



# The importance of conflict-induced mortality for conservation planning in areas of human–elephant co-occurrence



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## ABSTRACT

Multiple-use zones around protected areas are designed to balance human resource needs with wildlife conservation, but conflicts between wildlife and people in these areas of co-occurrence (CA) can seriously undermine their conservation potential. We evaluated this issue by assessing the effects of conflict-induced mortality in CAs around an inviolate core, on long-term population viability of the endangered, wide-ranging, and conflict-prone Asian elephant (*Elephas maximus*). Using a single-sex, age-structured density-dependent matrix population model to simulate elephant population dynamics over a period of 500 years, we: (1) assessed the existence of extinction thresholds arising from the interaction of mortality due to human–elephant conflict (HEC) and habitat degradation, and (2) evaluated whether and to what extent habitat supplementation by the CA is devalued by detrimental effects of conflict-induced mortality. We parameterized our model using published survival and fecundity rates. We considered different scenarios of core to CA configurations, and simulated the population under HEC-induced mortality rates ( $HEC_m$ ) ranging from 0 to 0.1. Population persistence was adversely affected by  $HEC_m$ , and its detrimental effects were magnified as the proportion of core habitat declined. Under moderate  $HEC_m$ , small increments in mortality rates necessitated disproportionately large increases in core area availability to avoid quasi-extinction. Furthermore, benefits of CA supplementation were driven more by CA quality than size, and these benefits declined as  $HEC_m$  increased. We emphasize the need to minimize conflict-induced mortality, or to maintain adequate refugia from such anthropogenic threats, to successfully conserve conflict-prone species in human-dominated landscapes.

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## 1. Introduction

Growing human populations and associated anthropogenic threats are at the forefront of global population declines in wildlife species (Sanderson et al., 2002a; Cardillo et al., 2004; Karanth et al., 2010). A central focus of conservation policy is therefore to identify strategies that can minimize threats to wildlife populations. One such strategy is the spatial separation of wildlife populations from anthropogenic presence, and hence, threats. Protected areas (PAs) are envisioned to achieve this separation to varying degrees and to provide refuge to wildlife species from anthropogenic threats in heterogeneous landscapes (Margules and Pressey, 2000; Hansen and DeFries, 2007). Inviolate core areas devoid of human presence, however, are often limited in size (Woodroffe and

Ginsberg, 1998), and species persistence in heterogeneous landscapes hinges on the ability of faunal assemblages to use the intervening areas of human presence (Saunders et al., 1991; Ricketts, 2001). Therefore, conservation programs increasingly encompass multiple-use areas around inviolate cores that can augment available wildlife habitat and population size (Pimm et al., 1988) while allowing for human activities (e.g., Sanderson et al., 2002b; Wikramanayake et al., 2004; Athreya et al., 2013).

Studies from across the globe suggest that the greatest challenge to the mutual well-being of humans and wildlife in areas of their co-occurrence (henceforth, 'co-occurrence areas') arises from the conflict that occurs between them (Naughton-Treves, 1998; Woodroffe et al., 2005; Karanth et al., 2013a). Large-bodied mammals are particularly prone to conflicts with humans as their expansive home-range needs (Karanth and Sunquist, 2000; Fernando et al., 2008) force them to directly compete with people for limited space and resources. Although a certain level of conflict is inevitable at any interface between humans and large mammals

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(Madhusudan, 2003), loss and degradation of core habitat, in addition to increasing wildlife populations, agricultural intensification and livestock depredation opportunities outside PAs (Gubbi, 2012; Karanth et al., 2013b; Suryawanshi et al., 2013), are likely to cause a greater spillover of animals into co-occurrence areas (CAs). Large mammal species that can 'adapt' to a human-dominated environment may occur in the CA in relatively high densities (e.g., Athreya et al., 2013). However, given that large mammal persistence in heterogeneous landscapes is increasingly threatened by human-induced mortality due to human-wildlife conflict, CAs can potentially act as population sinks (Woodroffe and Ginsberg, 1998; Balme et al., 2010; Newby et al., 2013). As such, anthropogenic mortality of wide-ranging megafauna within these CAs can greatly devalue their role as proxy habitat around inviolate core areas.

The Asian elephant *Elephas maximus* is a prime example of a large-bodied, wide-ranging, conflict-prone species that is increasingly threatened by anthropogenic activities across its geographical range. Almost half of the 873,000 km<sup>2</sup> of habitat that harbors elephants in Asia is both fragmented and heavily impacted by humans (Leimgruber et al., 2003). Growing human populations, deforestation and agro-developmental land conversion are resulting in ever-shrinking habitat islands interspersed within a human-dominated landscape (Leimgruber et al., 2003). This, in combination with an upswing in incidents of human-elephant conflict (HEC) (Sukumar, 2003), is severely exacerbating the endangered status of the species. Long-term conservation of the Asian elephant therefore requires a greater understanding of the implications of increasing HEC, particularly in the context of habitat loss and degradation (Goswami et al., 2007).

The impact of conflict-induced mortality on the viability of elephant populations in heterogeneous landscapes is largely unknown. We address this issue by extending a density-dependent age-structured matrix population model (Armbruster and Lande, 1993; Armbruster et al., 1999) to project Asian elephant population viability in the light of HEC-induced mortality within CAs. Our goal was to understand how the interplay of anthropogenic mortality and modifications to existing habitat could shape the future of elephant populations. We defined our hypothetical area of interest as comprising inviolate core areas surrounded by CAs, and explored elephant population persistence under different configurations of the core and co-occurrence areas and varying levels of HEC-induced mortality. We use our results to make recommendations about elephant conservation in the face of growing anthropogenic pressures.

## 2. Methods

### 2.1. Density-dependent model of elephant demography

We constructed a deterministic, females-only age-structured matrix model (Caswell, 2001) with 60 1-year age classes using previously reported age-specific survival and fecundity rates for female Asian elephants (Sukumar et al., 1998). We estimated fertility rates for age class  $i$  ( $F_i$ ) using a post-breeding census formulation, as the product of the age-specific survival ( $P_i$ ) and fecundity  $m_i$  rates, i.e.  $F_i = P_i \times m_i$ . We then parameterized a population projection matrix using  $P_i$  and  $F_i$ . Population growth rate (dominant eigenvalue,  $\lambda$ ), stable age distribution (right eigenvector,  $w$ ) and reproductive value (left eigenvector,  $v$ ) were estimated as per Caswell (2001).

We adopted the approach used by Armbruster and Lande (1993), and Ambruster et al. (1999) to model density-dependence such that elephant density ( $D$ ; females per km<sup>2</sup>) affected reproductive parameters (age at first reproduction and calving intervals).

We modeled age at first reproduction ( $\alpha$ ) and calving interval in years ( $CI$ ) as functions of density ( $D$ ), whereby  $\alpha = \alpha_{min} + \beta_1 D$  and  $CI = CI_{min} + \beta_2 D$ . Here,  $\alpha_{min}$  and  $CI_{min}$  correspond to  $\alpha$  and  $CI$  prior to the effects of density-dependence. We set  $\alpha_{min}$  as 16 years following Sukumar et al. (1998) and calculated  $CI_{min}$  as the reciprocal of annual fecundity rates (Armbruster and Lande, 1993). We obtained our density estimate from a population survey within a PA in southern India that reported a density of 3.13 elephants km<sup>-2</sup> and a female-biased sex ratio of 3:1 (Goswami et al., 2007). Therefore we estimated female elephant density as  $3.13 \times 0.75 = 2.35$  female elephants km<sup>-2</sup>. We then parameterized  $\beta_1 = \beta_2 = 3.77$  such that equilibrium population size in core areas yielded a density of 2.35 female elephants km<sup>-2</sup>.

We estimated density-dependent fecundity rates ( $m_{i(DD)}$ ) for each age class as  $1/CI$  following Armbruster and Lande (1993), and used these to derive density-dependent fertility rates ( $F_{i(DD)}$ ). For each set of simulations, we used a starting population size of 2350 females. This initial population size approximated the equilibrium population size for a 1000 km<sup>2</sup> core area ( $K_{core}$ ), estimated as the abundance of female elephants given an equilibrium density of 2.35 female elephants km<sup>-2</sup>. The starting population size was distributed according to the estimated stable age distribution, which was used as the initial population vector. All simulations were run for 500 years. Parameters values are provided in Table 1.

### 2.2. Mortality due to human-elephant conflict

Our model imposes two forms of control on elephant populations: (a) density-dependence through its influence on reproduction, and (b) HEC-induced mortality in the CA affecting elephant survival rates. Our goal was to test for the effects of the latter on elephant population viability. To achieve this we conceptualized a hypothetical modeling space  $Area_{tot}$  comprised of a circular core region of size  $Area_{core}$  and radius  $R_{core}$ , surrounded by a multiple-use CA. We defined the core area as an inviolate space free of human presence to represent an undisturbed PA. The CA, on the other hand, accommodates human activities to varying extents, thus leading to differing CA quality and HEC-induced mortality scenarios. As such, HEC-induced mortality was restricted to the CA.

We allowed elephants in our model to move between the core and the CA within limitations of their biological movement capabilities and quantified by a movement parameter ( $M$ ). We assumed that elephants could move from the core to the CA provided they are within a distance  $M$  from the core-CA edge. We estimated  $M = 8.7$  km as the radius of a circle of size 237 km<sup>2</sup>, equivalent in area to the average of reported minimum convex polygon home range sizes for Asian elephants in telemetry studies where animals were tracked for longer than six months ( $n = 34$  individuals or herds) (Olivier, 1978; Bhaskaran et al., 1995; Joshua and Johnsingh, 1995; Fernando and Lande, 2000; Williams, 2002; Venkataraman et al., 2005; Fernando et al., 2008; Alfred et al., 2012). Effectively, the core area of our modeling space could be partitioned into (1) an interior refuge of size  $Area_{ref}$  and radius  $R_{ref}$  where  $R_{ref} = R_{core} - M$  and (2) a movement zone of width  $M$  (hereafter, movement zone). We assumed that elephants inhabiting the interior refuge did not move to the CA, and thus were not exposed to HEC-induced mortality. However, elephants were allowed to move between the movement zone and the CA, and this section of the population encountered HEC-induced mortality.

The realized HEC-induced mortality rate ( $HECm_{real}$ ) was modeled as a function of the probability of human-elephant encounters  $p(encounter)$  in the CA and naïve annual HEC-induced mortality rate ( $HECm$ ) as:

$$HECm_{real} = p(encounter) \times HECm$$

where

**Table 1**Annual survival and reproductive parameters used in the females-only elephant population projection model.<sup>a</sup>

Age class ( <i>i</i> )	Baseline survival rates ( $P_i$ )	Fecundity rates ( $m_i$ )	Initial fertility rates <sup>b</sup> ( $F_i$ )	Minimum calving interval <sup>b</sup> ( $CI_{min}$ )
1	0.9000	0	0	0
2–5	0.9600	0	0	0
6–15	0.9850	0	0	0
16–20	0.9970	0.2250	0.2243	4.4444
21–50	0.9850	0.2250	0.2216	4.4444
51–60	0.9000	0.2000	0.1800	5.0000

<sup>a</sup> Age at first reproduction ( $\alpha_{min} = 16$ ), and annual survival and fecundity rates were obtained from Sukumar et al. (1998).<sup>b</sup>  $F_i$  was estimated as  $P_i \times m_i$ , and  $CI_{min}$  as  $1/m_i$ .

$$p(\text{encounter}) = (Area_{tot} - Area_{core}) / (Area_{tot} - Area_{ref}) \quad (1)$$

We assumed that  $HECm$  was additive to natural mortality due to factors such as predation, disease, malnutrition, and accidents (Sukumar, 2003). Therefore, we estimated realized survival ( $P_{i[real]}$ ) for the fraction of the population exposed to HEC-induced mortality as the product of baseline survival rates ( $P_i$ ; i.e., survival rates in the absence of  $HECm$ ), and the probability of surviving HEC as:

$$P_{i[real]} = P_i \times (1 - HECm_{real}) \quad (2)$$

Survival rates of elephants inhabiting the interior refuge were assumed to be unaffected by  $HECm$ .

### 2.3. Scenarios of human–elephant conflict and habitat alteration

We started with a set of scenarios focused on evaluating the ramifications of HEC-induced mortality for populations faced with increasing habitat degradation i.e., core habitat converted to CA of varying quality. We first simulated the dynamics of an initial population of 2350 female elephants, distributed among age classes as per the estimated stable age distribution, in a core area of 1000 km<sup>2</sup>. We then simulated scenarios of increasing conversion of core area to CA. We also considered four scenarios of CA quality such that: (a) the carrying capacity of CA,  $K_{CA} = 0.25 \times$  carrying capacity of the core,  $K_{core}$ , (b)  $K_{CA} = 0.5K_{core}$ , (c)  $K_{CA} = 0.75K_{core}$ , and (d)  $K_{CA} = K_{core}$ . To isolate the effects of HEC-induced mortality we controlled for equilibrium population size in our modeled space  $Area_{tot}$  by supplementing core area loss with a CA area of equivalent carrying capacity. For example, when  $K_{CA} = 0.5K_{core}$ , 1 km<sup>2</sup> of core habitat lost was compensated by 2 km<sup>2</sup> of CA habitat to maintain equilibrium population size of  $Area_{tot}$ . We considered four scenarios of habitat degradation: 0%, 25%, 50% and 100% loss of core habitat. For this simulation we used  $HECm = 0.05$ . We considered this to be a moderate rate of HEC-induced mortality as this value approximately corresponds to natural mortality rates faced by adult Asian elephants (Armbruster et al., 1999).

Our second set of scenarios was designed to identify extinction thresholds for the Asian elephant brought about by the interaction of HEC-induced mortality and habitat degradation. Like above, we allowed  $Area_{core}$  to range from 0 to 1000 km<sup>2</sup>, and compensated the loss of core habitat with CA. To represent a range of plausible HEC-induced mortality rates, we used a range of  $HECm$  from 0 to 0.1, highlighting the following rates: low (0.025), moderate (0.05), and high (0.10). Our definition of high  $HECm$  was based on Sukumar et al. (1998), who considered annual female elephant mortality rates of  $\geq 8\%$  as high. For each simulation we quantified the time taken by our hypothetical population to reach ‘quasi-extinction’, defined as a decline in elephant abundance to 10% of its original size as per earlier studies (Engen et al., 2002; Inchausti and Halley, 2003). Thereafter, we estimated equilibrium population size with respect to  $Area_{core}$  as the average population size for the last 100 years of our simulation. We confirmed that the population had in fact attained equilibrium during this time period by ensuring that  $\lambda \sim 1$ . For each  $HECm$  scenario, we

evaluated minimum  $Area_{core}$  required to avoid quasi-extinction in our hypothetical population.

For our final set of simulations, we investigated whether the positive effects of increased habitat availability through the addition of a CA are negated by the detrimental effects of HEC-induced mortality. We considered a reference population of Asian elephants in a core habitat of area 1000 km<sup>2</sup> supplemented by a CA of varying size and habitat quality. Thus, we included scenarios where (1) CA width ( $W_{CA}$ ) was equal to and half of  $M$  and (2)  $K_{CA}$  was equal to and half of  $K_{core}$ . For each set of simulations, we used  $HECm$  values ranging from no  $HECm$  (0), low (0.025), moderate (0.05) and high (0.10). For time  $t$ , we evaluated each scenario based on the difference in projected population size ( $N_t$ ) for that particular scenario and the projected population size for the reference population, where the habitat was composed entirely of core ( $Base N_t$ ). Therefore, for a scenario corresponding to  $x$  CA width,  $y$  CA carrying capacity, and  $z$   $HECm$ , our parameter of interest, difference in population size for time  $t$  ( $\Delta N_t$ ), was given by:

$$\Delta N_t[x, y, z] = N_t[x, y, z] - Base N_t \quad (3)$$

All our models were implemented in MATLAB (MATLAB 2009) and our figures were created in R (R Development Core Team, 2013). The code is available on request.

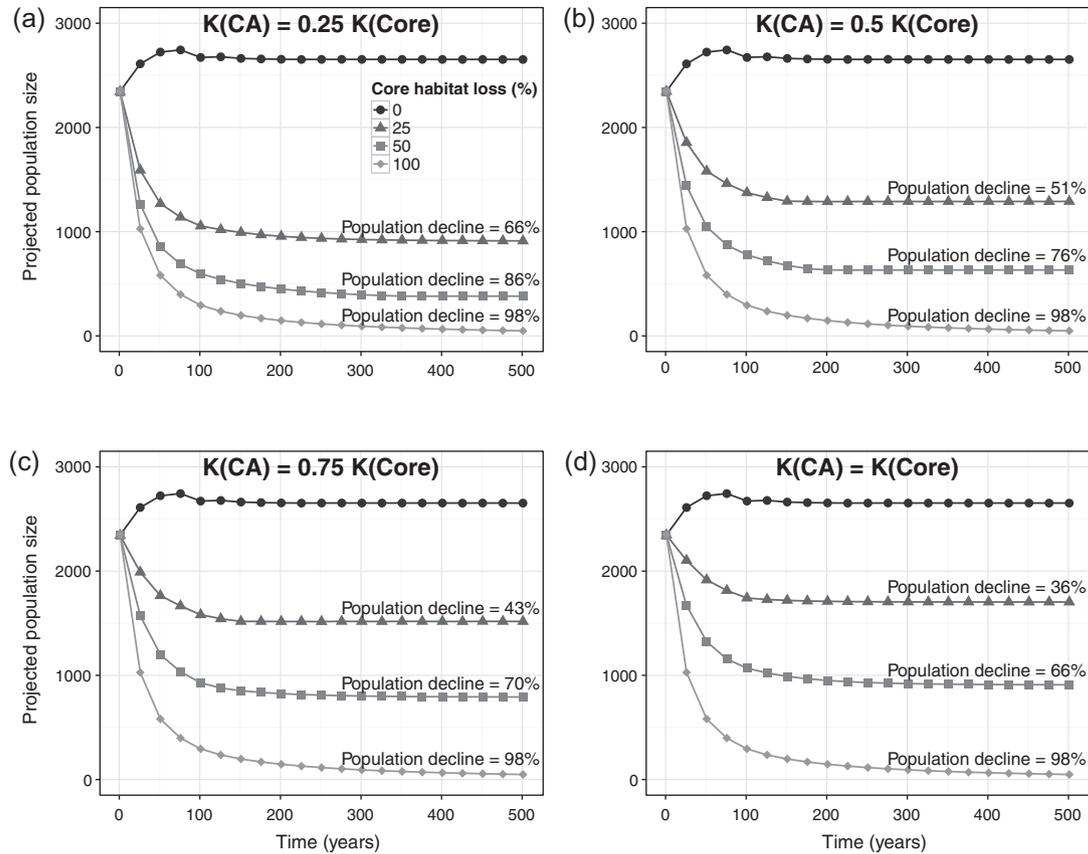
## 3. Results

### 3.1. Effects of $HECm$ on population viability

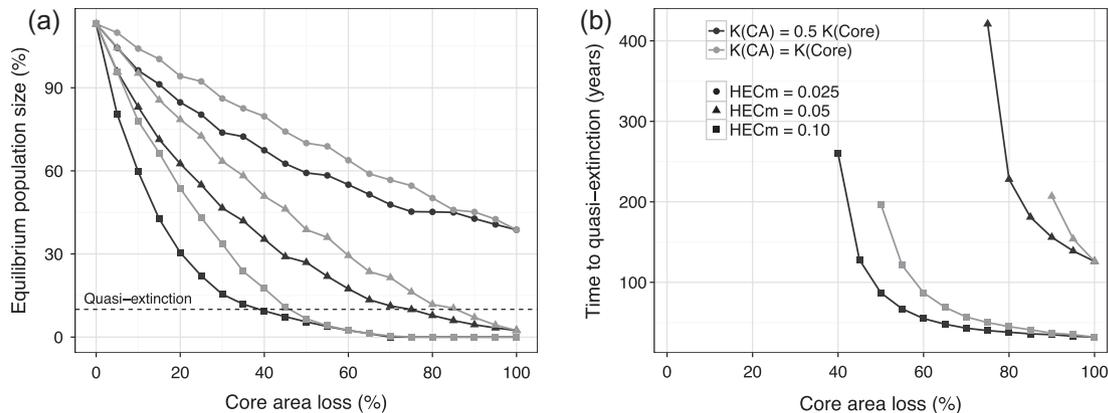
HEC-induced mortality had a substantial negative impact on our hypothetical Asian elephant population (Fig. 1). Our results indicate a disproportionate HEC-induced decline in elephant numbers with increasing conversion of the core to the CA. For example, when the carrying capacity of the CA and the core were equivalent (i.e.,  $K_{CA} = K_{core}$ ), the initial population declined by 36% with a 25% reduction in  $Area_{core}$ , and by 66% when  $Area_{core}$  was reduced to 50% of the original 1000 km<sup>2</sup> of core habitat (Fig. 1d). This population decline was more severe as CA quality (i.e., its carrying capacity,  $K_{CA}$ ) decreased relative to the carrying capacity of the core,  $K_{core}$  (Fig. 1).

### 3.2. Interplay of $HECm$ and habitat degradation

Our study population declined to a functionally quasi-extinct state (10% of the original population) when  $HECm > 0.05$  and available core habitat was less than critical minimum levels (Fig. 2a). For example, when CAs were qualitatively equivalent to the interior core,  $Area_{core}$  of 10% and 50% were required to avoid quasi-extinction for  $HECm$  of 0.05 and 0.10, respectively (Fig. 2a and b). Below these levels of  $Area_{core}$ , time to quasi-extinction diminished with core habitat loss for a given  $HECm$  (Fig. 2b). With increasing core area loss, time to quasi-extinction declined more rapidly for  $HECm$  of 0.05 than  $HECm$  of 0.10. For example, with a decline in



**Fig. 1.** Asian elephant population projections over time for scenarios where the carrying capacity of the co-occurrence area  $K(CA)$  is (a) one-fourth that of the core, (b) half of the core, (c) three-quarters of the core and (d) equivalent to the core. For all models, initial population size was 2350 female elephants in a core area of 1000 km<sup>2</sup>, and the rate of  $HEC_m$  was 0.05.

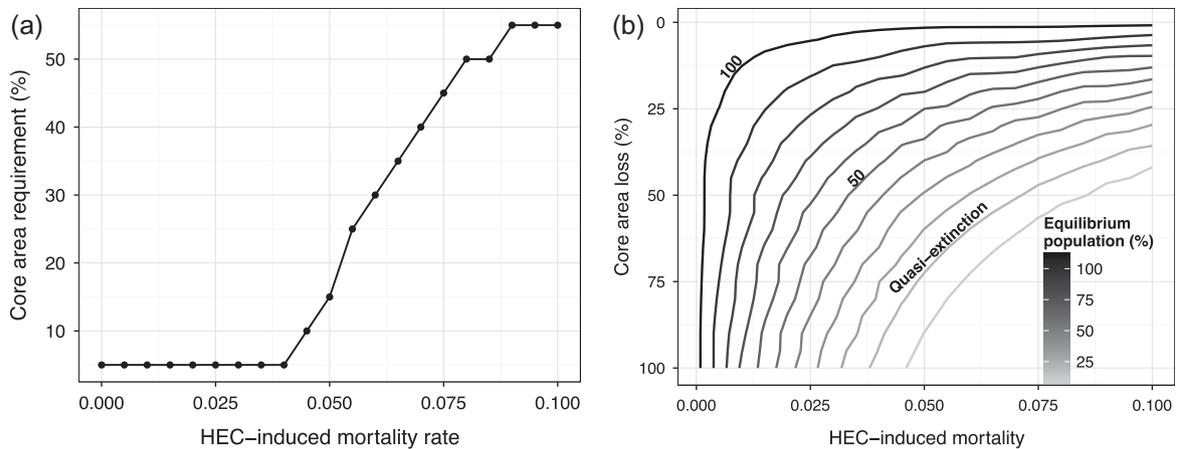


**Fig. 2.** (a) Equilibrium population size and (b) time to quasi-extinction as a function of percentage core area loss and increasing  $HEC$ -induced mortality for scenarios where the carrying capacity of the co-occurrence area  $K(CA)$  is half and equal to the carrying capacity of the core  $K(Core)$ . The dashed line represents the quasi-extinction threshold at which elephant populations declined to 10% of their original size.

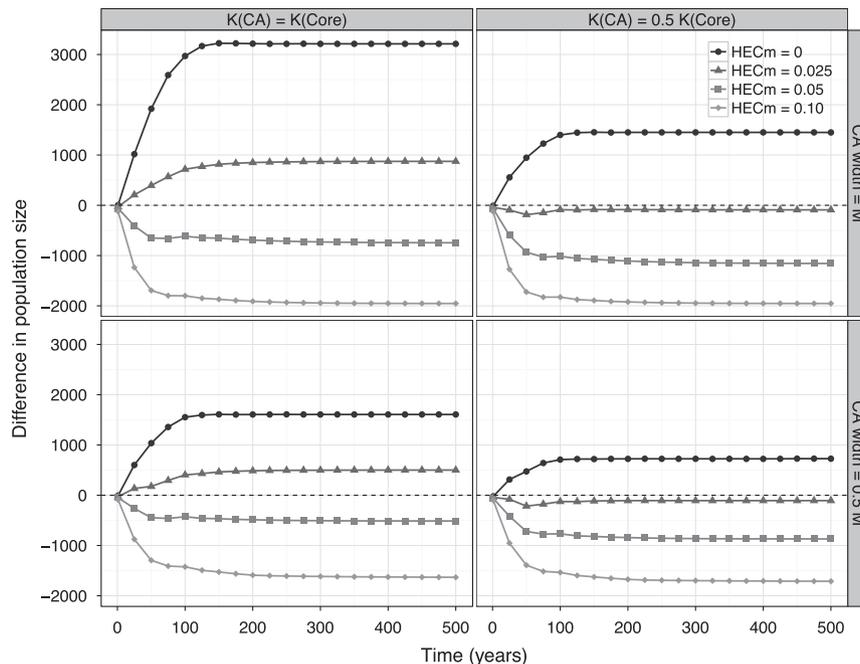
$Area_{core}$  from 10% to 0%, time to quasi-extinction reduced by 39% for  $HEC_m = 0.05$  and by 14% for  $HEC_m = 0.10$ , when  $K_{CA} = K_{core}$ .

These results indicate (1) the existence of extinction thresholds arising from the interaction of mortality due to  $HEC$  and habitat degradation, and (2) that this threshold is most sensitive to  $HEC_m$  in the range of moderate (0.04) to high (0.08). Small increments of  $HEC_m$  in this range necessitated disproportionately large increases in  $Area_{core}$  to prevent quasi-extinction (Fig. 3a and b). With the exception of high  $Area_{core}$  (>80%), this threshold effect was also reflected in substantial declines in equilibrium popula-

tion size with increasing  $HEC_m$  (Fig. 3b). Therefore, a small increase in  $HEC_m$  needed to be accompanied by large additions to  $Area_{core}$  extents to maintain a given equilibrium population size (Fig. 3b). On the other hand, elephant populations faced with low  $HEC_m$  (e.g., 0.02) did not become quasi-extinct (Fig. 3a), but were maintained at approximately 30–40% of the original population even when core habitat was  $\leq 10\%$  of the total habitat area (Fig. 3b). Results presented in Fig. 3 were for  $K_{CA} = K_{core}$ ; these results showed similar patterns, albeit with greater intensity when  $K_{CA} = 0.5 K_{core}$ .



**Fig. 3.** Interactive effects of HEC-induced mortality rates ( $HEC_m$ ) and percentage core area loss on elephant population dynamics where the carrying capacity of the co-occurrence area is equal to that of the core, as shown by (a) critical percentage core area requirements to avoid quasi-extinction with varying  $HEC_m$  and (b) a contour plot of equilibrium population size with varying  $HEC_m$  and percentage core area loss. Contour lines represent percentages of a starting population size of 2350 individuals.



**Fig. 4.** Difference in Asian elephant population size between scenarios of co-occurrence area (CA) width and quality, and a reference population in a core area of 1000 km<sup>2</sup> with no CA. We used a core area of 1000 km<sup>2</sup> supplemented by a CA where (1) CA width was equal to and half of the average movement distance for elephants ( $M$ ) and (2) carrying capacity of the CA,  $K(CA)$ , was equal to and half the carrying capacity of the core,  $K(CA)$ .  $HEC$ -induced mortality ranges from absent ( $HEC_m = 0$ ) through low ( $HEC_m = 0.025$ ) and moderate ( $HEC_m = 0.05$ ) to high ( $HEC_m = 0.10$ ).

### 3.3. Habitat benefits versus mortality drawbacks in co-occurrence areas

Although the addition of a CA zone to core habitat accrued benefits due to increased space and resource availability for the elephant population, these benefits were negated by moderate (0.05) to high (0.10)  $HEC_m$  (Fig. 4). In the absence of HEC-induced mortality, the size and quality of the CA zone around a core was positively associated with an increase in elephant population size. The benefits from a smaller CA with the same quality as the core ( $BW = 0.5M$ ,  $K_{CA} = K_{core}$ ) (Fig. 4b) were comparable to a larger CA of poorer quality ( $BW = M$ ,  $K_{CA} = 0.5K_{core}$ ) (Fig. 4c). Interestingly, however, CA quality was more important than CA size for elephant

population viability in the presence of conflict-induced mortality ( $HEC_m = 0.025$ ).

## 4. Discussion

Conservation focus in the last two decades has undergone a decided shift towards embracing lands outside strictly inviolate PAs (e.g., Sanderson et al., 2002b; Wikramanayake et al., 2004). This move addresses ethical concerns of human displacement (Adams and Hutton, 2007) while increasing the space and resources available to wildlife (Bali et al., 2007). A consequence of this paradigm shift, however, is increased interactions between

people and wildlife, which for some species can imply heightened incidence of human–wildlife conflict. Conservation of the Asian elephant typifies this chain of events, whereby the wide-ranging nature of the species necessitates conservation measures in areas larger than those encompassed by PAs. Yet, the increased interface between such species and people in the larger landscape aggravates the incidence of human–wildlife conflict (e.g., Naughton-Treves, 1998; Madhusudan, 2003; Karanth et al., 2013a). It is imperative therefore to carefully consider the implications of human–wildlife conflict for the long-term viability of species before undertaking landscape-scale conservation measures. Our results emphasize the need for caution and indicate that human–wildlife conflict can have a strong detrimental influence on wildlife populations.

Theoretical studies posit that there exists a critical habitat level below which a given population cannot persist (Lande, 1987; Fahrig, 2001). We assessed the synergistic influence of habitat degradation and HEC on population viability, and found evidence for a threshold determined by interactions between core habitat availability and  $HEC_m$  (Figs. 2 and 3). Our results suggest that as conflict induced mortality increases, a greater percentage of core area may be required to avoid quasi-extinction (Fig. 3a), or substantial population decline (Fig. 3b). We highlight that populations may be highly sensitive to a specific range of conflict-induced mortality; under the assumptions of our study, this range extended between  $HEC_m$  that we considered to be moderate to moderate-high. Within this range, a small increment in  $HEC_m$  necessitated a disproportionately large increase in  $Area_{core}$  to avoid quasi-extinction. Thus, conservation efforts will need to maintain conflict-induced mortality rates at lower levels than that identified as critical ranges, and more significantly, be sensitive to even small increments in mortality to ensure long-term population viability of conflict-prone species.

These threshold effects make it imperative that data on conflict-related mortality of endangered species be collected regularly and systematically. Reports of the number of animals killed due to human–wildlife conflict exist for some species. For example, the Monitoring of Illegal Killing of Elephants (MIKE) program of the Convention on International Trade in Endangered Species (CITES) maintains records of anthropogenic elephant mortality across Africa and Asia. While these data have been used to estimate the ratio of number of carcasses illegally killed to the total number of carcasses encountered (e.g., Burn et al., 2011), there are difficulties and assumptions associated with translating raw numbers of elephants killed to a mortality rate. Chelliah et al. (2013) used a modeling approach to arrive at a likely conflict-induced 5-year mortality rate of 0.015 for female elephants in Nagarhole National Park, India. Although this mortality rate is low relative to the  $HEC_m$  range we used in our study, data on other conflict-prone species indicate that annual human-caused mortality rates outside PAs can be very high: 20.3% for African wild dogs *Lycaon pictus* (Woodroffe et al., 2007), 39.0% for African lions *Panthera leo* (Woodroffe and Frank, 2005), and 35.8% for leopards *Panthera pardus* (Balme et al., 2010). Therefore, it is important to test the effects of an entire range of plausible HEC-induced mortality rates on elephant population dynamics so as to encompass future scenarios of increasing conflict and landscapes for which mortality rates are either unreliable or unavailable. We chose a plausible  $HEC_m$  upper limit of 0.10 based on Sukumar et al. (1998), who considered annual female elephant mortality rates of  $\geq 8\%$  as high. Threats such as poaching need to be quantified in a similar manner as they can have an additional deleterious effect on survival (Blake and Hedges, 2004) and thereby lead to population declines at much lower conflict-induced mortality rates. Furthermore, we note that species with long generation times might show a delayed response to factors that adversely affect their populations (e.g., conflict-

induced mortality), as well as those that ameliorate threats to survival (i.e., conservation interventions) (Tilman et al., 1994; Armbruster et al., 1999). This is evident in our results on time to quasi-extinction (Fig. 2b).

The interactive effects of habitat availability and HEC on population persistence assume significance in the context of the area falling under inviolate core areas in India, and elsewhere. For example, while the average area covered by Elephant Reserves in India is 2383 km<sup>2</sup>, only 37% of this area on average is occupied by PAs (Government of India, 2005). Although PAs are generally purported to serve as refuges against anthropogenic threats (Margules and Pressey, 2000; Hansen and DeFries, 2007), it is important to note that they can also include 'areas of co-occurrence' and resultant human–wildlife conflict (e.g., Banerjee et al., 2013). Thus, many conflict-prone species may in reality face human-induced mortality in significant proportions of their habitat (Woodroffe and Ginsberg, 1998; Robinson and Bennett, 2000; Mills, 2012). Based on our results, we strongly suggest that any increase in conflict-induced mortality needs to be simultaneously compensated by augmentation of inviolate core habitat and vice versa. In contrast, both habitat loss and conflict-induced mortality are likely to increase in many contexts (e.g., Chartier et al., 2011), suggesting that these threats are synergistically pushing conflict-prone species towards extinction.

Extending conservation measures to CAs outside inviolate core areas can be an effective strategy to reduce extinction risk through increased space- and resource-availability (Athreya et al., 2013). However, there exist few guidelines to aid in conservation decisions regarding trade-offs between the quality of CAs—defined for example in terms of resource availability and existence of anthropogenic threats—and their size. Our results indicate that CAs can augment population abundance provided HEC-induced mortality is low (Fig. 4). Importantly, at a low  $HEC_m$  of 0.025, a relatively small but good quality CA was associated with greater benefits (Fig. 4b) than a CA twice its size but inferior in quality (Fig. 4c). Thus, our results suggest that habitat restoration and conflict resolution in the CA may be as important as, or more important than, securing large CAs. This is a key finding in the context of conservation planning in areas where humans and wildlife co-occur.

Conservation landscapes that support wildlife populations may be comprised of multiple inviolate core areas interspersed within a CA (e.g., Sanderson et al., 2002b; Wikramanayake et al., 2004). We found that alternative core configurations (i.e., a single core versus multiple cores summing up to the same area) led to different equilibrium population sizes, with multiple cores leading to smaller equilibrium population size. However, core habitat loss was substantially more important in influencing elephant population dynamics than the core area configuration per se (Fig. A2). We acknowledge the possibility of scenarios where  $K_{CA} > K_{core}$  given the generalist feeding habits of the Asian elephant and their potential preference for resources available in a moderately disturbed CA (Fernando, 2006; Fernando and Leimgruber, 2011). Under such scenarios, equilibrium population size would be higher than those reported here when  $HEC_m$  is low. At higher  $HEC_m$ , however, detrimental effects of anthropogenic mortality will likely exceed benefits of additional habitat offered by the CA. Asian elephants generally occur in lower densities in primary rainforests than dry and more open forests (Sukumar, 2003). Therefore, scenarios where  $K_{CA} > K_{core}$  can potentially occur in regions where PAs are largely comprised of rainforests, and surrounding CA regions are relatively less disturbed. However, protected areas in countries that support a majority of the extant Asian elephant population (India and Sri Lanka) include drier forests and grasslands (Sukumar, 2003; Fernando and Leimgruber, 2011). In addition, there is little evidence from Asia or Africa to suggest a higher

carrying capacity for elephants in the CA as compared to the core; in fact, studies from Africa suggest that elephant population density in CA regions is at best equivalent to that in the core (Stokes et al., 2010), and can be as low as 17% of core densities (Blake et al., 2007).

Asian elephant densities vary considerably throughout their range, from as low as 0.25 elephants km<sup>-2</sup> to >3 elephants km<sup>-2</sup>, as used in this study (de Silva et al., 2013). Furthermore, some elephant populations may be less productive and have lower fecundity than that used to parameterize our model (de Silva et al., 2013); populations characterized by low fecundity may be rendered less resilient to HECm. We tested the generality of our results by modeling elephant population dynamics under conditions of (a) lower density estimates, (b) lower fecundity estimates, and (c) a combination of lower density and lower fecundity. We found that the interactive effects of HECm and core habitat loss were more pronounced particularly in populations with low densities, but also in less fecund populations (Fig. A3). Populations characterized by low density and/or low fecundity faced detrimental effects of HECm even under scenarios of minimal core habitat loss, and their extinction times were considerably lower. We further note that the negative effects of core habitat loss and HECm on small populations are likely to be greater than our study suggests because our deterministic model did not consider environmental and demographic stochasticity, both of which would increase extinction probabilities (Armbruster et al., 1999).

We recognize that behavioral adaptations of species, arising from their perception of the CA and resultant decisions to use these areas of co-occurrence (e.g., Srinivasaiah et al., 2012), might lead to results different than those reported here. For example, animals might be drawn towards the CA because of the availability of nutrient-rich resources in crop fields or prey in the form of livestock (Sukumar, 2003; Treves and Karanth, 2003). This possible preference in combination with heightened mortality risk might render the CA an ecological trap (Robertson and Hutto, 2006). Conversely, species might show behavioral adaptations to avoid the risk-prone CA. We tested the likely implications of these behavioral adaptations: when HECm = 0.10, CA avoidance facilitated population persistence while an ecological trap scenario reduced equilibrium population size in relation to a 'no behavioral adaptation' scenario (Fig. A4).

Effective conservation of wide-ranging large mammals must necessarily encompass areas of human presence in addition to inviolate core areas. However, we suggest a note of caution while promoting conservation measures in regions delegated as CAs to core habitat. With continuing human–wildlife conflict, retaliatory killings by people in the CA will likely have a strong impact on population viability, as evidenced by this study. We therefore emphasize the need to take counter-measures to effectively reduce human–wildlife conflict and associated mortality (reviewed in Treves et al., 2009). The close juxtaposition of people and wildlife clearly poses a challenge for the conservation of endangered, conflict-prone fauna; ironically, it is these human-dominated landscapes that perhaps offer species like the Asian elephant the best chance of survival over time.

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## Appendix A. Supplementary material

Schematic representation of our model; effects of (1) core area configuration, (2) variation in population size and fecundity, and (3) behavioral adaptations on elephant population viability under scenarios of increasing HECm and core habitat loss. Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2014.05.026>.

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