



Note

Mortality Patterns of Asian Elephants in a Region of Human–Elephant Conflict

CHASE A. LADUE ¹, *Department of Environmental Science and Policy, George Mason University, 4400 University Drive, Fairfax, VA 22030, USA*

IMIRA ERANDA, *Department of Biological Sciences, Rajarata University of Sri Lanka, Mibintale—50300, Sri Lanka*

CHANDANA JAYASINGHE, *Department of Wildlife Conservation, Battaramulla—10120, Sri Lanka*

RAJNISH P. G. VANDERCONE , *Department of Biological Sciences, Rajarata University of Sri Lanka, Mibintale—50300, Sri Lanka*

ABSTRACT Many wildlife species suffer from human–wildlife conflict, especially crop-raiding. Long-term analyses of mortality patterns are needed to assess the efficacy of management strategies that address this issue. We report mortality patterns from necropsies of 498 Asian elephants from 2009–2018 in an area of northwestern Sri Lanka. Deaths were lowest in July and highest in October, a period of peak crop availability. Most (about 70%) deaths were human-related, and males were killed in these incidents more frequently than females. As gunshot deaths decreased, other forms of human-related deaths increased. Additionally, causes of death differed between districts, with more intentional human-related mortality observed in the district with the highest percent of protected land. These results highlight the importance of understanding the long-term spatial and temporal variation in wildlife mortality to effectively address human–wildlife conflict. © 2021 The Wildlife Society.

KEY WORDS Asian elephant, crop-raiding, *Elephas maximus*, human–wildlife conflict, mortality, necropsy.

Human–wildlife conflict (HWC) is widespread and involves a diversity of dimensions and species, ranging from granivorous invertebrates, rodents, and birds to large megaherbivores such as Asian elephants (*Elephas maximus*; Messmer 2000, Pimentel et al. 2005, Dickman 2010, Nyhus 2016, Fernando et al. 2021). Crop-raiding in particular threatens the existence of small, stakeholder farms adjacent to protected areas, motivating negative responses by people towards many threatened wildlife species (Hill 2018). These agricultural areas provide food security to many communities, but more broadly, crop-raiding has catastrophic global economic effects (Treves et al. 2007, Tscharrntke et al. 2012). Hence, mitigating HWC—and more specifically, crop-raiding, a form of HWC—is a priority for conservation. A number of strategies based on modifying the behavior of wildlife (Chelliah et al. 2010), and human behavior and perceptions (Lischka et al. 2020), have been used to mitigate HWC with varying degrees of success (Woodroffe et al. 2005, Chelliah et al. 2010, Branco et al. 2019). Often, their application occurs at limited spatial scales; hence, their effect on managing HWC more widely is unclear. The analysis of indices of HWC, such as human-induced mortality in wildlife over broad spatial and temporal scales, may offer insights into the effectiveness of mitigation strategies.

Human–elephant conflict (HEC), most often through crop-raiding, is a major impediment to the wellbeing of humans and elephants in elephant range countries. Asian elephants are threatened primarily by habitat loss and

fragmentation, exacerbating HEC in areas with growing human populations (Choudhury et al. 2008, Barua et al. 2013, Wilson et al. 2015, Anuradha et al. 2019, Menon and Tiwari 2019). At the same time that HEC threatens the safety and livelihood of local human communities, elephants are also critically important to the normal functioning of the ecosystems where they live (Blake and Hedges 2004, Campos-Arceiz and Blake 2011, Tscharrntke et al. 2012). Despite its small size, Sri Lanka hosts among the highest concentrations of Asian elephants of any range country, with a population between 6,000 to 7,000 elephants, about 12–15% of the global population (Leimgruber et al. 2003, Choudhury et al. 2008, Fernando et al. 2011, Department of Wildlife Conservation [DWC] 2012). Human–elephant conflicts are prevalent in Sri Lanka; humans occupy almost 70% of elephant range on the island and a large proportion of the elephant population lives outside the protected area system (Fernando et al. 2021). Sri Lanka's DWC recorded >360 elephant deaths and 100 human deaths in 2019 from HEC alone, with compelling evidence that this problem has increased dramatically over the past few decades (Santiapillai et al. 2010, Fernando and Pastorini 2011, Prakash et al. 2020). Therefore, there is strong motivation to find solutions to HEC that uphold human safety and ensure the preservation of this ecologically important species.

More recently across the Asian elephant's range, long-term solutions to HEC focus on evidence-based strategies that consider temporal and spatial variation. In Sri Lanka, HEC intensity is unevenly distributed; a recent survey indicated that the North Central and North Western

Received: 7 October 2020; Accepted: 5 January 2021

¹E-mail: cladue@gmu.edu

provinces—where agriculture is common and other forms of human development are more sparse—experience high HEC levels, placing the heavy burden of HEC on a relatively small subset of the human population (Gunawardhana 2018, Fernando et al. 2021). To address this issue, residents often rely on short-term, nonlethal methods such as noise, firecrackers, and spotlights to discourage crop-raiding with mixed success (Davies et al. 2011). Although illegal in Sri Lanka, lethal forms of human retaliation during HEC are common, with gunfire and poisoning most often reported. Throughout Sri Lanka, improvised explosives hidden among crops (i.e., hakkapatas) are increasingly prevalent too (Fernando et al. 2011). Human–elephant conflict mitigation in Sri Lanka is primarily carried out by the DWC, and includes activities such as establishing new protected areas, habitat enrichment, capture and translocation of problem animals, driving herds into protected areas, and establishing biological and electrical fencing around villages and protected areas (Perera 2009). Although a number of researchers have examined the effect of HEC on humans and elephants in Sri Lanka and the short-term success of these strategies (Campos-Arceiz et al. 2009, Santiapillai et al. 2010, Fernando et al. 2011, Gunawardhana 2018, Prakash et al. 2020), none have explored long-term regional and temporal variation of human-related elephant mortality in Sri Lanka. Such studies can elucidate spatial and temporal variation in mortality and their causes, and they also provide valuable insights into the efficacy of HEC mitigation strategies, which are fundamental to progress in this area.

In this light, the purpose of this study was to describe elephant mortality patterns over a 10-year period (2009–2018) in an area of Sri Lanka where HEC is prevalent. It is standard practice for DWC veterinarians to perform gross necropsy examinations on all elephants that have been discovered dead, providing the opportunity to understand temporal and regional variation in elephant mortality, including incidents that may be linked to HEC. We tested the hypothesis that certain elephant demographics are more often engaged in HEC as has been suggested by other studies and predicted that human-caused mortality would be more prevalent among male elephants, especially adults and subadults. Furthermore, we predicted that the prevalence and the causes of human-related deaths would vary temporally and geographically over the region (e.g., as a function of the amount of protected land vs. agriculture in an area), with mortality resulting from HEC being more common in agricultural areas during times of peak harvest. Additionally, we examined the hypothesis that various anthropogenic mortality events would be interrelated and predicted that increased or decreased frequencies of certain anthropogenic mortality events would affect the frequency of other human-related causes over time.

STUDY AREA

Sri Lanka's DWC recognizes 7 discrete wildlife regions on the island that correspond to distinctive landscape types and geographic features (Fig. 1). We analyzed mortality patterns

from 2009 through 2018 in the Northwestern Wildlife Region of Sri Lanka, which experiences high rates of HEC and includes parts of the Northern, North Central, and North Western provinces and all or part of each of the following districts (Department of Census and Statistics of Sri Lanka 2012, Prakash et al. 2020): Anuradhapura (North Central; 7,179 km²; 2012 human population = 860,757), Kurunegala (North Western; 4,702 km²; 2012 human population = 1,618,465), Mannar (Northern; 730 km²; 2012 human population = 99,570), and Puttalam (North Western; 3,072 km²; 2012 human population = 762,396; Fig. 1). The study area is a mosaic of human activity—mostly agriculture, principally rice—and protected landscapes. Most of the area is rural, but several major towns exist: Puttalam (127,844 people in 2012), Anuradhapura (50,595 people), Kalpitiya (64,908 people), Kurunegala (30,315 people), and Chilaw (24,712 people).

In this area there are 2 inter-monsoon seasons, March to April and October to November. The elevation of the Northwestern Wildlife Region ranges from 8 m to 120 m, and the forest cover is predominantly dry semi-evergreen forests, which is the characteristic forest type in the dry zone of Sri Lanka. There is, however, considerable variation in the floral composition across its geographic range (Dittus 1977, Vandercone 2011). In general, the vegetation is dominated by tree species such as the weera (*Drypetes sepiaria*), thampanai tree (*Mischodon zeylanicus*), kalukadumberiya (*Diospyros oocarpa*), kaluwara gas (*Diospyros ebenum*), and rayan tree (*Manilkara hexandra*; Dittus 1977, Vandercone 2011). Dominant fauna in the area include Asian elephants, water buffalo (*Bubalus bubalis* and *B. arnee*), spotted deer (*Axis axis*), sambar (*Rusa unicolor*), and leopard (*Panthera pardus kotiya*; although no wildlife species in Sri Lanka feed upon or are major competitors of elephants). The Northwestern Wildlife Region comprises 15,683 km² (~24% of the total area of Sri Lanka), of which 4,589 km² (29% of the region) is protected as a national park, sanctuary, or other similar area; few of these areas are fenced adequately, allowing for elephant movement across much of the area. This region is in Sri Lanka's dry zone, experiencing between 1,000 mm and 1,500 mm of precipitation annually (rainfall peaks at the height of the rainy season around Oct) and annual temperatures from 22.5°C to 30.0°C (Department of Meteorology, Sri Lanka). The 4 districts can be ordered from highest to lowest percent of land within the Northwestern Wildlife Region that is protected: Mannar (62.6%), Puttalam (44.7%), Anuradhapura (27.6%), and Kurunegala (12.8%). In 2011, the DWC censused 1,189 total elephants in the Northwestern Wildlife Region; this is thought to be the most accurate estimate of elephant density in the region available during the study period (DWC 2012).

METHODS

During the study period (2009–2018), DWC veterinarians conducted all necropsies assigned to the Northwestern Wildlife Region shortly after a deceased elephant was found with oversight by C. Jayasinghe. Research methods that

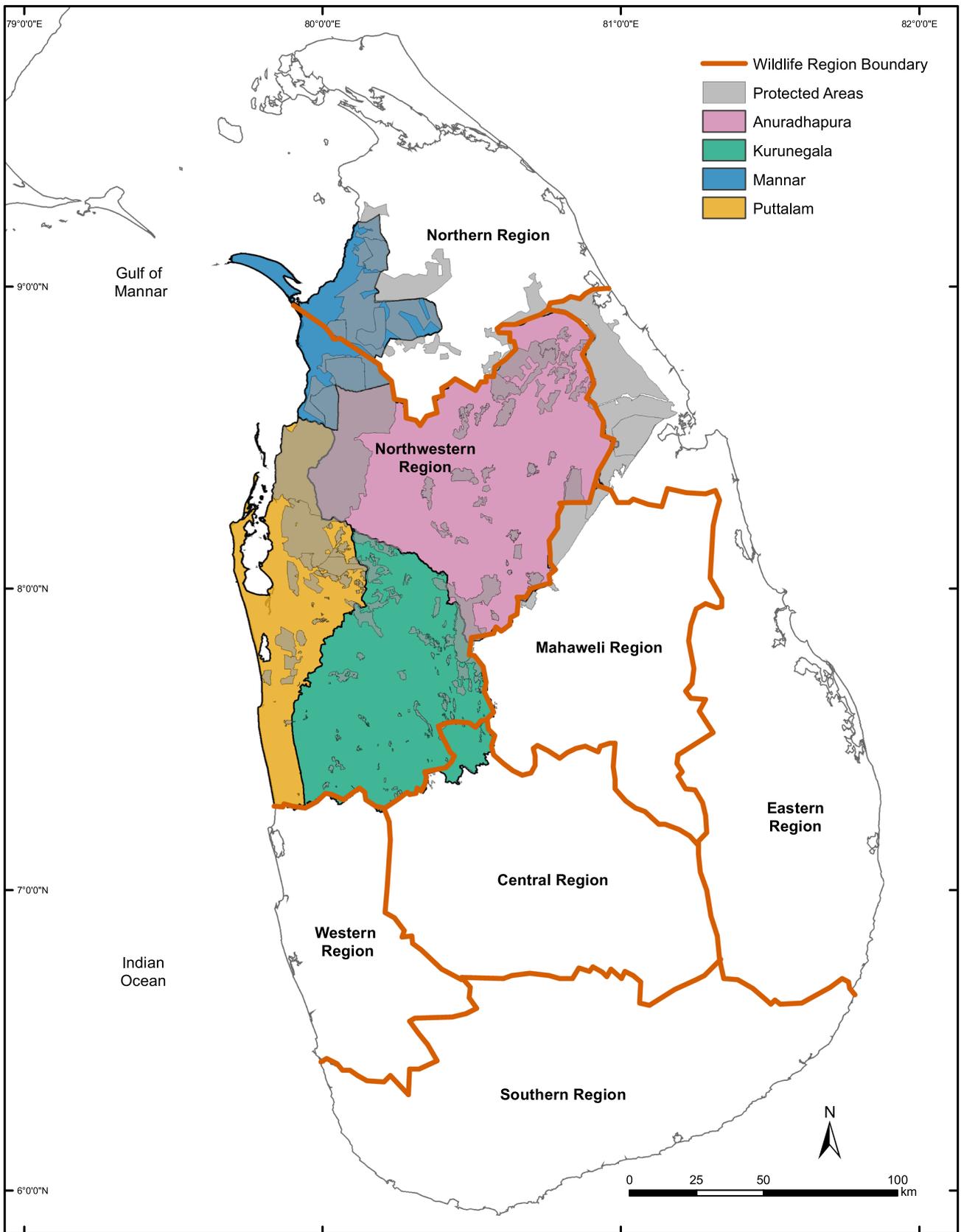


Figure 1. Sri Lanka with Department of Wildlife Conservation wildlife regions outlined in red (accurate as of Dec 2020). Districts at least partially included in the Northwestern Region are colored, with protected areas in these districts shaded in gray.

ensured animal welfare were approved by the DWC and Rajarata University of Sri Lanka (permit number WL/3/2/44/15); raw necropsy data are property of DWC (all of which is summarized here), available upon reasonable request. At each necropsy, veterinarians recorded the sex, height, estimated age, and cause of death (if known). We categorized causes of death into those intentionally caused by humans (gunshot, hakkapatas, or poisoning), unintentional deaths (electrocution, vehicle or train injury, trap or snare, or landmine), and natural deaths (e.g., septicemia, worm infections, physical injuries, dehydration, starvation). Human-related deaths were almost always easily identified upon gross examination, as were most forms of natural deaths. If cause of death could not be confirmed, unknown was listed in the report. On-site veterinarians estimated age based on several factors, including dentition, height, body condition, and depigmentation patterns (elephants tend to acquire more and larger areas of skin depigmentation as they age). If an estimate included an age range, we used the average of that range for our analysis. Additionally, we assigned each elephant to 1 of the following age categories: calf (<1 yr), juvenile (1–5 yrs), subadult (>5–15 yrs), adult (>15 yrs), or unknown (Arivazhagan and Sukumar 2008). When veterinarians could not estimate age, we used height-based criteria (Table 1).

We used chi-square tests to compare observed mortality patterns (e.g., by year, district, cause of death) to those expected by equal distribution; for comparisons between districts, we adjusted expected values for land area of each district. We used a *t*-test to compare age at death between males and females. We used an analysis of variance (ANOVA) to compare average mortality rates between months, with a Tukey's honest significant difference (HSD) *post hoc* test to reveal pairwise differences between months. Lastly, to test for changes in the frequency of mortality over time (including specific causes of death), we used Pearson's correlation tests. We set statistical significance at $\alpha = 0.05$. We carried out all analyses out using R (version 3.6.3; R Core Team 2020), using the package ggplot2 for plots (Wickham 2016).

RESULTS

We collated reports from gross necropsy examinations for the 498 elephants that died in Sri Lanka's Northwestern Wildlife Region districts during 2009–2018. The average annual mortality was 49.8 ± 13.3 (SD) elephants, with no

Table 1. Age and height criteria used to group Asian elephants into mutually exclusive age classes, based on Arivazhagan and Sukumar (2008).

	Age range (yrs)	Height (m)
Male		
Adult	>15	>2.5
Subadult	>5–15	>1.8–2.5
Female		
Adult	>15	>2.1
Subadult	>5–15	>1.8–2.1
Juvenile	1–5	1.2–1.8
Calf	<1	<1.2

apparent increasing or decreasing trend over 10 years ($t_8 = 1.840$, $P = 0.209$, $r = -0.432$). The number of deaths was higher in 2009 (60 deaths), 2011 (73 deaths), 2012 (61 deaths), and 2016 (62 deaths) than in other years ($\chi^2_9 = 32.080$, $P \leq 0.001$; Fig. 2). Monthly mortality rates differed ($F_{11} = 2.201$, $P = 0.019$); mortality was highest in October at the peak of the rainy season ($11.8\% \pm 3.5\%$ of annual deaths) and lowest in July ($5.1\% \pm 3.0\%$ of annual deaths; Fig. 3).

Sex was reported in 430 necropsy reports, with males comprising 65.3% of deaths ($n = 281$); 15.7% of those males ($n = 44$) had visible tusks, but there were no apparent differences in mortality patterns between tuskers and non-tuskers. One female was pregnant when she was found dead. Age estimates were available for 425 elephants of known sex. Males and females died at similar ages ($t_{373} = -0.429$, $P = 0.668$); the average age of death for males was 21.1 ± 14.5 years and for females it was 20.5 ± 13.0 years. When calves and juveniles were excluded from the dataset, the average death age for males was 24.1 ± 13.4 years and for females it was 22.2 ± 12.2 years. The 2 oldest males were approximately 60 years old (1 died of gunshot, the other poisoned); the oldest female was approximately 85 years old (died of septicemia).

Definitive causes of death were assigned to 482 elephants; 51.4% of deaths were intentionally human-caused (gunshot, hakkapatas, or poisoning), and 18.5% resulted from unintentional human activity (Table 2). Adult and subadult males comprised 52.3% of intentional deaths (compared to 30.5% for adult and subadult females); unintentional deaths were 51.1% male, and 28.3% female (Fig. 4). Males died more often from human-related deaths than females: intentional ($\chi^2_1 = 14.792$, $P \leq 0.001$) and unintentional ($\chi^2_1 = 6.041$, $P = 0.014$).

Intentionally caused deaths occurred most frequently through gunshots (53.9%). The percent of annual deaths due to gunfire decreased from 2009 through 2018 ($t_8 = -2.983$, $P = 0.018$, $r = -0.726$; Fig. 5). As gunfire-related deaths decreased, other forms of human-related deaths (intentional and unintentional) increased ($t_8 = -4.682$, $P = 0.002$, $r = 0.856$). Hakkapatas were the most common cause of death for juveniles (26.1% of all deaths) and subadult males (45.5%); 38.5% of hakkapatas victims were subadult males. Poisoning affected most sex and age demographics evenly. Electrocution comprised the majority of unintentionally caused, human-related deaths (72.8%), and mortality from train collisions was relatively rare (4.4% of total deaths). Septicemia was the most commonly reported natural death (41.8% of natural deaths), but more specific causes related to this condition could not be determined. Other common forms of natural mortality included worm infection (12.7% of natural deaths), physical injury (11.9%), dehydration and starvation (10.4%), and respiratory obstruction (10.4%). Confirmed deaths by other elephants occurred only among adult males ($n = 6$), and in 1 juvenile and 1 calf.

Over the study period, the majority of elephant deaths were recorded in Anuradhapura ($n = 309$, 62.0%); 89 deaths

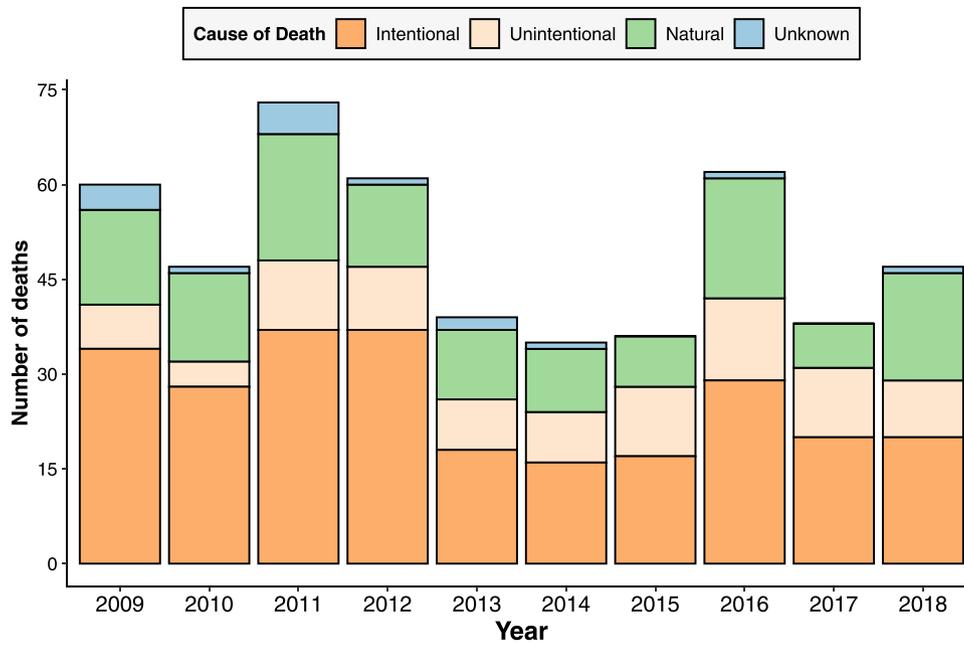


Figure 2. Number of Asian elephant deaths in Sri Lanka's Northwestern Wildlife Region from 2009–2018 by year. Intentional and unintentional deaths are human-related.

(17.9%) were recorded in Puttalam, 73 (14.7%) in Kurunegala, and 27 (5.4%) in Mannar district. This progression was almost exactly what would be expected based on the area of each district (the most deaths occurred in the largest district, and the fewest in the smallest district), and the distribution of the causes of death within each district generally followed the overall patterns described above. There were, however, significant inter-district differences in the mortality patterns observed over the study period, even when standardized for land area (Fig. 6). The percentage of elephant deaths due to intentional human events was high

in Mannar district (59.2%) and relatively low in Kurunegala district (38.4%; $\chi^2_3 = 66.266$, $P \leq 0.001$). Unintentional human events caused higher mortality rates in Kurunegala (27.4% of all deaths in the district), but these deaths were rarer in Mannar (only 7.4%; $\chi^2_3 = 15.510$, $P = 0.001$).

DISCUSSION

Human–elephant conflict is a major concern for elephant conservation, as is evident by our results from this area of Sri Lanka, where 69.9% of elephant deaths were human-related in 2009–2018. Monthly variation in elephant mortality

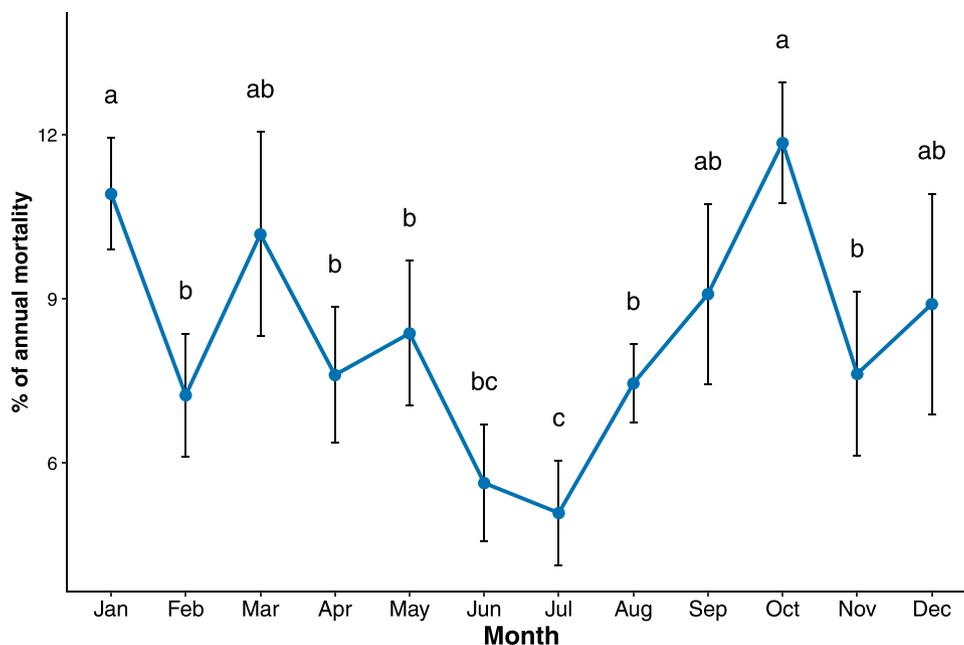


Figure 3. Monthly mortality rates of Asian elephants in Sri Lanka's Northwestern Wildlife Region from 2009–2018, expressed as average annual percentages. Error bars indicate standard error, with statistically significant differences via Tukey's honest significant difference noted by different letters.

Table 2. Causes of death for Asian elephants in Sri Lanka's Northwestern Wildlife Region from 2009–2018. Values in each category indicate number of elephants necropsied by Department of Wildlife Conservation veterinarians.

	Male		Female		Juvenile	Calf	Unknown	Total
	Adult	Subadult	Adult	Subadult				
Intentional	87	47	60	18	18	5	21	256
Gunshot	66	15	39	2	3	2	11	138
Hakkapatas ^a	8	30	12	10	11	2	5	78
Poisoning	13	2	9	6	4	1	5	40
Unintentional	40	7	20	6	4	1	14	92
Electrocution	35	5	10	1	2		14	67
Train injury	3	2	9	5	2	1		22
Landmine	1							1
Trap or snare	1							1
Vehicle injury			1					1
Natural	48	12	20	9	19	8	18	134
Septicemia	27	4	14	2	1		8	56
Worm infection			1	2	7	4	3	17
Physical injury	4	1	2	2	3	2	2	16
Dehydration or starvation	6	1	2	2	3			14
Respiratory obstruction	4	4		1	2		3	14
Elephant attack	6				1	1	1	9
Other	1	2	1		2	1	1	8
Unknown	2		2	1	1	1	9	16
Total	177	66	102	34	42	15	62	498

^a improvised explosives.

coincided with timing of highest crop availability; the highest number of deaths occurred during harvest months (Weerakoon et al. 2011), suggesting that mortality as a result of crop-raiding incidents is still common. Over half of human-caused deaths were from gunfire, most likely resulting from farmers trying to deter elephants from agriculture (Fernando et al. 2011). Illegal hunting is not yet a major threat to Sri Lankan elephants, especially because most males on the island lack tusks (Santiapillai and Wijeyamohan 2013); this is supported by our findings of no

mortality-related differences between tuskers and non-tuskers. Sustained HEC intensity may promote illegal killing (Compaore et al. 2020), emphasizing the urgent need for effective mitigation strategies.

Furthermore, mortality due to intentional human causes did not decrease over the study period; even though gunfire-related deaths became rarer, other human-caused forms of mortality (e.g., hakkapatas, electrocution, poisoning) became more prevalent. Gunfire-related mortality fell sharply after the first 2 years of this study period (although it increased again precipitously in 2017 for unknown reasons). This likely coincided with improved patrolling in these areas after the end of the Sri Lankan Civil War—and thus the decreased prevalence of firearms—and more severe consequences for owning firearms or using them to persecute wildlife. The Civil War ended in 2009, with active fighting taking place in Mannar, and the other districts in this area bordered areas where fighting took place. This finding emphasizes the fact that prohibiting or discouraging 1 form of lethal deterrent (i.e., gunfire) does not eliminate conflict, especially when people are not compensated adequately for elephant damage (Gunawardhana 2018). Instead, it simply motivates the unregulated development of other lethal practices. Mortality from intentionally caused deaths was more common than unintentional causes. It is illegal to kill an elephant in Sri Lanka, but when pressed, people have strong motivation to protect themselves and their property (Anuradha et al. 2019). Equally as important to preserving elephants is ensuring the well-being of the people that live around them, as coexistence is largely dependent upon tolerance by local communities (Barua et al. 2013, Kansky et al. 2016, Saif et al. 2020).

There were also observed inter-district differences in mortality patterns, as have been described in other studies

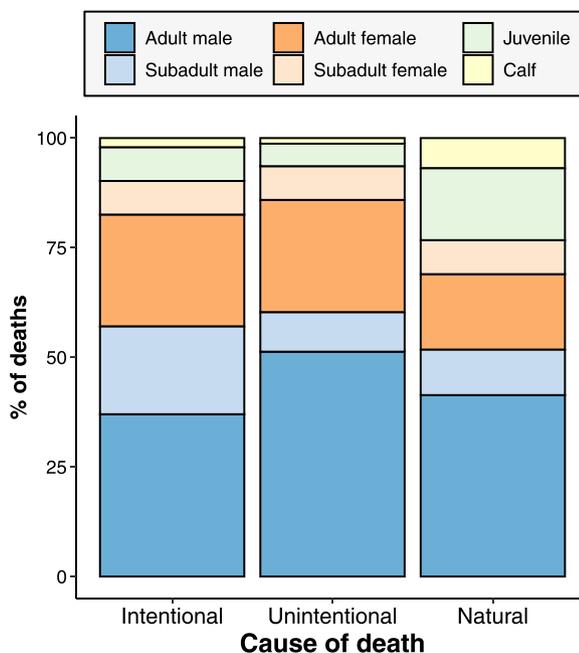


Figure 4. Causes of death for different age classes of Asian elephants in Sri Lanka's Northwestern Wildlife Region from 2009–2018.

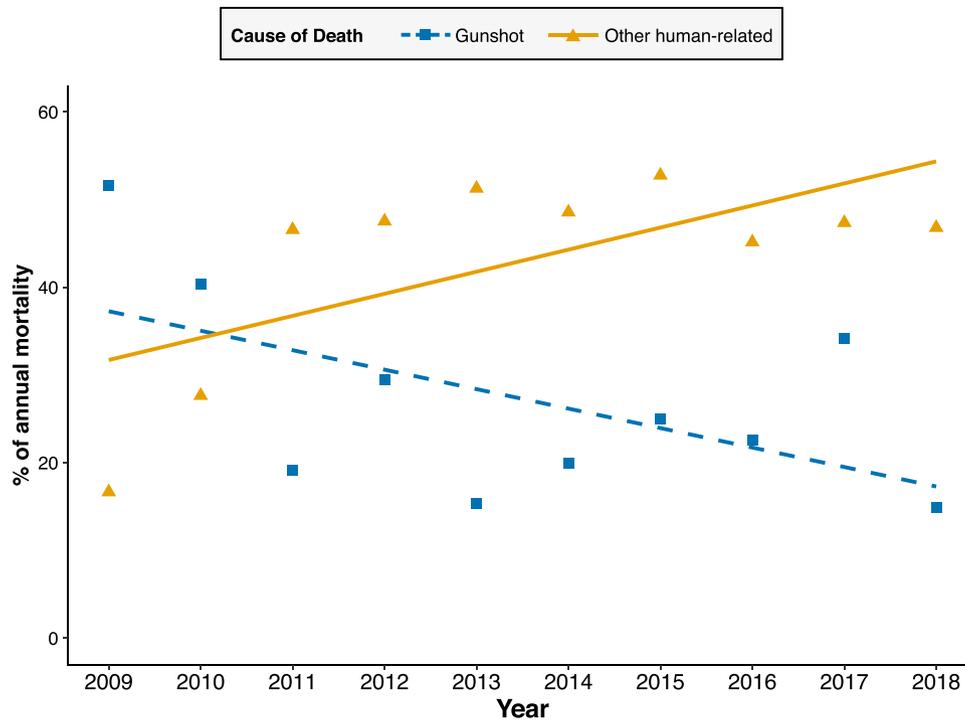


Figure 5. Percent of annual mortality due to gunshot (blue squares) and all other forms of human-related causes (orange triangles) for Asian elephants in Sri Lanka's Northwestern Wildlife Region from 2009–2018. Linear regression lines are shown for gunshots (dashed blue line) and other human-related causes (solid orange line).

(Prakash et al. 2020). Unsurprisingly, most elephant deaths occurred in the largest of the 4 districts within this wildlife region (Anuradhapura). Intentional human-related deaths were most prevalent in the district with the largest percent of protected land (Mannar, 62.6% protected) and least prevalent in the district with the lowest percent of

protection (Kurunegala, 12.8%). This finding is supported by other studies. For example, elephants have been reported to travel in larger groups farther from protected areas, making crop-raiding events more intense and increasing the likelihood of HEC-related deaths surrounding human activity (Chiyo et al. 2014). Furthermore, the perceived value of protected land for wildlife can diminish over time, perhaps also decreasing the motivation of local communities to rely on nonlethal deterrents for crop-raiding elephants (Ogra and Badola 2008, MacKenzie et al. 2017). Beginning in the 1950s, elephant management strategies in Sri Lanka focused on segregating people and wildlife, moving as many elephants as possible to confined, protected areas (Fernando 2015). These strategies that focus on sequestering elephants to protected land have received criticism from scientists and conservationists in Sri Lanka (Santiapillai et al. 2010, Fernando et al. 2021), and these practices may inadvertently promote HEC because the elephants that remain often become problem elephants, more likely to engage in crop-raiding (Fernando 2015). Furthermore, translocated elephants easily outgrow the carrying capacity of many protected areas, wandering into nearby farmlands to forage at night and quickly moving back into protected areas during the day (Ekanayaka et al. 2011). Instead of a protected area approach, a newer, *in situ* model that aims for coexistence between people and elephants is currently being incorporated by DWC into its forthcoming National Policy for Elephant Conservation and Management in Sri Lanka.

Additionally, we found that male elephants disproportionately died in human-related incidents, which

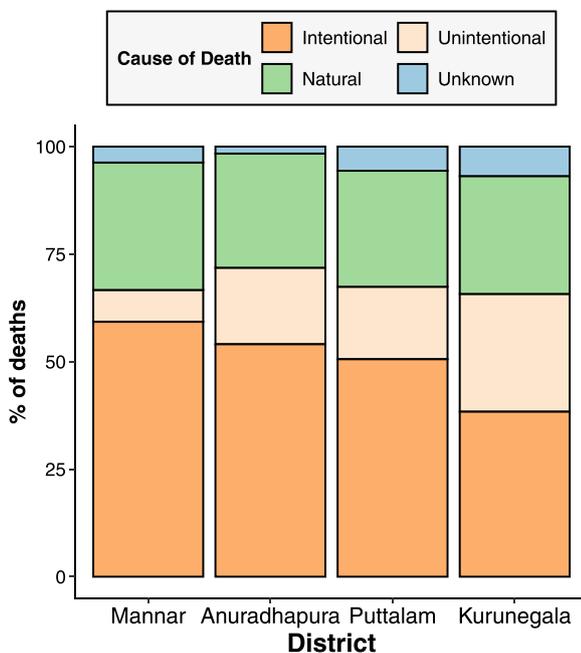


Figure 6. Causes of death for Asian elephants in Anuradhapura, Kurunegala, Mannar, and Puttalam districts, Sri Lanka, from 2009–2018, expressed as percent of total deaths per district.

indicates that a strategy that targets particular elephant demographics may be necessary. Male elephants, especially those in a heightened reproductive state (i.e., musth) engage in crop-raiding more frequently and are more likely to take risks and traverse more dangerous, human-inhabited areas (Ekanayaka et al. 2011, Prakash et al. 2020, Fernando et al. 2021). Therefore, conventional, nonlethal crop-raiding deterrents may be less effective for male elephants. When government-sanctioned firecracker deterrents fail, people may turn to lethal deterrents for persistent crop-raiders (Fernando et al. 2011). Notably, the recent proliferation of hakkapatas is concerning. These explosives disproportionately affect subadult male elephants, perhaps because this demographic is more likely to explore new areas and occupy low-quality habitat (Srinivasaiah et al. 2019). Given their propensity to engage in crop-raiding, research on the ecology of male elephants in particular could assist with management strategies, lending insight into the environmental and behavioral motivation to engage in HEC (Srinivasaiah et al. 2012, Mumby and Plotnik 2018). There is a pressing need for a multidisciplinary approach to HEC, referencing conservation psychology research and animal-based perspectives to explain historical trends and provide recommendations moving forward.

We have shared and discussed these findings with DWC so that appropriate measures can be implemented in this region and throughout the rest of the island. Taken together, these mortality statistics suggest that HEC is dynamic, changing over spatial and temporal scales. Almost certainly, individualized approaches are necessary to mitigate this problem on at least the district level, and perhaps occasionally even at the animal level. As our results suggest, careful monitoring of new management strategies will be required because a variety of factors influence the patterns of HEC. Only by addressing the changing needs of humans and elephants will survival of elephants in Sri Lanka and elsewhere be possible. Furthermore, we have illustrated that analyzing HWC at a broader temporal scale offers insight to address specific practices such as crop-raiding.

MANAGEMENT IMPLICATIONS

These results have broader implications for addressing HWC, and more specifically, the pressing challenge of crop-raiding. Several times in the recent past, Sri Lanka has implemented strategies to mitigate and reduce HWC, similar to various regions globally with elephants and other species. Despite these attempts, the dynamic dimensions of HWC challenge short-term mitigation strategies. For example, in this region it was clear that elephant deaths from gunfire decreased dramatically with increased gun control among civilians. Other forms of intentional killing increased over the same period, demonstrating the continued persistence of the conflict. Only long-term studies of wildlife mortality such as this one can shed light on the efficacy of management strategies that address HWC. The changing nature of HWC and crop-raiding at temporal and spatial scales also necessitates adaptive response strategies. For example, in this study there were differences in mortality

patterns between adjacent districts based on the proportion of protected land available (and concomitantly, human density), requiring an approach that considers regional and local differences in habitat quality and food and crop availability for wildlife. Despite the efforts of various groups (e.g., DWC and related agencies in Sri Lanka) to foster coexistence between wildlife and people, it is clear that human agricultural communities will turn to lethal deterrents when their physical safety and financial security are at risk. The burden of HWC may disproportionately affect a subset of an area's human population, but such conflict has wide-ranging consequences for food security and economic prosperity. Long-term studies have the potential to assist with mitigation strategies that adapt to changing pressures and factors leading to HWC.

ACKNOWLEDGMENTS

We thank the Department of Wildlife Conservation of Sri Lanka for performing and providing information about elephant necropsies, and S. M. Farinelli for making the map of our study area. This work was carried out under the permit issued to R. P. Vandercone of Rajarata University of Sri Lanka (permit number WL/3/2/44/15) by the Department of Wildlife Conservation. C. A. LaDue was supported by the Fulbright United States Student Program (U.S.–Sri Lanka Fulbright Commission).

LITERATURE CITED

- Anuradha, J. M. P. N., M. Fujimura, T. Inaoka, and N. Sakai. 2019. The role of agricultural land use pattern dynamics on elephant habitat depletion and human–elephant conflict in Sri Lanka. *Sustainability* 11:2818.
- Arivazhagan, C., and R. Sukumar. 2008. Constructing age structures of Asian elephant populations: a comparison of two field methods of age estimation. *Gajah* 29:11–16.
- Barua, M., S. A. Bhagwat, and S. Jadhav. 2013. The hidden dimensions of human–wildlife conflict: health impacts, opportunity and transaction costs. *Biological Conservation* 157:309–316.
- Blake, S., and S. Hedges. 2004. Sinking the flagship: the case of forest elephants in Asia and Africa. *Conservation Biology* 18:1191–1202.
- Branco, P. S., J. A. Merkle, R. M. Pringle, L. King, T. Tindall, M. Stalmans, and R. A. Long. 2019. An experimental test of community-based strategies for mitigation human–wildlife conflict around protected areas. *Conservation Letters* 13:e12679.
- Campos-Arceiz, A., and S. Blake. 2011. Megagardeners of the forest—the role of elephants in seed dispersal. *Acta Oecologica* 37:542–553.
- Campos-Arceiz, A., S. Takatsuki, S. K. K. Ekanayaka, and T. Hasegawa. 2009. The human–elephant conflict in southeastern Sri Lanka: type of damage, seasonal patterns, and sexual differences in the raiding behavior of elephants. *Gajah* 31:5–14.
- Chelliah, K., G. Kannan, S. Kundu, N. Abilash, A. Madhusudan, N. Baskaran, and R. Sukumar. 2010. Testing the efficacy of a chilli-tobacco rope fence as a deterrent against crop-raiding elephants. *Current Science* 99:1239–1243.
- Chiyo, P. I., J. W. Wilson, E. A. Archie, P. C. Lee, C. J. Moss, and S. C. Alberts. 2014. The influence of forage, protected areas, and mating prospects on grouping patterns of male elephants. *Behavioral Ecology* 25:1494–1504.
- Choudhury, A., D. K. L. Choudhury, A. Desai, J. W. Duckworth, P. S. Easa, A. J. T. Johnsingh, P. Fernando, S. Hedges, M. Gunawardena, F. Kurt, et al. 2008. *Elephas maximus*. The IUCN Red List of Threatened Species 2008:e.T7140A12828813.
- Compaore, A., D. Sirima, E. M. Hema, B. Doamba, S. N. Ajong, M. D. Vittorio, and L. Luiselli. 2020. Correlation between increased human–elephant conflict and poaching of elephants in Burkina Faso (West Africa). *European Journal of Wildlife Research* 66:24.

- Davies, T. E., S. Wilson, N. Hazarika, J. Chakrabarty, D. Das, D. J. Hodgson, and A. Zimmermann. 2011. Effectiveness of intervention methods against crop-raiding elephants. *Conservation Letters* 4:346–354.
- Department of Census and Statistics of Sri Lanka. 2012. ජනන ජනන [Census of Population and Housing]. Department of Census and Statistics of Sri Lanka, Battaramulla, Sri Lanka.
- Department of Wildlife Conservation [DWC]. 2012. The first national survey of elephants in Sri Lanka. Department of Wildlife Conservation of Sri Lanka, Battaramulla, Sri Lanka.
- Dickman, A. J. 2010. Complexities of conflict: the importance of considering social factors for effectively resolving human–wildlife conflict. *Animal Conservation* 13:458–466.
- Dittus, W. P. J. 1977. The ecology of a semi-evergreen forest community in Sri Lanka. *Biotropica* 9:268–286.
- Ekanayaka, S. K. K., A. Campos-Arceiz, M. Rupasinghe, J. Pastorini, and P. Fernando. 2011. Patterns of crop raiding by Asian elephants in a human-dominated landscape in southeastern Sri Lanka. *Gajah* 34: 20–25.
- Fernando, P. 2015. Managing elephants in Sri Lanka: where we are and where we need to be. *Ceylon Journal of Science (Biological Sciences)* 44:1–11.
- Fernando, P., M. K. C. R. De Silva, L. K. A. Jayasinghe, H. K. Janaka, and J. Pastorini. 2021. First country-wide survey of the endangered Asian elephant: towards better conservation and management in Sri Lanka. *Oryx* 55:46–55.
- Fernando, P., J. Jayewardene, T. Prasad, W. Hendavitharana, and J. Pastorini. 2011. Current status of Asian elephants in Sri Lanka. *Gajah* 35:93–103.
- Fernando, P., and J. Pastorini. 2011. Range-wide status of Asian elephants. *Gajah* 35:15–20.
- Gunawardhana, L. M. A. P. 2018. An analysis of human–elephant conflict as a disaster: a case study in Anuradhapura district of Sri Lanka. *Journal of Tropical Environment* 1:40–55.
- Hill, C. M. 2018. Crop foraging, crop losses, and crop raiding. *Annual Review of Anthropology* 47:377–394.
- Kansky, R., M. Kidd, and A. T. Knight. 2016. A wildlife tolerance model and case study for understanding human wildlife conflicts. *Biological Conservation* 201:137–145.
- Leimgruber, P., J. B. Gagnon, C. Wemmer, D. S. Kelly, M. A. Songer, and E. R. Selig. 2003. Fragmentation of Asia's remaining wildlands: implications for Asian elephant conservation. *Animal Conservation* 6:347–359.
- Lischka, S. A., T. L. Teel, H. E. Johnson, C. Larson, S. Breck, and K. Crooks. 2020. Psychological drivers of risk-reducing behaviors to limit human–wildlife conflict. *Conservation Biology* 34:1383–1392.
- MacKenzie, C. A., J. Salerno, J. Hartter, C. A. Chapman, R. Reyna, D. M. Tumusiime, and M. Drake. 2017. Changing perceptions of protected area benefits and problems around Kibale National Park, Uganda. *Journal of Environmental Management* 200:217–228.
- Menon, V., and S. K. Tiwari. 2019. Population status of Asian elephants *Elephas maximus* and key threats. *International Zoo Yearbook* 53:17–30.
- Messmer, T. A. 2000. The emergence of human–wildlife conflict management: turning challenges into opportunities. *International Biodeterioration & Biodegradation* 45:97–102.
- Mumby, H. S., and J. M. Plotnik. 2018. Taking the elephants' perspective: remembering elephant behavior, cognition and ecology in human–elephant conflict mitigation. *Frontiers in Ecology and Evolution* 6:122.
- Nyhus, P. J. 2016. Human–wildlife conflict and coexistence. *Annual Review of Environment and Resources* 41:143–171.
- Ogra, M., and R. Badola. 2008. Compensating human–wildlife conflict in protected area communities: ground-level perspectives from Uttarakhand, India. *Human Ecology* 36:717–729.
- Perera, B. M. A. O. 2009. The human–elephant conflict: a review of current status and mitigation methods. *Gajah* 30:41–52.
- Pimentel, D., R. Zuniga, and D. Morrison. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics* 52:273–288.
- Prakash, T. G. S. L., A. W. Wijeratne, and P. Fernando. 2020. Human–elephant conflict in Sri Lanka: patterns and extent. *Gajah* 51:16–25.
- R Core Team. 2020. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Saif, O., R. Kansky, A. Palash, M. Kidd, and A. T. Knight. 2020. Costs of coexistence: understanding the drivers of tolerance towards Asian elephants *Elephas maximus* in rural Bangladesh. *Oryx* 54:603–611.
- Santiapillai, C., and S. Wijeyamohan. 2013. The first national survey of elephants in Sri Lanka. *Current Science* 105:153–154.
- Santiapillai, C., S. Wijeyamohan, G. Bandara, R. Athurupana, N. Dissanayake, and B. Read. 2010. An assessment of the human–elephant conflict in Sri Lanka. *Ceylon Journal of Science (Biological Sciences)* 39:21–33.
- Srinivasaiah, N., V. Kumar, S. Vaidyanathan, and R. Sukumar. 2019. All-male groups in Asian elephants: a novel, adaptive social strategy in increasingly anthropogenic landscapes of southern India. *Scientific Reports* 9:8678.
- Srinivasaiah, N. M., V. D. Anand, S. Vaidyanathan, and A. Sinha. 2012. Usual populations, unusual individuals: insights into the behavior and management of Asian elephants in fragmented landscapes. *PLoS One* 7:e42571.
- Treves, A., R. B. Wallace, L. Naughton-Treves, and A. Morales. 2007. Co-managing human–wildlife conflicts: a review. *Human Dimensions of Wildlife* 11:383–396.
- Tscharntke, T., Y. Clough, T. C. Wanger, L. Jackson, I. Motzke, I. Perfecto, J. Vandermeer, and A. Whitbread. 2012. Global food security, biodiversity conservation and the future of agricultural intensification. *Biological Conservation* 151:53–59.
- Vandercone, R. 2011. Dietary shifts, niche relationships and interspecific competition in the sympatric grey langur (*Semnopithecus entellus*) and the purple-faced langur (*Trachypithecus vetulus*) in Sri Lanka. Dissertation, Washington University, Saint Louis, Missouri, USA.
- Weerakoon, W. M. W., M. M. P. Mutunayake, C. Bandara, A. N. Rao, D. C. Bhandari, and J. K. Ladha. 2011. Direct-seeded rice culture in Sri Lanka: lessons from farmers. *Field Crops Research* 121:53–63.
- Wickham, H. 2016. *ggplot2: elegant graphics for data analysis*. Springer-Verlag, New York, New York, USA.
- Wilson, S., T. E. Davies, N. Hazarika, and A. Zimmermann. 2015. Understanding spatial and temporal patterns of human–elephant conflict in Assam, India. *Oryx* 49:140–149.
- Woodroffe, R., S. Thirgood, and A. Rabinowitz. 2005. *People and wildlife: conflict or coexistence?* Cambridge University Press, Cambridge, United Kingdom.

Associate Editor: Ryan Long.