying the risk of encroaching on human agriculture for males. Another explanation, not necessarily mutually exclusive, is that a higher body condition attained through feeding on crops helps mitigate the inherent stress from inhabiting human-dominated landscapes (Pokharel *et al.* 2019). Assuming that many of the scars we observed among the males in the present study were incurred during crop-foraging, the benefits accrued from foraging on nutritious crops outweighed any potential risks from encountering humans. If true, it makes the HEC problem even more troublesome for wildlife managers seeking sustainable, non-lethal solutions.

Proportionally more scars were located towards the front of male elephants than of females, a pattern that was amplified as males aged. In comparison to large female groups that include offspring, male elephants in Sri Lanka that are more solitary may be better able to occupy substandard, human-dominated habitats to acquire necessary resources (Fernando *et al.* 2021). Elephant behaviour is also plastic in changing environments. For example, Srinivasaiah *et al.* (2019) reported that uniquely stable, all-male groups form in a southern Indian elephant population outside of forested areas. Similar social strategies have not been observed in our population in Sri Lanka, but even temporary male–male associations outside of the musth period may facilitate information transfer that make them adept at feeding on crops (Evans and Harris 2008; Keerthipriya *et al.* 2020). Our results suggest that males adopt different crop-foraging strategies as a result of previous exposure; younger male elephants run away from gunfire (evidenced by proportionally more scars on the rump), whereas older males may face human threats head-forward. Another explanation for these male scar patterns is that farmers are less tolerant of habitual crop foragers; as males accumulate more crop-foraging incidents with age, local farmers may be more apt to fire gunshot towards more critical body regions in these older elephants (i.e. towards the head or thoracic region). Many people who live among elephants in Sri Lanka depend on guns to deter elephants from feeding on their crops (Fernando *et al.* 2011). However, it appears that the threat of gunfire is not necessarily a lethal risk to elephants, as scars were exceedingly common in this population. So-called ‘problem’ elephants commonly habituate to human presence when they do not feel threatened (Fernando 2015), and so, these older male elephants could have simply learned that the benefits of foraging on crops outweighed any potential risk from human retaliation. The fact that the relative position of these scars on the body appears to change over time implies that these elephants are active parties in HEC, adapting to human-dominated landscapes over time. If this is the case, dynamic HEC mitigation strategies are warranted that account for individual variation among elephants.

We are unsure of the significance between the major and minor wounds we observed. Personal firearms are strictly limited in Sri Lanka (people who kill elephants are most often prosecuted, even in cases of farmers defending property), but rifles and shotguns are the most commonly owned guns throughout the island (Edirisinghe and Kitulwatte 2010). It is possible that large wounds resulted from guns shot at close range and/or subsequent wound infection. Very few scars that we saw ($n < 5$) included visible exposed tissue, but all of these wounds were all large in size. Therefore, another possibility exists that the major scars were more recently acquired than smaller scars. Most of what we understand about wound healing in elephants comes from captive specimens under veterinary treatment (Mikota 2006). It is noteworthy that the elephants in this study apparently survived many gunfire incidents. Besides penetrating trauma to vital organs, skin infection resulting from gunfire may also cause more generalised infection or inanition in elephants, which can be fatal, especially in areas of the body where skin is thinner (Sutradhar *et al.* 2018). Still, the relative thickness and unique anatomy of the skin across much of the body seems to protect elephants from at least some gunfire (Luck and Wright 1964; Mikota 2006; Smith 1890; Spearman 1970). Following wound progression on wild elephants living in forests is difficult, and further research is needed to better interpret the complete meaning of our results. Beyond conservation and management importance, such studies would enhance the survival and well being of individual elephants inhabiting human landscapes and surrounding areas.

Despite their historical and cultural significance in Sri Lanka, public perception of elephants in modernity is increasingly negative on the island and is counterproductive to many conservation efforts (Bandara and Tisdell 2003; Fernando *et al.* 2005; Santiapillai and Wijeyamohan 2016). These sentiments are prevalent in human populations in which adequate compensation schemes for affected people are not present and as the magnitude of HEC incidents increase (Gunawardhana 2018; Anuradha *et al.* 2019). Some conservationists assert that true coexistence with defined landscapes for elephants and human activity via a segregation model is unfeasible (Fernando *et al.* 2021; Santiapillai *et al.* 2010). Instead, sustainable solutions should focus on building tolerance in these communities over shared land while acknowledging the significant hardships these people face on a daily basis by living with elephants (Jadhav and Barua 2012; Barua *et al.* 2013; Saif *et al.* 2020). This will depend on determining the factors that influence wildlife tolerance (including tangible costs and benefits), involving interdisciplinary research that combines social science with a strong emphasis on understanding the basic biology and ecology of elephants and other species (Kansky and Knight 2014; Kansky *et al.* 2016). These patterns vary temporally and spatially across the range of environments where Asian elephants are found.

The present study has contributed to these efforts by identifying elephants that are most apt to engage in HEC, including how these tendencies change over time. So as to understand how HEC varies geographically, the scar patterns we describe here may be a more effective way to conduct surveys around Sri Lanka than are other current methods. Considering the elephants’ perspective in HEC will involve taking into account individual variation in response patterns to ever-changing environments (Mumby and Plotnik 2018). Our results, combined with those of other studies, indicated that elephants differ in their propensity to be involved in various forms of HEC. Studies such as these emphasise how HEC mitigation strategies should adapt on the basis of the identities of elephants in a particular area. HEC is constantly evolving, necessitating dynamic conflict resolution plans that integrate both human and animal perspectives in real-time. Our study showed the changing responses of elephants to human landscapes, with contributing factors such as sex and age, by using a method that is efficient and requires few resources. By targeting and characterising the elephants, communities and landscapes involved in specific areas of concern, more effective management plans can be developed for an increasingly modernised world.

## Conflicts of interest

The authors declare no conflicts of interest.

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