Conservation conflict in Nepal: An examination of the pattern and ecological dimension of human-wildlife conflict and wildlife conservation

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Eidesstattliche Versicherung

Declaration

Hiermit erkläre ich an Eides statt, dass ich die vorliegende Dissertationsschrift selbst verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe.

I hereby declare, on oath, that I have written the present dissertation by my own and have not used other than the acknowledged resources and aids.

Hamburg, 02.05. 2018

(Krishna Prasad Acharya)

Summary

Human-wildlife conflict is recognized as one of the most challenging conservation issues worldwide. The problems have been compounded by unsustainable exploitation of forest areas to meet human needs that often contradict with needs of wildlife species. The problem is particularly acute where the mega-herbivore and charismatic carnivores such as tigers, rhinoceros, leopards, elephants and bears come into conflict with humans. These species have already suffered the highest shrinkage of habitat range. Consequently, conservation planning has evolved to consider multi-level approaches, while accounting for species-specific requirements, to maximize conservation outputs. Human-wildlife conflict, however, has remained unabated — even escalating in several previously unreported sites. The need to create an extensive forest landscape with no human intrusion and fragmentation has become increasingly evident, but in practice the aim to protect all areas of biological significance is unrealistic. The central focus of a conservation strategy should include an understanding of species-specific conflict patterns and their underlying mechanisms. The following summary of this cumulative dissertation presents key issues of wildlife conservation in the face of growing human-wildlife conflict at the landscape level. These issues included (a) the spatial and temporal pattern of human-wildlife conflict, (b) drivers of human-wildlife conflict, and (c) conservation of non-conflict species.

The first part of the comprehensive summary provides the thematic context of three articles. This thematic context consists of the theoretical and empirical background associated with human-wildlife conflict, species conservation and management. It introduces human-wildlife conflict and wildlife conservation and presents the main terms and definitions. Then, a 'framework of human-wildlife conflict and conservation' focuses on three key issues: (a) pattern of human-wildlife conflict, (b) drivers of human-wildlife conflict, and (c) conservation in the face of conflict. The 'conservation in the face of conflict' provides short summaries of four candidate species studied in this dissertation.

The second part of the comprehensive summary integrates the three articles that constitute the cumulative dissertation into the thematic context. The first article focuses on the nationwide pattern of human fatalities and injuries caused by attacks by Bengal tigers (*Panthera tigris*

tigris), Asiatic elephants (*Elephas maximus*), one horned rhinoceros (*Rhinoceros unicornis*) and common leopards (*Panthera pardus*). The paper presents a pattern of wildlife-induced human death and injury over a five-year period, and examines the pattern by seasons, months and locations. The paper shows that while conservation is paying off, there is a growing trend of conservation conflict throughout country. The second paper examines the role of habitat requirements and forest fragmentation in creating human-wildlife conflict. The paper demonstrates that a large undisturbed forest is needed to reduce human-wildlife conflict although there are considerable variations between wildlife species. The third article focuses on the status of population recovery of gharials (*Gavialis gangeticus*) in Nepal. It shows that the gharial population is growing, but faces critical conservation challenges. The gharial populations are sex-biased and limited within a protected area system.

Each article is presented with an abstract, followed by a discussion of the respective article in the thematic context, showing the implications and recommendations of the findings for the issues presented in the first part. Based on the results of the articles and their discussion in the thematic context, specific conclusions on the conservation in the face of conflict are drawn. The first part of the conclusion shows that human-wildlife conflict is pervasive and growing outside of protected areas. The second part shows that landscape-based protection is not panacea of all conservation problems of all species. There is a need for a multi-species focused conservation strategy to sustain the wildlife population throughout landscapes.

The complete versions of the three articles, together with the comprehensive summary, constitute this cumulative dissertation.

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Part I. Thematic context

1. Introduction

Nepal is known for its exceptionally high biodiversity and successful conservation of globally threatened fauna such as tigers, leopards, rhinoceros and crocodiles through several in-situ and ex-situ conservation programs (Richard et al., 2013). In the past, conservation largely depended on national parks controlled by central governments. This approach is now increasingly recognized to be impacted at several levels, often related to the socio-economic and cultural dimensions of the people who depend on forests for their livelihood (Bookbinder et al., 1998; Brown, 1998; Heinen and Yonzon, 1994). This is important for Nepal because nearly 85% of the population in rural areas is actively engaged in agriculture, forestry and fishery (CBS, 2012), where forests provide basic and vital livelihood support such as firewood, livestock fodder, medicinal herbs and timber (Baral et al., 2007; Bookbinder et al., 1998; Brown, 1998). There are strong debates about the conservation and social benefits of such integrated approach (Jansen and Shen, 1997). In some cases, public support for conservation has deteriorated as the human-wildlife conflict (HWC) increases (Madden, 2004). Studies suggest that human-wildlife conflict has been reported from different parts of the country (Pandey et al., 2015; Pant et al., 2015). Most of such conflict involved large iconic mega-fauna that have global conservation significance (Bhattarai and Fischer, 2014; Gurung et al., 2008; Jnawali, 1989; Pant et al., 2015). Conservation biologists need to understand whether conservation success and conflict are mutually evolving (Treves et al., 2007), and if conflict is always counterproductive to conservation (Inskip and Zimmermann, 2009).

Human–wildlife conflict is a conservation problem that increasingly threatens the continued existence of some of the world's most endangered species (Dowie and Dickman, 2010). It occurs when wildlife species and humans compete with each other for space, food and life (Treves et al., 2007). With the expansion of human population and subsequent infrastructure development, forest areas have been fragmented and are subjected to intense human modifications (Bhattarai et al., 2012). Consequently, human-wildlife conflict has become a complex conservation problem in Nepal. The conflict occurs in many forms such as crop raiding, property damage, interruption of normal activities of local people, death and injury of people and retaliatory killings of wildlife species involved (Treves et al., 2007). A number of methods have been used to mitigate and prevent human-wildlife conflicts, which range from physical barriers (e.g., ditches and canals, biological and electric fences), chasing conflict wildlife by noise making (e.g., shouting, drum-beating and use of fire crackers), translocation and culling of conflict animals, plantation of unpalatable crops, compensation and insurance schemes to use of modern technology such as satellite telemetry (Distefano, 2015; Madden, 2004; Sugumar and Jayaparvathy, 2013). Such measures, however, are not always successful in improving human-wildlife co-existences (Distefano, 2015; Treves et al., 2007). This thesis focuses on conservation conflict and conservation success and explores the relationship between humans and wildlife in the increasingly complex ecological contexts. In doing so, this thesis —in particular — addresses the following key research questions:

1. Are globally threatened wildlife species found in Nepal involved in conflict with humans?
2. What are the spatial and temporal patterns of conflict by the species across a large landscape?
3. Does landscape fragmentation drive wildlife into conflict with humans?
4. Are species that are not involved in conflict such as gharials (*Gavialis gangeticus*) better protected?

A particular focus is given to four wildlife species, namely, common leopard (*Panthera pardus*), Bengal tiger (*Panthera tigris tigris*), one horned rhinoceros (*Rhinoceros unicornis*) and Asiatic elephant (*Elephas maximus*) to assess patterns of conflict and their relationship with habitat requirement and forest fragmentation. The conservation status of gharials (*Gavialis gangeticus*) is assessed as a case study of a non-conflict species.

1.1 Wildlife conservation in Nepal: A retrospect

Nepal has a long history of wildlife conservation, dating back several centuries when it was guided by religions, spiritual beliefs and traditions (Spiteri and Nepal, 2006). Modern conservation began shortly after the 1950s with the downfall of the Rana autocracy in 1951. Nepal's first planed development policy, the five-year plan (1956-1961), acknowledged the importance of conservation and management of flora and fauna (BPP, 1995). The first rhino sanctuary was established in 1964 (Heinen and Shrestha, 2006). Conservation policies in this period were mainly 'preservation oriented' —advocating for centralized regulatory control (Mehta and Kellert, 2017). The rhino sanctuary was expanded to create the Chitwan National Park in 1973. Nepal made remarkable progress in establishing protected areas of various categories (e.g., national parks, wildlife reserves) in the 1970s (Bhattarai et al., 2012), which involved relocation of human settlements, translocations of wildlife populations and allocation of budget in conservation (Brown, 1997; Heinen and Shrestha, 2006; Müller-Böker and Kollmair, 2015). This approach was successful in restoring the diminishing populations of tigers, elephants, rhinoceros and gharials (Basnet, 2014; Martin et al., 1996; Paudel et al., 2012). However, the strict conservation approach with little or no regard to the needs of the local community eventually eroded community support for conservation (Heinen and Shrestha, 2006; Martin et al., 1996). Consequently, the conservation approach failed to mitigate human caused threats to large mammals such as human disturbance, retaliatory killings and wildlife poaching (Basnet, 2014; Ferraro, 2002; Keiter, 1995; Seeland, 2000).

Nepal gradually adopted community-based conservation strategies starting in the early 1980s to address the problems arising from the 'preservation oriented' conservation approach. Integrated conservation and development programs (ICDPs) were implemented to foster community participation in wildlife conservation while providing local livelihood support (Spiteri and Nepal, 2006). Conservation area rules and buffer zone management regulations were formulated to provide legal and institutional infrastructure used to involve local communities in protected area management (Heinen and Shrestha, 2006; Sharma, 1990; Stræde and Treue, 2006). Thus, people living in the periphery of protected areas, known as the buffer zone, are recognized as the major stakeholder of wildlife conservation. The buffer zone is an area of human settlements and forests surrounding core area of parks where local people are actively involved in forest conservation

(Stræde and Treue, 2006). Amendments of National Parks and Wildlife Conservation Act (NPWCA 1972) were made to channel back 30-50 % park revenue for community development works in buffer zone (Mehta and Heinen, 2001; Sharma, 2017).

The buffer zone program was instrumental in ameliorating the park-people relations. However, the isolated protected areas alone were insufficient in maintaining the meta-population of large mammals, especially tigers, rhinoceros, leopards and elephants (Wikramanayake et al., 2004, 2011). Thus, the need became clear for a conservation strategy beyond the protected areas — referred to as landscape conservation— that would create wildlife corridors between core areas and maintain ecological functions and services (Smith et al., 1998; Wikramanayake et al., 2004). Nepal began landscape conservation in the early 2000s with the implementation of Terai Arc Landscape (TAL), which successfully restored diminishing tiger populations (Smith et al., 1998; Thapa et al., 2017; Wikramanayake et al., 2011; MoFSC, 2015). Currently five conservation landscapes (Chitwan Annapurna Landscape, Sacred Himalayan Landscape, Kanchenjunga Landscape, Kailash Sacred Landscape and Terai Arc Landscape) have been adopted with different conservation priorities (MoFSC, 2015). These conservation landscapes cover as much as two-thirds of Nepal's land area, including non-protected areas.

1.2 Human wildlife interaction and conflict

Human–wildlife interaction is inevitable. However, the extent of interaction and its consequence vary in a wide variety of contexts (Angelici, 2015; Rissman et al., 2007). The interactions have potential for significant impacts on both humans and wildlife. This requires a better understanding of the different dimensions of human-wildlife interactions. When humans and wildlife come into proximity and compete for common but limited food (Distefano, 2015) and space (Carter et al., 2012), there are usually negative interactions, which result in various types of conflicts such as the killing of wildlife (Oli et al., 1994; Paudel, 2012), death or injury of humans (Gurung et al., 2008; Saberwal et al., 1994), crop damage/destruction (Gillingham and Lee, 2003; Heinen, 1993; Linkie et al., 2007; Sapkota et al., 2014; Thapa, 2010), property damage (Peterson et al., 2010) and loss of livestock (Dar et al., 2009; Karanth et al., 2013).

Human-wildlife conflict has existed for centuries (Kruuk, 2002), which ranges from the loss of both conflict wildlife and humans to wildlife extinction and economic loss (Woodroffe et al., 2005). For example, the Tasmanian tiger was hunted to extinction because farmers perceived existential threats to their sheep (Paddle, 2002). Similarly, risks posed by wildlife to aviation (e.g., collusion of birds with aircraft) is one of the several examples of growing new types of problems (Martin et al., 2011).

Livestock depredation by wild carnivores impacts nearly 12% of the annual net family income in areas bordering wildlife reserves in Zimbabwe (Butler, 2000). Chomba et al. (2012) conducted a nationwide study on the pattern of human death by wildlife attacks in Zambia and found more than half of human deaths (53%) were caused by Nile crocodiles, followed by hippos (19%) and elephants (18%). Hundreds of people are killed by lions and crocodiles annually in Mozambique, Tanjania and Kenya (Dunham et al., 2010; Packer et al., 2005). In the Golan heights of Israel, golden jackle (*Canis aureus*) are responsible for the deaths of 1.5-1.9 % calves on average born each year (Yom-Tom et al., 1995). In Asian countries, large mammals such as tigers and elephants, snow leopards, Tibetan wolfs, Asian lions and leopards are often reported as major sources of conflicts in areas where they share habitats with humans (Karanth et al., 2013; Mishra, 1997; Nyhus and Tilson, 2004; Oli et al., 1994; Pant et al., 2015; Saberwal et al., 1994).

1.3 Ecological aspects of human-wildlife conflict

Human-wildlife conflict occurs when resource use overlaps between wildlife and humans. In general, wild animals avoid humans by avoiding or underutilizing disturbed areas (Harihar and Pandav, 2012; Paudel and Kindlmann, 2012). However, the extent of the responses varies markedly among the species in question (Arroyo-Rodríguez and Dias, 2010; Beale and Monaghan, 2004; Kerley et al., 2002). Studies have suggested that human-wildlife conflict has both a socio-cultural and ecological context (Dowie and Dickman, 2010). Carter et al. (2012) noted that tigers co-existed with humans in human disturbed areas of Chitwan National Park by temporarily avoiding disturbed areas during day time.

Much attention has been given to the pattern of conflicts (Saberwal et al., 1994; Thapa, 2010), mitigation strategies (Thirgood and Redpath, 2008), and behavior of humans and wildlife in question. However, human-wildlife conflict has not been assessed through a landscape ecology perspective based on spatial patterns of habitats and their fragmentation (e.g., shape, size and connectivity of forest habitat and their diversity). This is important for two reasons: First, human disturbance on biodiversity is increasing mainly due to expanding human populations and infrastructure development (e.g., roads, highways, industries etc) (Sanderson et al., 2009). Thus, an increasing proportion of global biodiversity is located in human-modified landscapes (de Thoisy et al., 2010). Second, landscape conservation has been identified as an effective strategy to address problems of insular populations confined within small forest patches in the human dominated landscape (Carroll, 2007; Coppolillo et al., 2004). Thus, in such areas, conservation is now, in a broader sense, managing both humans and wildlife populations. Human dominated forest landscapes are subjected to varying degrees of human disturbances, and creating a win-win situation for wildlife and human is a serious challenges (Beier and Noss, 1998; Simberloff and Cox, 1987). Thus, it is important to understand the relative effects of landscape composition and configuration on wildlife distribution and abundance.

1.4 Conservation milestones in Nepal in the face of conflict

Nepal now has a protected area system that covers more than 23% of its national territory, and many endangered species are now more secure in Nepal despite a rapid human population growth, various political conflicts and the country's poor economic conditions (Baral and Heinen, 2007, 2009). Outside the protected areas, the forest cover has increased over time mostly due to the successes of community forestry programs (Acharya, 2002; Gautam et al., 2002). This has contributed to the restoration of locally extinct species in their former historical range. Although biodiversity conservation is an unexpected benefit of community forestry in Nepal (Mikkola, 2002), it —however— emerged as a practical conservation model for involving local people in the landscape conservation.

Recent studies have shown that conservation is paying off: populations of tigers, rhinoceros, crocodiles and elephants have been increased and restored in some of their historical ranges (DNPWC, 2016, 2017; Subedi et al., 2013; Wikramanayake et al., 2004). However, increasing incidences of human-wildlife conflict throughout the country including in previously unreported areas suggest that challenges to wildlife conservation are more serious than expected (Bhattarai and Fischer, 2014; Pandey et al., 2015; Pant et al., 2015). Consequently, species may face multiple threats such as illegal hunting and trade and non-compliance of conservation law (Lenzen et al., 2012). Illegal hunting of rhinoceros in Nepal remained unabated for several decades— despite having strict penalties and being strictly guarded by the Nepalese army in the protected area. Nepal, however, successfully controlled rhinoceros poaching by adopting a multi-stakeholder partnership with local communities serving as a cautious observant of any suspicious activities in community (Acharya, 2016). Community support, therefore, is important in the conservation landscapes where rhinoceros are recently reestablished. Landscape conservation with particular focus on flagship species is expected to protect non-targeted species that share the same habitats (Caro, 2010), although there is considerable debate about the usefulness of this approach (see review (Rodrigues and Brooks, 2007; Zacharias and Roff, 2001). There is little information about the fate of species that are not involved in conflict with humans in the conflict hotspots.

1.5 Structure of the comprehensive summary

The comprehensive summary provides a snapshot of key issues needed to understand conservation conflict in Nepal, particularly human-wildlife conflict involving fatalities and injuries from attacks of one horned rhinoceros, Bengal tiger, Asiatic elephant and common leopard. The thesis provides a nationwide overview of spatial and temporal patterns of conflict and explores to what extent landscape fragmentation affects conflict. The thesis presents gharials as a special case to assess the conservation status of species that for several reasons are not involved in conflict. Firstly, gharials rarely attack humans, and therefore people have little or no animosity towards them (Stevenson, 2015). However, human induced threats such as fishing, sand mining and river pollution are major determinants of their endangerment (Maskey and Percival, 1994). Secondly, gharials share the same riverine landscape protected for rhinoceros, elephants and tigers in Nepal. Thirdly, gharials conservation involves both in-situ and ex-situ conservation, and conservation of gharials, in part, depends on wider public support —which may be largely determined by levels of conflict with rhinoceros, elephants and tigers.

The articles are briefly summarized and discussed in the context of the framework in the second part of this comprehensive summary.

These articles are:

Acharya, K.P., Paudel, P.K., Neupane, P.R., Köhl, M., 2016. Human-wildlife conflicts in Nepal: Patterns of Human fatalities and injuries caused by large mammals. Plose ONE 1–18.

Acharya, K.P., Paudel, P.K., Jnawali, S.R., Neupane, P.R., Köhl, M., 2017. Can forest fragmentation and configuration work as indicators of human–wildlife conflict? Evidences from- human death and injury by wildlife attacks in Nepal. Ecol. Indic. 80, 74-83. https://doi.org/10.1016/j.ecolind.2017.04.037

Acharya, K.P., Khadka, B.K., Jnawali, S.R., Malla, S., Bhattarai, S., Wikramanayake, E., Köhl, M., 2017. Conservation and Population Recovery of Gharials (*Gavialis gangeticus*) in Nepal. Herpetologica 73, 129–135.

1.6 Definitions

1.6.1 Human-wildlife conflict

Human–wildlife conflict is defined and interpreted in a variety of ways. Peterson et al. (2010) reviewed 422 research papers related to human wildlife conflict and found that the term referred to the conflict related to human food, human safety and property damage; and less attention was given to the coexistence between humans and wildlife. The focus is related to the human side of the equation. The 5th World Park Congress brought human wildlife conflict (HWC) to the global stage as a part of an effort to address current challenges facing protected area management and conservation. A technical workshop, part of the World Park Congress, defined the conflict in a balanced approach:

> "Human-wildlife conflict occurs when the needs and behavior of wildlife impact negatively on the goals of humans or when the goals of humans negatively impact the needs of wildlife. These conflicts may result when wildlife damage crops, injure or kill domestic animals, threaten or kill people" (Madden, 2004).

This definition, however, does not specifically discuss property damage caused by wildlife such as damage to houses, livestock-sheds and more. Such damage is acute in the elephant home ranges, where elephants are prone to damage houses in search of food (Santiapillai and Jackson, 1990; Sugumar and Jayaparvathy, 2013; Pant et al., 2015).

1.6.2 Habitat fragmentation and metapopulation

Species specific habitat fragmentation assessment is important for the conservation of threatened animals because each species has a different ecological niche and dispersal capabilities. The concept of the ecological niche was introduced by Grinnell to focus on the habitat requirements need by a species to survive and reproduce (Grinnell, 1917). Hutchinson (1959) expanded this term by separating the habitats into the multiple resources required by a species. It included, among others, abiotic and biotic conditions as well as interspecies interactions.

Metapopulation analysis is a part of fundamental ecological research that provides both an empirical and conservation framework for conserving wildlife in fragmented landscapes (McCullough, 1996). This is because wildlife populations become more isolated as human activity increases in their habitat, and many populations are already in danger of extinction locally, regionally and globally (Wiens, 1996). A metapopulation is defined as " a set of location populations which interact via individuals moving between local populations" (Hanski and Gilpin, 1991). Interaction of wildlife populations is affected by loss and fragmentation of natural habitats, which has a detrimental effect on the structure and composition of their communities (Bender et al., 1998). Wildlife populations in small and fragmented habitats are at risk of extinction because of demographic stochasticity and inbreeding depression (Keller and Waller, 2002). Therefore, a large area is required to be set aside for wildlife conservation, which, however, is not possible because many areas of biological importance are already degraded beyond restoration (Sarkar, 2014).

Levin (1970) first coined the term metapopulation referring to “population of populations” as a part of his seminal work on insect populations in a “patchy environment”. Levins (1970) examined the rates of recolonization and extinction of species in patches and determined how metapopulations would persist through time. The idea regained attention, after being dormant for nearly 20 years, as natural habitats underwent rapid and rampant fragmentation leading to the local, regional and global extinction of several species (Wilcox and Murphy, 1985). Many of such fragmented patches are now designated as reserves, functioning much like habitat “islands” in a sea of unsuitable habitats (or developed areas) (Hilty et al. 2006). This contributed to the application of island biogeography: the study of the distribution and dynamics of species in island environments.

The importance of metapopulation structure in conservation planning came into prominence with the advent of new technologies and tools (e.g., radiotelemetry and GPS collars, GIS software) that enabled the handling of large data used to study how wildlife populations are distributed in the fragmented landscapes. This suggested an urgency of landscape level conservation with a focus on restoring wildlife corridors that facilitate wildlife movement between patches (Beier and Noss, 1998; Bennett, 1990; Harrison and Bruna, 2011). Corridors minimize the negative effect of habitat fragmentation and isolation by allowing movement between spatially separated habitat patches (Keller and Waller, 2002; Wilcox and Murphy, 1985).

2. Framework of human-wildlife conflict and conservation

The following chapter outlines the pattern of human-wildlife conflict. First, a brief outline of human-wildlife conflict is given. It is followed by drivers of human-wildlife conflict, especially ecological drivers in the context of landscape conservation of large mammals in the human-dominated landscapes. The framework is completed by a brief description of the current status of rhinoceros, tiger, elephant, common leopard and gharial populations in Nepal.

2.1 Pattern of human-wildlife conflict

In a predominately agrarian society like Nepal, human-wildlife conflict has different dimensions than those of developed and industrial countries, partly because of different socio-cultural aspects (Dowie and Dickman, 2010; Thirgood and Redpath, 2008). Local people rely on forest for land, subsistence resources (e.g., fodder, firewood, medicine) and commercial products (e.g., timber) (Primack, 2012). The patterns of conflict, therefore, are different, reflecting socio-cultural aspects of the local community and wildlife species involved. The common patterns of conflict under scientific investigation in Nepal include (a) crop damage (Jnawali, 1989; Thapa, 2010), (b) livestock damage (Jackson et al., 1996, 2004), and (c) property damage (Pant et al., 2015). The conflict patterns also have a spatial dimension, especially within protected areas or adjoining corridors (Carter et al., 2012; Pandey et al., 2015). Conflict occurring outside the protected area is poorly investigated. The species-specific conflict patterns are also reported in Nepal such as human-tiger conflict (Bhattarai and Fischer, 2014; Gurung et al., 2008), human-elephant conflict (Pant et al., 2015), human-rhinoceros conflict (Jnawali, 1989) and human-snow leopard conflict (Oli et al., 1994). Recent research suggests that human-wildlife conflict (HWC) continues to be a major problem in Nepal's biodiversity hotspots (Karanth and Nepal, 2012). All these studies are confined to a few protected areas and provided little information on human fatalities and injuries caused by wildlife attacks. (Karanth et al., 2013) noted that there were co-occurrence of conflict and human death and injury constitute a serious conservation challenge. The common human reaction is to retaliate against wildlife involved in the conflict (Woodroffe et al., 2005).

2.2 Drivers of human wildlife conflict

While studying the patterns of human-wildlife conflict provides crucial information on the dynamics of HWC, it offers little information about the underlying mechanisms. Several conflict mitigation tools have been used in the past, but none proved successful in reducing human-wildlife conflicts. This is attributed to faulty mitigation strategies that often focus on the technical aspects of conflict reduction while ignoring the ecological drivers of human-wildlife conflict (Dowie and Dickman, 2010; Manfredo and Dayer, 2004). Effective conservation of wildlife populations requires an appropriate assessment of how habitat fragmentation influences the spatial patterns of habitat occupancy across landscapes (Hilty et al., 2006). Fewer studies have utilized key ecological traits, such as behavior of species in fragmented patches, to develop a well-founded strategy for conflict mitigation (Bélisle, 2005).

2.3 Conservation in the face of challenges

Biodiversity conservation is a complex conservation problem, which is the result of an unprecedented level of threats resulting from unsustainable exploitation of resources, climate change and environmental pollution including wildlife trade and poaching (Rands et al., 2010). There have, however, been some examples of conservation successes despite these challenges (Ferraro, 2002; Jepson and Whittaker, 2002; Rodrigues and Brooks, 2007). Although measurement of conservation success is subjective and difficult to ascertain, the increasing public support for conservation and improved scientific understanding of ecosystem and wildlife ecology have led to significantly more effective conservation strategies (Hannah, 2011). Nepal has made an exemplary conservation milestone for protecting rhinoceros, tigers, elephants and gharials. The following sections provide an overview of these species.

2.3.1 Rhinoceros

The greater one horned rhinoceros (*Rhinoceros unicornis*) is one of the three rhinoceros species found in Asia: the other two being the Javan rhinoceros (*Rhinoceros sondaicus*) and the Sumatran rhinoceros (*Dicerorhinus sumatrensis*) (Foose et al., 1997). Two other rhinoceros species, the black rhinoceros (*Diceros bicornis)* and white rhinoceros (*Ceratotherium simum*) are limited to Africa (Emslie, 1999). The greater one horned rhinoceros —hereafter rhinoceros— is now very rare and confined to a few scattered, isolated populations within its former geographical range (Subedi et al., 2013) . Rhinoceros are now extinct in Myanmar, southern China and Indo-China (Grubb, 2005). Currently, a total of 3500 individuals exist in the few isolated protected areas in Nepal and India, including nearly 645 individuals in Nepal (DNPWC, 2017). Rhinoceros are protected in Nepal by the National Parks and Wildlife Conservation Act (NPWCA 1973). They are listed as vulnerable (VU) in the IUCN's Red List (IUCN, 2018) and naturally assessed as an VU in Nepal. They are included in Appendix 1 of CITES (http://checklist.cites.org).

Figure 1: The greater one horned rhinoceros (*Rhinoceros unicornis*) in Chitwan National Park (Photo by Sagar Giri)

Rhinoceros in Nepal are found in three separated national parks —Chitwan, Bardia and Shuklaphanta— and their surrounding areas (DNPWC, 2017): the latter two protected areas (PAs) include a small, reintroduced population. In the early 1950s, Nepal had an estimated 1,000 individual living rhinoceros (DNPWC, 2017). Chitwan valley, a prime habitat of rhinoceros, lost a large tract of forest areas with the influx of human migrants from nearby hills. Consequently, the rhinoceros population declined to fewer than 100 individuals by the end of the 1960s (DNPWC, 2017; Richard et al., 2013). However, conservation measures taken by late 1950s helped to avert a total collapse of the rhinoceros population, but until 1986 all were confined to the Chitwan National Park (CNP) (Dinerstein and Price, 1991). Such a small population is at risk of extinction due to various environmental and genetic stochasticity. Therefore, a total of 87 rhinoceros were translocated between 1986 and 2003 from Chitwan National Park (CNP) to Bardia National Park (BNP), as well as four rhinoceros to Sukhlaphanta Wildlife Reserve (now Shuklaphanta National Park- SnNP) in 2003 to create a third population in Nepal (DNPWC, 2017). However, the number of rhinoceros in BNP dropped to 31 in 2007 from 67 in 2000 partly due to heavy poaching during a phase of armed conflicts (Thapa et al., 2013). With end of armed conflict, an additional five rhinoceros were reintroduced in 2017 to supplement this small population (DNPWC, 2013).

Now, rhinoceros are found in CNP, BNP, SnNP and conservation landscapes adjoining these protected areas (Subedi et al., 2013). These conservation landscapes include forest areas that have been successfully restored with the implementation of Terai Arc Landscape. Barandabhar Forest Corridor of CNP and Khata Corridor of BNP, for example, are conservation landscapes, outside of protected areas, that harbor rhinoceros (DNPWC, 2017). At the same time, human-rhinoceros conflict has been reported in these new areas. Rhinoceros are a habitat specialists and prefer tall and short grasslands and riverine forests— avoiding the sal (*Shorea robusta*) forest (Dinerstein and Price, 1991). Availability of suitable habitats in the landscapes is important for rhinoceros conservation, which, otherwise, may drive them into agriculture lands and create conflict.

2.3.2 Elephant

The Asiatic elephant (*Elephas maximus*) is the largest surviving terrestrial mega-fauna of Asia, and one of the two elephant species (African savanna elephant *Loxodonta africana*). The Asiatic elephant (hereafter elephant) is an endangered (EN) species by IUCN's Red list of threatened species (IUCN, 2018). Elephants were widely distributed through much of Sumatra, Java, and Borneo, West Asia along the Iranian coast into the Indian subcontinent, South-east Asia including, and into China at least as far as the Yangtze-Kiang, covering an estimated area of 9 million km^2 (Sukumar, 1992, 2003, 2006). They are locally extirpated from much of their former geographical range and survive in a few and small fragmented populations in India, Bangladesh, Bhutan, Nepal, and Sri Lanka in South Asia and Cambodia, China, Indonesia (Kalimantan and Sumatra) Lao PDR, Malaysia (Peninsular Malaysia and Sabah), Myanmar, Thailand, and Viet Nam in South-east Asia.

Figure 2: Asiatic elephant (*Elephas maximus*) in Bardia National Park (Photo by Ashok Ram)

Elephants found in Nepal, Bhutan and India were once a large metapopulation of Indian elephants but after a long period of isolation formed into four distinct subpopulations: 1) North and Northeast India, 2) Central India, 3) Nilgiri, and 4) Anamalai - Periyar (Vidya et al., 2005). Nepal's elephants occupy the centerfold for the north and northeast Indian elephant populations which covers a large swath of area from Meghalaya to Uttar Pradesh (2,000 km). Wild elephants in Nepal are found in four clusters: eastern population (50-70 individuals including 10-13 resident individuals), central population (40-50 individuals) in Chitwan-Parsa complex, (3) the far western population (2-18 individuals) in the Churia foothills (DNPWC, 2008). These populations are the remnants of a large population of elephants (e.g., North and Northeast India). The eastern and possibly central populations of Nepal are a part of northeastern population whereas the western and far-western population is represented by the north population (Vidya et al., 2005). These populations used to roam along seasonal migratory paths along the Nepal-India border. With the expansion of human populations and forest fragmentation, elephants were increasingly restricted to small partially or completely isolated groups (Pradhan et al., 2011).

2.3.3 Tiger

Tigers (*Panthera tigris tigris*) are considered an iconic wildlife species in ecosystems where they are found (Dinerstein et al., 2007). This is because tiger conservation generally leads to conservation of entire ecosystems and wildlife communities, including their prey species (Wikramanayake et al., 1998). They were widely distributed throughout Asia, from Persia to Indonesia, and north to far eastern Russia and Korea (Sanderson et al., 2010). Tigers are extirpated from nearly 93% of historical range and confined into a few isolated protected areas and their adjoining forests in Bangladesh, Bhutan, Cambodia, China, India, Indonesia, Lao PDR, Malaysia, Myanmar, Nepal, Russia, Thailand and Vietnam (Dinerstein et al., 2007) (Table 1).

Photo 3: Royal Bengal Tiger (*Panthera tigris tigris*) in Chitwan National Park (Photo by Sagar Giri)

Of the nine sub-species of tigers, three species are extinct (Table 1). Bengal tiger (*Panthera tigris tigris)* are found primarily throughout the Indian sub-continent, mainly in Nepal (198 individuals), India (1706 individuals), Bangladesh (440 individuals) and Bhutan (75 individuals) (DNPWC, 2016). In Nepal, tigers are mostly found within protected areas: Parsa National Park, Chitwan National Park, Banke National Park, Bardia National Park and Suklaphanta National Park (DNPWC, 2016). Historically, Bengal tigers in Nepal were distributed along a large swatch of contiguous lowland forests, also known as ***Char Koshe Jhadi***, (Smith et al., 1999). Hunting records and anecdotal accounts suggest that they were present in the east of the Bagmati River (e.g., Trijuga forest and Koshi Tappu Wildlife Reserve) in the early 1970s (DNPWC, 2016).

Table 1: Range and status of different sub-species of tigers		
SN/Common Name	*Scientific name*	Range/status
1. Bengal tiger	*P. t. tigris*	Indian sub-continent
2. Caspian tiger	*P. t. virgata*	Formerly in Turkey through central and west Asia (extinct)
3. Amur tiger	*P. t. altaica*	Amur River region of Russia and China, and North Korea
4. Javan tiger	*P. t. sondaica*	Formerly in Java, Indonesia (extinct)
5. South China tiger	*P. t. amoyensis*	South-central China
6. Bali tiger	*P. t. balica*	Formerly in Bali, Indonesia (extinct)
7. Sumatran tiger	*P. t. sumatrae*	Sumatra, Indonesia
8. Indo-Chinese tiger	*P. t. corbetti*	Continental South-east Asia
9. Malayan tiger	*P. t. jacksoni*	Malay Peninsula

Source: Adapted from Tiger Action Plan, 2016 (DNPWC, 2017)

The government of Nepal initiated a systematic tiger conservation plan in the late 1960s. Chitwan National Park and Bardia National Park were established for tiger conservation (Heinen and Shrestha, 2006). The first Tiger Conservation Action Plan for Nepal was prepared in 1999 and was revised in 2007. Subsequently, a five-year Tiger Conservation Action Plan 2008-2012 was implemented (DNPWC/MoFSC/GoN, 2007). Meanwhile, the government developed a National Tiger Recovery Program (NTRP) in 2010 for five years. The second Tiger Conservation Action Plan (2016-2020) is an updated version of the first Tiger Conservation Action Plan. These series of conservation plans have been instrumental for successful implementation of the Terai Arc Landscape (TAL) strategy and action. The landscape strategy helped to restore tiger populations in their historical ranges in Nepal, particularly in Barandabhar corridor and protected forest (BCPF), Banke National Park (BaNP), Kailali-Kanchanpur complex (KKC), Khata corridor and protected forest (KCPF), Basanta corridor and protected forest (BCPF), Laljhadi corridor and protected forest (LCPF) and Bramhadev corridor (BC) (DNPWC, 2016). Periodic tiger census in Nepal suggests that tiger distribution is steadily expanding, and its population has been increased by 63% (198 individuals) since 2010 (DNPWC, 2016).

2.3.4 Common Leopard

Common leopards (*Panthera pardus*) are widely distributed throughout Africa and Asia but they are extirpated from much of their home range. Remaining populations are severely dwindled because of habitat fragmentation, isolation, deterioration, prey base declines and human prosecution (Lindsey et al., 2013; Selvan et al., 2014; Thorn et al., 2013). Leopards are listed as vulnerable (VU) in the IUCN's Red List (IUCN, 2018) and included in the Appendix 1 of CITES (http://checklist.cites.org). They are one of the wild distributed felids and found in a variety of habitats ranging from desert to tropical forests, to grasslands, rainforest and high mountains (Jnawali et al., 2011; Sunquist and Sunquist, 2002). This attributed to their extremely high adaptability to different habitats and diets (Hayward et al., 2006).

Common leopard (*Panthera pardus fusca*) is a subspecies found in the Indian subcontinent. In Nepal, leopards are found throughout the country, but they had very sparse distribution in the mid-hills mountain (Jnawali et al., 2011). The mid-hills was the first area occupied by major settlers of Nepal (Mikkola, 2002), which could have contributed to the sparse leopard population here. The region later witnessed an unprecedented reforestation, driven by community forests (Acharya, 2002) . Recent reports of leopard sightings including increased trend of human-leopard conflict and body parts seizures suggest that leopards are recolonized and their populations are increasing in Nepal (Paudel, 2016).

Figure 4: Common leopard (*Panthera pardus fusca*) in Chitwan National Park (Photo by Sagar Giri)

Leopard conservation in Nepal is a multi-faceted challenge. The soaring number of reported human causalities and injuries and livestock losses by the attacks of leopards suggests that site specific conservation programs are urgently needed (Paudel, 2016). In lowland Nepal, leopards share both habitat and prey-species with the more dominant large cat, the Bengal tiger (*Panthera tigris tigris*) (Jnawali et al., 2011). (Odden et al., 2010) found that leopards are displaced by tigers into park periphery and forest fringes outside of protected areas in Bardia National Park. This may be true for all lowland protected areas of Nepal. (Thapa, 2015) reported the human induced mortality of 45 individual leopards between (2009-2013) in Nepal. Recent reports showed that 22 leopards were retaliatory killed and 14 were rescued in last five years in Kaski district (DFO Kaski, 2018). This suggests that retaliatory killings could be many times higher than reported as most of such cases go unreported. Thus, there is an urgent need to assess the conflict and its underlying mechanism.

2.3.5 Gharials

The gharials (*Gavialis gangeticus)* are a critically endangered species according to IUCN's Red List of threatened species (IUCN, 2018). Gharials were once distributed across approximately 20,000 km^2 of riverine habitat of the Indus, Ganges, Brahmaputra, and Irrawady river systems. They are now limited to a few places in select river stretches in India and Nepal (e.g., National Chambal Sanctuary, Katerniaghat Sanctuary; Chitwan National Park, Son River Sanctuary, Satkosia Gorge Sanctuary (Groombridge, 1987; Stevenson, 2015).

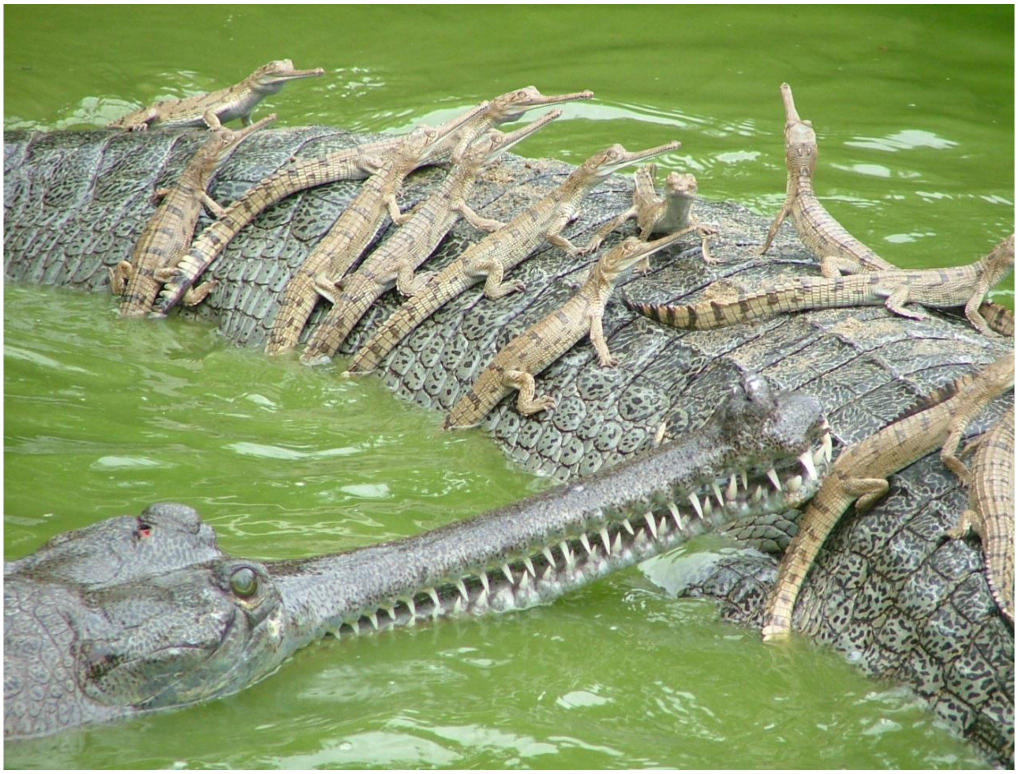

Figure 5: Gharial (*Gavialis gangeticus)* in Chitwan National Park (Photo by Krishna Acharya)

The breeding populations of the gharials survive mainly in three rivers in Nepal: Narayani-Rapti, Karnali and Babai (Maskey and Percival, 1994). Because of a very low first-year survival rate under natural conditions (7.7%) (Hussain 1999) and anthropogenic threats (e.g., sand and boulder mining, fishing, hunting for eggs), this species faced a serious rate of decline and extirpated much of its range (Stevenson, 2015). The government of Nepal launched a captive breeding program in 1978. Over a 27 year period (1981-2007), a total of 691 gharials were reared in captivity and reintroduced back into their natural habitats (Ballouard et al., 2010).

Gharials are regarded as "aquatic tigers," because their presence indicates an unpolluted river and the presence of abundant prey species such as fish, similar to tigers in a forest. Nepal has pioneered innovative strategies combining both ex-situ and in-situ conservation to protect gharials in the river systems. The government of Nepal endorsed a Gharial Conservation Action Plan on wetland day of 2018 (DNPWC 2018). The plan prioritizes the upgrading of scientific knowledge, its prey base and habitat, and strengthening in-situ conservation program.

2.4 Central issues of ecological and human interactions of wildlife conservation in this thesis

2.4.1 Spatio-temporal pattern of conflict

Nepal has been successful in protecting rhinoceros, elephants, leopards, gharials and tigers from the verge of local extinction. All these species mainly survive in the human dominated forest landscape, even outside of protected areas. With the exception of gharials, human-wildlife conflict involving these wildlife is common. The conflict is a dynamic interaction and varies over time and space based on the species in question and socio-cultural status of the people. Crop raiding is perhaps the most common form of HWC, and people show some degree of resilience towards such damages (Karanth and Nepal, 2012). Human fatalities and injuries are extreme forms of conflict because human death/injury constitutes a deep retribution among the victim's family and society and disrupts the normal activity of entire villages. Consequently, the conflict may erode public support for conservation. This thesis examines spatial and temporal patterns of human death and injury by (a) type of species involved in conflict, (b) seasonality of conflict, and (c) location of conflict.

2.4.2 Habitat heterogeneity, fragmentation and configuration

Habitat fragmentation is a process during which a large expanse of habitat is transformed into a number of smaller patches of smaller total area, isolated from each other by a matrix of unsuitable habitats (Wilcove et al., 1986). According to Fahrig (2003), qualitatively categorization of habitat fragmentation includes four process: (a) reduction in habitat amount, (b) increase in number of habitat patches, (c) decrease in sizes of habitat patches, and (d) increase in isolation of patches. Quantitative measures of these habitat fragmentation indices provide useful ecological measures of species in question (Harrison and Bruna, 2011). However, fragmentation measures vary widely; some include only one effect (e.g., reduced habitat amount or reduced patch sizes). This thesis evaluates species specific responses (e.g., human death and injury) in relation to fragmentation indices as outlined by Fahrig (2003).

Part II. Integration of the articles into the thematic context

Part I provides a detailed account of human-wildlife conflict and conservation using a theoretical background and its contextual consideration. Human-wildlife conflict has several dimensions based on the species in question. This is particularly important when conservation involves a human dominated landscape. The core issues of wildlife conservation in the face of conflict include understanding patterns of human-wildlife conflict, its connection with forest fragmentation, and conservation of non-conflict animals.

This part summaries core research papers following by a detailed description of papers in the context of the thesis. The methods and results are described in detail in the articles.

1. Acharya et al. (2016): “Human-Wildlife Conflicts in Nepal: Patterns of Human Fatalities and Injuries Caused by Large Mammal”

This first paper is a part of this thesis. The paper was written by Krishan P. Acharya, Prakash K. Paudel, Prem Raj Neupane and Michael Köhl. It is published in the peer reviewed international journal ‘PLoS one’ in 2016.

1.1 Summary of the paper (Acharya et al., 2016)[1]

Injury and death from wildlife attacks often result in people feeling violent resentment and hostility against the wildlife involved and, therefore, may undermine public support for conservation. Although Nepal, with its rich biodiversity, is doing well in its conservation efforts, human-wildlife conflicts have been a major challenge in recent years. The lack of detailed information on the spatial and temporal patterns of human-wildlife conflict at the national level impedes the development of effective conflict mitigation plans. We examined patterns of human injury and death caused by large mammals using data from attack events and their spatiotemporal dimensions collected from a national survey of data collected in Nepal over five years (2010–2014). Data were analyzed using logistic regression and chi-square or Fisher's exact tests. The results show that Asiatic elephants and common leopards are most commonly involved in attacks on humans in terms of attack frequency and fatalities. Although one-horned rhinoceros and bears had a higher frequency of attacks than Bengal tigers, tigers caused more fatalities than each of these two species. Attacks by elephants peaked in winter and most frequently occurred outside protected areas in human settlements. Leopard attacks occurred almost entirely outside protected areas, and a significantly greater number of attacks occurred in human settlements. Attacks by one-horned rhinoceros and tigers were higher in the winter, mainly in forests inside protected areas; similarly, attacks by bears occurred mostly within protected areas. We found that human settlements are increasingly becoming conflict hotspots, with burgeoning incidents involving elephants and leopards. We conclude that species-specific conservation strategies are

[1] Acharya, K.P., Paudel, P.K., Neupane, P.R., Köhl, M., 2016. Human-Wildlife Conflicts in Nepal: Patterns of Human Fatalities and Injuries Caused by Large Mammals. Plose ONE 1–18. https://doi.org/10.1371/journal.pone.016171

urgently needed, particularly for leopards and elephants. The implications of our findings for minimizing conflicts and conserving these imperiled species are discussed.

1.2 Discussion of the first paper in the thematic context

The first article provides a robust assessment of spatial and temporal patterns of human death and injury resulting from human-wildlife conflict in Nepal. It provides detailed answers to the following questions:

a) Which species are involved in the conflict?
b) Are there any different between patterns of conflict by species involved?
c) Is there any temporal pattern of conflict by wildlife species?

The article shows that elephants (30%) are most often involved in human-wildlife conflicts resulting in death and injury of humans followed by leopards (21%), rhinoceros (18%), bears (12%), and tigers (10%). There is an increasing trend of frequency of wildlife attacks from 2010 to 2014 for bears ($r = 0.91$), leopards ($r = 0.67$), elephants ($r = 0.11$) and tigers ($r = 0.87$), except for rhinoceros ($r = -0.13$). The article shows a strong species specific seasonal pattern of conflict for elephants and rhinoceros, with consistently high frequency of attacks in winter. In terms of attack location, human use landscapes (e.g., farmland and home) are conflict hotspots for elephants and leopards, unlike tigers and rhinoceros which mostly attacked people in the forests within protected areas.

Elephants are the largest terrestrial mammal and roam vast areas while foraging for large quantities of food (Sukumar, 1992, 2003). The high human-elephant conflict may be the result of (a) loss of forests along seasonal migratory routes (Santiapillai and Jackson, 1990; Sukumar, 1992, 2003); (b) shrinkage of available forest areas (Hoare, 1999; Zhang and Wang, 2003); and (c) direct contact with human populations who are dependent on subsistence agriculture (Distefano, 2015). The high elephant-human conflict in the dry season may be related to the limited forage in the forest. The same is true for leopards, whose attacks peaks in April, the driest time of the year, when forests are short of prey species and water sources. Attacks by rhinoceros occur mainly in the dry season (winter) in forests and farmland. People searching for firewood and fodder are most likely to be killed. The article provides four main findings: (a) attacks by elephant and leopards are most frequent, (b) attacks are common outside of protected areas (spatial dimension), (c) attacks are associated with a high human death rate and (d) attacks are more frequent in winter seasons/months.

This article offers valuable input into the scientific understanding and conservation implications of wildlife in Nepal. The forests of human dominated landscape may provide a range of dispersion, an extension of habitat, and a corridor between habitat patches. However, the inconsistency echoing "conservation creates conflict" may be apparent if wildlife requirements are not comprehensively integrated into conservation planning in landscape conservation. The aspect of ecological drivers of human-wildlife conflict is also a part of this thesis which is discussed in the next paper.

2. Acharya et al. (2017) Can forest fragmentation and configuration work as indicators of human–wildlife conflict? Evidences from human death and injury by wildlife attacks in Nepal

The second article of this thesis is written by Krishna Prasad Acharya, Prakash K. Paudel, Shanta Raj Jnawali, Prem Prasad Neupane and Michael Köhl and published in the Ecological Indicators in 2017.

2.1 Summary of the paper (Acharya et al., 2017)[2]

Fragmented forests and heterogeneous landscapes are likely to have less natural vegetation and smaller core areas, a low degree of landscape connectivity, high prevalence of anthropogenic edges, and high landscape heterogeneity, which may alter—at varying degrees—behavior of wildlife species such as attacks on humans. We evaluated whether or not forest fragmentation

[2]Acharya, K.P., Paudel, P.K., Jnawali, S.R., Neupane, P.R., Köhl, M., 2017. Can forest fragmentation and configuration work as indicators of human–wildlife conflict? Evidences from human death and injury by wildlife attacks in Nepal. Ecol. Indic. 80. 74-83. https://doi.org/10.1016/j.ecolind.2017.04.037

(e.g., shape, size and distribution of forest patches measured as landscape shape index, effective mesh size, and landscape heterogeneity), habitats (proportion of bush and grassland, distance to water sources), and human disturbances (human population density) have a significant relationship with frequencies of human deaths and injuries by Bengal tiger (*Panthera tigris tigris*), common leopard (*Panthera pardus*), one-horned rhinoceros (*Rhinoceros unicornis*) and Asiatic elephant (*Elephas maximus*). Data on human injury and death were obtained from a national survey over five years (2010-2014). The relationship between wildlife attacks and landscape attributes were investigated using a zero-inflated Poisson regression model. Attacks by tigers were significantly and positively associated with forest fragmentation (effective mesh size which is high in a landscape consisting of disconnected small patches). Attacks by common leopards were strongly positively related with landscape heterogeneity, and negatively related to the proportion of bush and grassland. Attacks by one-horned rhinoceros were positively significantly related to the distance to water sources, and proportion of bush and grassland in the landscape. Attacks by elephants were strongly and positively associated with the forest fragmentation (landscape shape index, which increases as patches in the landscapes becomes disaggregated). These results suggest that forest fragmentation is inevitably a critical driver of human-wildlife conflicts, although the extent of effects varies depending on species specific habitat requirements.

2.2 Discussion of the second paper in the thematic context

This article refers to thematic context of this thesis ‘ecological aspects of human wildlife conflict’. It particularly correlates habitat characteristics (habitat heterogeneity, proportion of grasslands, water availability) and forest fragmentation with frequencies of human death and injury by large mammals and assesses their relative influences. Forest fragmentation was described by three variables: (a) landscape shape index and (b) effective mesh sizes which indicate size and configuration of a forest patch in a landscape, and (c) landscape heterogeneity (McGarigal et al., 2002). Landscape shape index measures edges of forest patches and their aggregation, whereas effective mesh size measures probability that two randomly chosen pixels are not in the same patches, and thus characterizes subdivision of a landscape independently of its size. Landscape heterogeneity is defined by Shannon's diversity index which measures abundances of habitat types (McGarigal et al., 2002), which included forest area, cultivated land, grassland, shrub land, wetland, water bodies, artificial surfaces, bare land, permanent snow and ice.

The foremost important aspect of this article is the identification of ecological drivers linked to the habitat requirements of the species in question. The probability of human death and injury by elephants and tigers in maximally compact and large forest patches is low. Leopard attacks are associated with highly heterogeneous landscapes, but rhinoceros attacks are related to water availability and grasslands. These findings match the spatial temporal pattern of conflict as discussed in the first paper and confirm that ecological drivers are an important determinant of human wildlife conflict. Forests in the human modified landscapes are small and have a high proportion of edges. It may be argued that such forests do not have enough food and shelter and consequently become conflict hotspots.

3. Acharya et al. (2017) "Conservation and population recovery of Gharials (*Gavialis gangeticus*) in Nepal"

The third article of this thesis is written by Krishna Prasad Acharya, Bed Kumar Khadka, Shant Raj Jnawali, Sabita Malla, Santosh Bhattarai, Eric Wikramanayake, and Michal Köhl and was published in Herpetologica in 2017.

1.1 Summary of the paper (Acharya et al., 2017)[3]

The remnant populations of gharials, *Gavialis gangeticus*, are now confined to the large, deep rivers of northern India and Nepal. In lowland Nepal, the populations are restricted to a few stretches of the Narayani–Rapti and Karnali–Babai river systems. Periodic censuses of the wild

[3] Acharya, K.P., Khadka, B.K., Jnawali, S.R., Malla, S., Bhattarai, S., Wikramanayake, E., Köhl, M., 2017. Conservation and Population Recovery of Gharials (*Gavialis gangeticus*) in Nepal. Herpetologica 73, 129–135.

populations have been made over the past 12 years. Here, we present population trends of gharials in the Narayani, Rapti, and Babai rivers based on these surveys. The results indicate that the combined numbers of adults and subadults have been gradually increasing since 2005, but the numbers of adults are low and female biased, with very few males recorded from all study sites. In 1978, Nepal established a captive breeding center in Chitwan National Park, from which captive-bred animals have been periodically released 4–7 years after hatching, at which time the animals are about 1.5 m total length. The detection of hatchlings and subadult classes that are smaller than these released animals in the rivers indicates that there is natural recruitment. Therefore, collecting all nests for ex-situ breeding might not be the best strategy until more rigorous field assessments are completed to determine the relative contributions of captive-bred versus natural recruitment. We suggest that more effort should be channeled toward field assessments, including mapping and monitoring habitat availability, habitat management to ensure necessary environmental flows to create sand banks and deep pools, and research to better understand the ecology and behavior of gharials in Nepal's rivers.

1.2 Discussion of the third paper in the thematic context

Acharya et al. (2016) discussed the pattern of human death and injury by large mammals and Acharya et al. (2017) discussed how forest fragmentations have contributed to increased human-wildlife conflict. This article suggests that wildlife conservation in the face of conflict is paying off. The detection of hatchlings and sub-adult classes that are smaller than these released animals in the rivers indicated that there was natural recruitment. Furthermore, a gradually increasing trend of gharials since 2005 suggests the importance of ex-situ conservation for gharial perseveration. However, there are certain gaps in gharial conservation. Gharials are largely confined within protected areas (Bardia National Park and Chitwan National Parks). Although large mammals (e.g., tigers, rhinoceros, and elephants) are established in their former habitats, including forests along rivers, these rivers are failed to restore the gharial population. Absence of gharials in outside of protected areas may be the result of sand mining, fishing and river pollution, which, to some extent, are tolerated by large mammals.

4. Conclusions of the cumulative dissertation

4.1 Temporal and spatial pattern of human fatalities and injuries by wildlife attacks

Human-wildlife conflict is one of the most serious conservation threats globally (Distefano, 2015). It is common in the human dominated forest landscapes inhabited by large carnivores and herbivores where subsistence agriculture is a mainstay occupation (Woodroffe et al., 2005). Studies suggest that crop damage is a common form of conflict and is tolerated to some extent (Hill, 2004). However, injury and fatalities by wildlife attacks result in serious resentment and greatly increased hostility towards the wildlife involved. The first article of this dissertation shows that human fatalities and injuries are caused mostly by globally threatened large herbivores and carnivores: elephants, common leopards, rhinoceros and tigers. Except one species of bear (*Ursus arctos*), all conflict species are globally threatened according to IUCN's Red List (IUCN, 2018). Human-elephant and human-leopard conflicts are the most frequent, especially in the human-dominated landscapes, outside of protected areas and in dry seasons (December-elephants, April-leopards). In December, natural food sources are very limited in the forest, so paddy crops (e.g., rice) that are ready for harvest become a target for hungry elephants. The same is true for leopards. Common leopards have made a comeback in their former habitats in Nepal's mid-hill mountains after the successful launch of the community forestry program. The high frequency of attacks in April may be related to a shortage of water and prey populations in small and fragmented forests in the mid-hill mountain forests.

Tiger attacks often occurred in forested areas, particularly in areas adjacent to the park boundaries. Although Carter et al. (2012) noted that tigers avoided park boundaries during day-time, pastoralists and fodder/firewood collectors are the most likely to be attacked. Rhinoceros attacked people primarily in the dry season (winter), and many attacks took place in forests and farmlands. This was probably because of the geographical and temporal overlap that occurs between rhinoceros and people. Rhinoceros are active during the early morning and wander into farmlands for opportunistic browsing, especially in the winter season when the quality and quantity of forage in forests are low (Jnawali, 1993). A rapid decline of tallgrass floodplain habitats and forage grass (e.g., *Saccharum spontaneum*), which are critical for rhinoceros, due to the succession of grasslands to woodlands and the invasion of exotic plants such as *Mikania micrantha* may have forced rhinoceros into human settlements.

In conclusion, large mammals that are threatened to extinction are mostly involved in human death and injury. The temporal and spatial pattern of conflict suggests that poor quality of habitat may be a major driver of such pattern.

4.2 Human-wildlife conflict in relation with forest fragmentation and habitat requirements

Fragmented forests have a high density of anthropogenic edges, high landscape heterogeneity, less natural vegetation and smaller core areas and a low degree of landscape connectivity, which may alter behavior of wildlife species such as attacks on humans. As described in the second article, human-elephant conflict is related to the level of forest fragmentation and habitat requirements. This matches the pattern of human-elephant conflict as described in the first paper. Asian elephants in Nepal were distributed throughout a vast region, most of which was taken over by humans for settlements, agricultural lands and industrial expansion (Pradhan et al., 2011; Sukumar, 2003). Consequently, forests became small, poorly connected and fragmented. The lowland Nepal is included Terai physiographic region, which is the home of elephants and tigers found in Nepal. This region covers 13% of Nepal's area and nearly 20% of it is covered by forests (FRA/DFRS, 2015) but it is the home for nearly 50% of Nepal's population (CBS, 2012).

Expanding infrastructure development is still the top most prioritized agenda, which will further fragment forest areas. The first article shows that human-leopard conflicts are common throughout the country including the entire mid hills of Nepal. This may be result from the comeback of leopards in Nepal's mid hills and lowlands after successful implementation of the community forestry program. Current community forestry is a strategy involving local people in the landscape conservation. However, the second article suggests that such forest patches, especially in the mid hills, have become a conflict hotspot. Mid-hill mountains were extensively settled, and forests were badly deteriorated. These forests areas, however, restored through the community forestry program, may not be adequate to sustain a viable metapopulation of leopards. The second article suggests that human–rhinoceros conflicts are high near water sources and in areas with a high proportion of bush and grasslands. This means that human-wildlife conflict is an ecological problem, and that size, shape and connectivity of forest patches and availability of species specific habitats are critical drivers. Biodiversity conservation in Nepal, therefore, should include these issues in conservation planning.

In summary, creating large and uninterrupted forests is important, but species-specific critical habitat requirements (e.g., grasslands, water sources, dense forest) also need to be considered for the conservation and management of wildlife populations.

4.3 Conservation of globally threatened mega-fauna in the face of conflict

The conservation of globally threatened wildlife populations is a multi-faceted challenge (Grenyer et al., 2006). Conservation biologists need to understand the conservation ecology of threatened species to make a well-informed conservation plan. Most species need a tailored-made solution based on their life history traits. Nepal has adopted a species-specific conservation strategy. This includes in-situ conservation (e.g., protected area system, habitat management, species reintroduction etc) and ex-situ conservation (e.g., captive breeding). Additionally, landscape conservation programs have been implemented in regions with more significant human populations and heterogeneous land ownership to provide dispersal opportunities for wildlife populations (MoFSC, 2015). Such landscape conservation focuses on select species which are expected to help conserve other species that share their habitats. The third paper covers the conservation status of gharials, a non-target and non-conflict species, in the landscape conservation framework.

The third paper confirms that population of critically endangered gharials is growing over last 10 years and the natural recruitment is being taken place (Acharya et al., 2017). However, gharials are still confined to river systems within protected areas, contrarily to tigers, elephants and rhinoceros. Absence of gharials outside of protected areas suggests that an umbrella effect may not hold true, which assumes that the conservation of flagship species will lead to the conservation of other sympatric species and structure of the landscape including the ecological function dependent on that function (Caro, 2010). Gharials may be less tolerant to human disturbance or there may be considerable incompatibility in habitat requirements or the flagship species may still tolerate. Furthermore, gharials may have been victims of ongoing conflict with tigers, rhinoceros and elephants. Therefore, there is a need for multi-species focused conservation programs, community participation, multi-agency involvement and strict implementation of rules and regulations. Species like gharials need to be seen as a flagship species in landscape conservation.

Although Nepal has made resounding progress in the conservation of globally threatened species, the third paper implies that conservation actions targeted on particular species and their habitats have both merits and demerits. The targeted actions on certain taxonomic list may compromise the conservation actions of less conspicuous species.

In conclusion, non-conflict species are not necessarily better protected than those of conflict species. There is a need for multi-species focused conservation programs to ensure conservation of diverse ecosystems.

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Annex I: Scientific articles and personal contribution

RESEARCH ARTICLE

Human-Wildlife Conflicts in Nepal: Patterns of Human Fatalities and Injuries Caused by Large Mammals

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Abstract

Injury and death from wildlife attacks often result in people feeling violent resentment and hostility against the wildlife involved and, therefore, may undermine public support for conservation. Although Nepal, with rich biodiversity, is doing well in its conservation efforts, human-wildlife conflicts have been a major challenge in recent years. The lack of detailed information on the spatial and temporal patterns of human-wildlife conflicts at the national level impedes the development of effective conflict mitigation plans. We examined patterns of human injury and death caused by large mammals using data from attack events and their spatiotemporal dimensions collected from a national survey of data available in Nepal over five years (2010–2014). Data were analyzed using logistic regression and chi-square or Fisher's exact tests. The results show that Asiatic elephants and common leopards are most commonly involved in attacks on people in terms of attack frequency and fatalities. Although one-horned rhinoceros and bears had a higher frequency of attacks than Bengal tigers, tigers caused more fatalities than each of these two species. Attacks by elephants peaked in winter and most frequently occurred outside protected areas in human settlements. Leopard attacks occurred almost entirely outside protected areas, and a significantly greater number of attacks occurred in human settlements. Attacks by one-horned rhinoceros and tigers were higher in the winter, mainly in forests inside protected areas; similarly, attacks by bears occurred mostly within protected areas. We found that human settlements are increasingly becoming conflict hotspots, with burgeoning incidents involving elephants and leopards. We conclude that species-specific conservation strategies are urgently needed, particularly for leopards and elephants. The implications of our findings for minimizing conflicts and conserving these imperiled species are discussed.

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Introduction

Conflicts between people and wildlife have been widely recognized as one of the most challenging issues for wildlife conservation worldwide [1,2]. Although problems have been well known for many years, the increase in conflicts, particularly in regions with high biodiversity, suggests that improved strategies are urgently needed to promote the co-existence of wild animals and people [2,3]. The continuous increase in the human population results in competition between people and wildlife for shared but limited resources, which manifest as various types of conflict, such as crop-raiding, livestock predation, property damage, human death and injury, and the retaliatory killing of wildlife [4,5]. Conflicts become extremely controversial when people are attacked by species that are endangered and legally protected. First, attacks by wildlife are life-threatening and thus are not acceptable to society, so people often retaliate by killing the animals involved in the conflict [6]. Second, large mammals are generally involved in the conflicts, and most of these species are threatened with extinction, so the retaliatory killings of threatened mammals further increases their extinction risk [7,8]. Third, the penalties for illegally killing endangered animals may further escalate hostile attitudes towards conservation efforts [9].

Several measures, ranging from the distribution of compensation and the promotion of wildlife deterrents to support the livelihoods of people, have been implemented to foster the co-existence of humans and wildlife [2,3,5,10]. However, the efficacy of such measures is largely uncertain due to the absence of information about the patterns of conflicts across various landscapes. Although human-wildlife conflicts have been extensively studied at local levels [11–13] and to some extent in Nepal [14–16], none of these studies report patterns of human fatalities and injuries caused by wild animals at the national level, with some exceptions in Africa [17,18].

Nepal, a central Himalayan country, has an exceptionally high level of biodiversity, partly because of the large variation in altitude (70–8,848 m) that occurs over short horizontal distances (~200 km) (Fig 1). The country has a disproportionately high diversity of flowering plants (~2% of the global number of species), mammals (8%) and birds (8.6%) in comparison with its proportion of global landmass (<0.01%) [19]. Maintaining biodiversity in this country is ranked as a very high global conservation priority, as demonstrated by efforts to maintain endemic bird areas [20] and the inclusion of areas of the country in the Global 200 ecoregions identified by the WWF [21]. Nepal has 23.24% of its land mass in protected areas (PAs) (Fig 1). Outside the PAs, approximately 29% of the forestland is managed under community forestry practices, where local communities play a significant role in forest management and decision-making about land use. Conservation challenges in such areas are complex and are mostly associated with the socio-cultural status of the people living there [19,22].

Protected areas in Nepal are disproportionately located at higher altitudes [23]. Consequently, the fauna of the lowland regions, especially large mammals, are not adequately protected, and most of them live in human-dominated forest landscapes [24]. The country has an unusually high proportion of globally threatened species of mammals in comparison to its area [8]. Nepal is a predominately agricultural country, with forests providing many life-supporting ecological goods and services. For example, firewood and fodder make up nearly 75% of the energy supply and 37% of the livestock feed, respectively, used by the country, and these are mostly harvested from forests [25]. A close link between society and the natural environment and their close physical proximity are a major cause of human-wildlife conflicts. Various reports suggest that there is an increasing incidence of human causalities and injuries due to wildlife interactions, even in areas with no previously reported incidents [12,14,16,26].

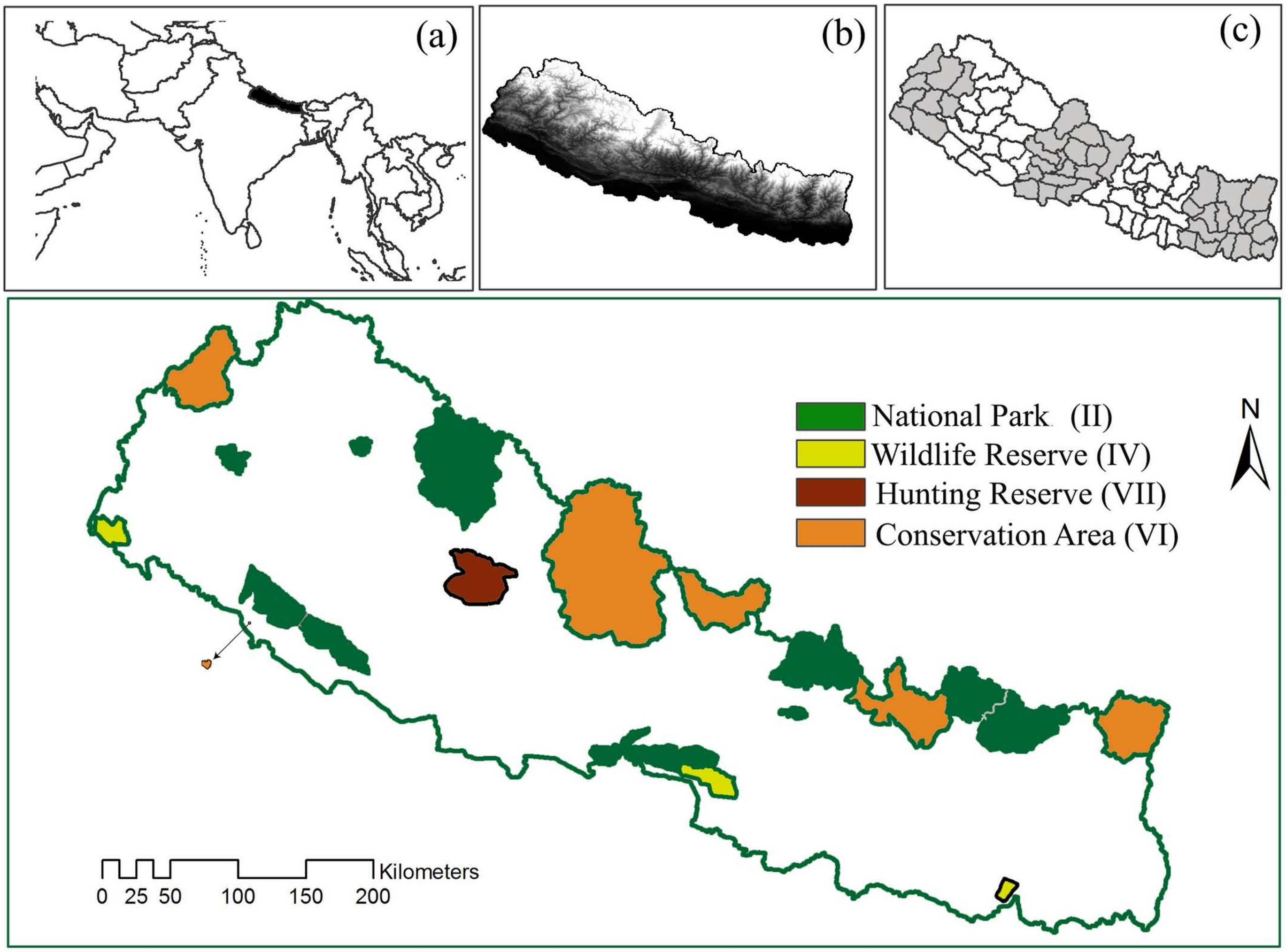

Fig 1. Map of protected areas in Nepal. Figures in parentheses indicate IUCN (World Conservation Union) protected area categories. In inset: (a) location of Nepal (dark color), (b) altitudinal gradient in Nepal (the lighter colors indicates higher altitudes), and (c) districts of Nepal. Five clusters of districts (indicated by shades of colors or white) indicate jurisdictions of the Regional Forest Directorate (RFD).

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Therefore, measures based on sound analyses of the spatial and temporal patterns of human casualties and injuries are needed to reduce the frequency of these conflicts.

In Nepal, people are attacked by large mammal species such as tigers, common leopards, rhinoceros, elephants and bears, but there is little discussion about the patterns of fatalities and injuries caused by wildlife or their underlying temporal dynamics [27]. Such information could provide essential guidance for establishing future conservation and research priorities in Nepal [19]. In this paper, we analyze data on human-wildlife conflicts collected over a five-year period (January 2010-December 2014) via a nation-wide survey of district forest offices and PA offices (districts and PAs are shown in Fig 1). The aims of this study were to (1) explore the temporal patterns (year, season and month) of wild animal attacks on people for different species, (2) determine the locations most vulnerable to attacks (e.g., home, forest and farmland), (3) identify conflict hotspots in Nepal, and (4) provide recommendations to support future conservation planning in Nepal.

Materials and Methods

Data assessment

We assessed data on human fatalities and injuries obtained from the Regional Forest Directorates (RFDs) and the Department of National Parks and Wildlife Conservation (DNPWC). The Ministry of Forests and Soil Conservation (MoFSC) implemented guidelines for relief payments for wildlife-related losses in 2006 (with an amendment in 2015). The guidelines provide a systematic procedure for providing financial support to victims or their dependents for various types of losses caused by wildlife: (1) loss of human life or injury, (2) loss of livestock, (3) loss of crops and stored food-grain, and (4) damage to houses and farm buildings. To avoid unjustified claims, the guideline stipulates a rigorous verification protocol that includes plausibility checks and objective evidence. According to the guidelines, the RFD is the entity responsible for the approval and disbursement of financial support to victims. (S1 File). In addition, we made telephone calls to district forest offices and PA offices to verify data and assess if there were any unreported and/or undocumented cases. We found that most relief claims were for human fatalities and injuries, while claims for crop and livestock loss were not common.

We prepared a database with 463 conflict cases involving death or injury of people caused by wildlife over a five-year period (2010–2014). The data indicate that bear, gaur (*Bos gaurus*), Asiatic elephant (*Elephas maximus*), common leopard (*Panthera pardus*), one-horned rhinoceros (*Rhinoceros unicornis*), Bengal tiger (*Panthera tigris tigris)*, wild water buffalo (*Bubalus arnee*) and wild boar (*Sus scrofa*) attacks on people all occurred during this period. For leopards, all attacks were by common leopards. Attacks by snow leopards (*Uncia uncia)* are very unlikely as they are not found below 3000 m [28], and our database suggests that leopard attacks occurred only in the mid-hills and the lowlands.

For each conflict event, we attempted to document the following data: (1) type of conflict (death or injury); (2) species involved; (3) time of incident (year, month, and season) (winter: December-February; spring: March-May; summer: June-August; autumn: September-November); (4) location of conflict (forest, farmland, or home); and (5) whether the conflict was inside or outside existing PA boundaries. The 'home' conflict location covers the homestead, including the house, livestock sheds, other structures, gardens and nearby vegetable plots, while 'farmland' includes land used for agricultural production (Table 1).

Data analysis

We classified each incident as either a fatality or injury, coded as 1 or0, respectively. Some species, such as gaur, wild water buffalo and wild boar were grouped in an "other" category as only

Table 1. Patterns of human death and injurydue to large-mammal attacks (mean and standard deviation) in the period from 2010–2014. Statistics for the 'other' category are not shown. Average (with ± SD).

Wildlife	Contribution [%]	Average number of attacks per year[a]	Average number of fatalities per year[a]	Average number of attacks per season[b]	Average number of fatalities per season[b]
Elephant	30	27.4 ±7.7	18 ±4.6	34.2 ±16.5	22.5 ±11.7
Leopard	21	19.4 ±11.6	8±5.4	24.2±3.8	10±6.6
Rhinoceros	18	17 ±4.3	3±1.2	21.2±16	3.7±3.5
Bear	12	11 ±4.3	1±1.2	13.7±2.6	1.2±1.2
Tiger	10	8.8±5.4	4.8±3.3	11±4.8	6±1.4

[a]observation period = 5 years

[b]number of seasons per year = 4

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a few cases involving these species were reported in certain seasons. We computed the kill prevalence and incident prevalence for each species as the percentage of the total number of fatal events and the percentage of the total number of incidents, respectively. Chi-square tests of independence or, in cases where there were a small number of observations, Fisher's exact tests were applied to compare the frequency of attacks (fatalities and injuries) by each wildlife species in relation to time (year, season, month), location (forest, farmland and home) and whether they were inside a PA boundary. We used a logistic regression (generalized linear model with a binomial error distribution and logit as the link function) for modeling season, wildlife category, and location (home, farmland and forest) as predictors of increased probabilities of fatalities and injuries in cases of attacks. The R statistical environment (R Development Core Team, 2015) was used for all analyses.

Results

Overall conflict pattern

Our data show that wildlife encounters with people resulting in death or injury in the five-year period from 2010 to 2014 involved the following animals: elephants (30%), leopards (21%), rhinoceros (18%), bears (12%), and tigers (10%) (Table 1, S2 File). On average, 7.7 attacks, including 2.9 fatalities, were reported per month (Table 1). The differences between the frequencies of fatalities and injuries were significant among wildlife species ($X^2 = 103.1$, df = 5, $P<0.001$) (Fig 2). Among the species analyzed, three were significantly associated with human deaths: elephants (kill rate = 0.66, $P<0.001$), leopards (kill rate = 0.41, P = 0.002), and tigers (kill rate = 0.55, P = 0.005) (Fig 2).

Overall, there was a significant difference between the incident prevalence and kill prevalence ($X^2 = 21.25$, df = 5, P = 0.0001), and for elephants and tigers, the kill prevalence exceeded the incident prevalence (Fig 3).

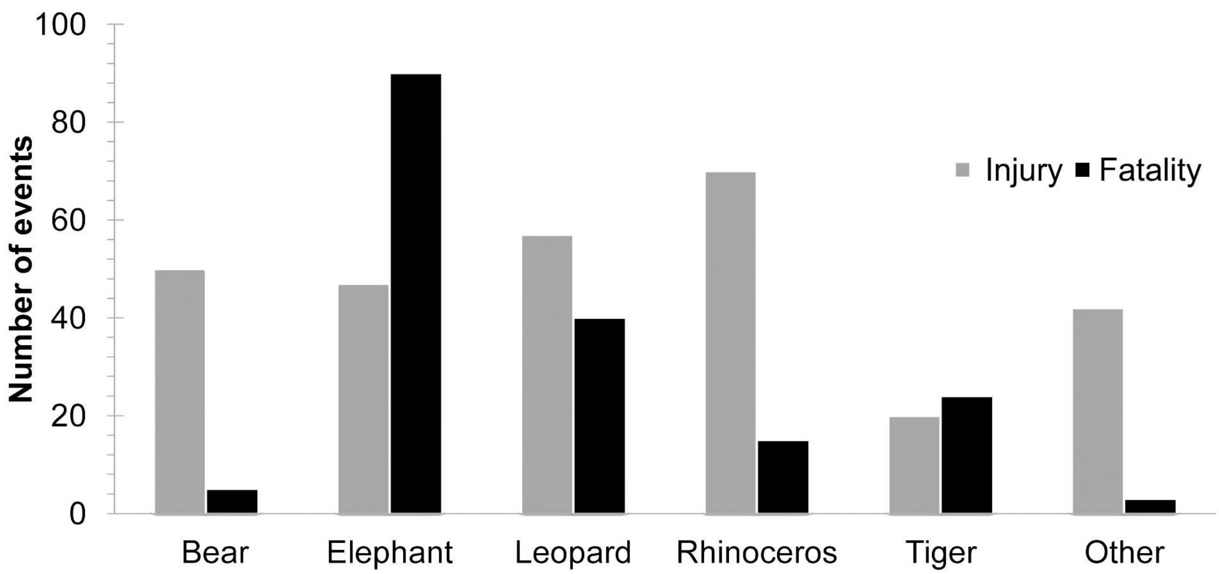

Fig 2. Frequency of attacks (fatalities and injuries) by bears, elephants, leopards, rhinoceros, tigers and others (gaur, water buffalo and wild boar) from 2010–2014.

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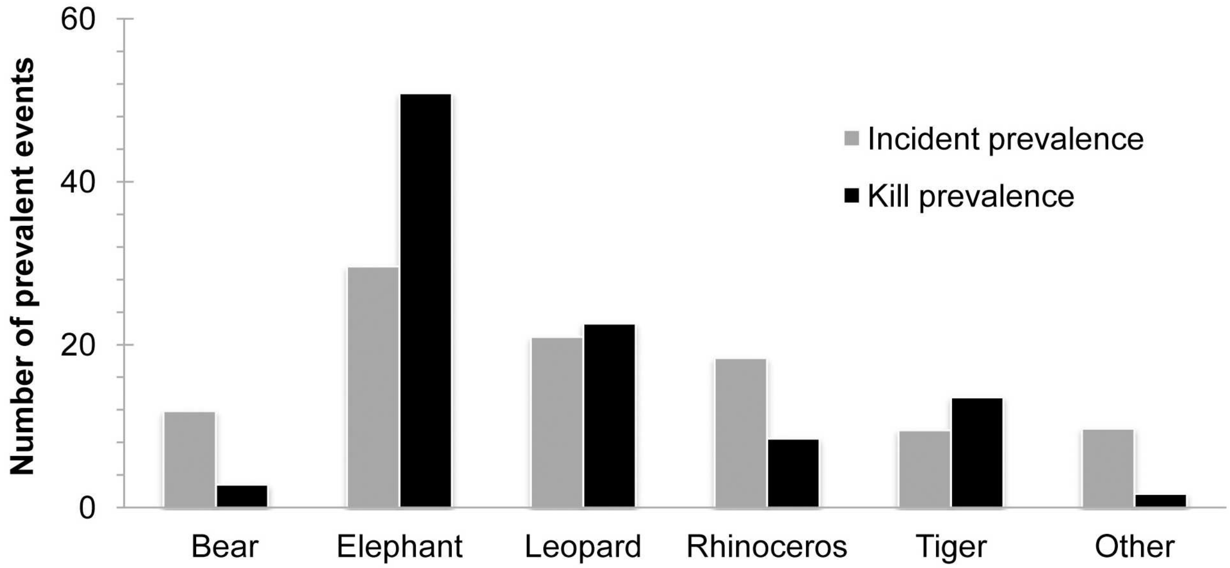

Fig 3. Incident prevalence and kill prevalence forbears, elephants, leopards, rhinoceros, tigers and others (gaur, water buffalo and wild boar) during the period from 2010–2014.

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Temporal pattern of human injuries and fatalities

We detected an increased frequency of wildlife attacks from2010 to2014 for bears ($R^2 = 0.91$), leopards ($R^2 = 0.67$), others ($R^2 = 0.45$) and tigers ($R^2 = 0.87$). For elephants, the trend was less pronounced ($R^2 = 0.11$), and it was negative for rhinoceros ($R^2 = 0.13$) (Fig 4). There were statistically significant differences among wildlife species in terms of total attacks ($X^2 = 38.7$, df = 20, P = 0.007) and kill rates ($X^2 = 153.43$, df = 20, $P < 0.001$).

We detected significant seasonal variations among the wildlife species when we analyzed the data for the frequency of attacks ($X^2 = 40.27$, df = 15, $P < 0.001$), frequency of deaths

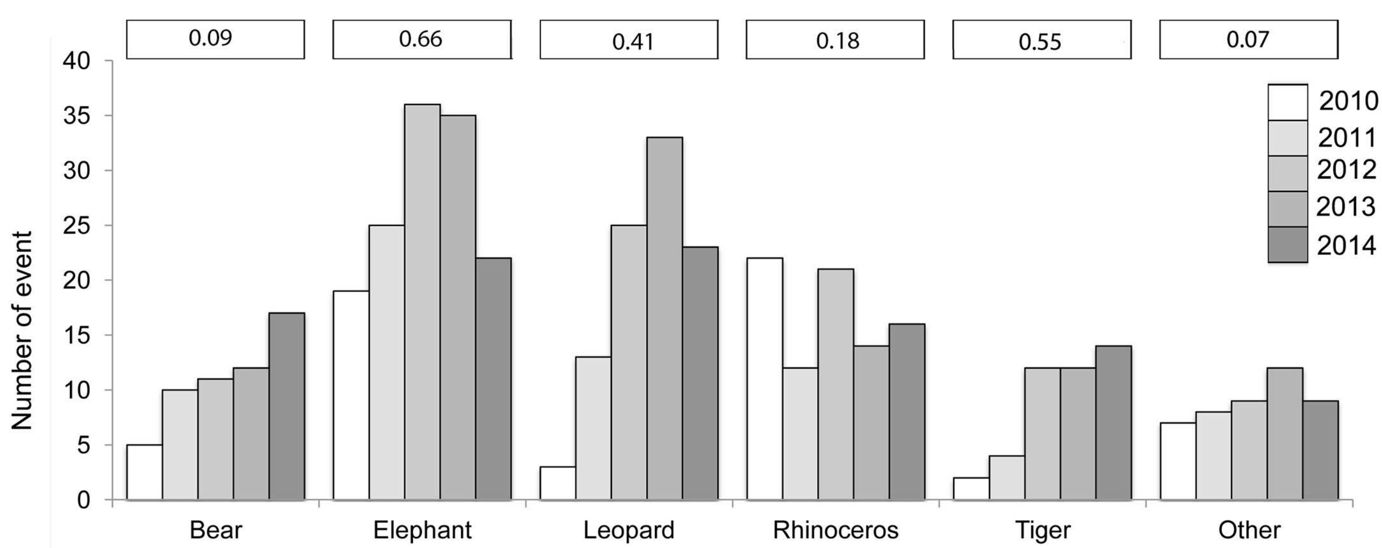

Fig 4. Frequency of attacks by bears, elephants, leopards, rhinoceros, tigers and others over a five-year period (2010–2014) by year. Numbers in a vertical line along the x-axis are the average kill rates of each wildlife species.

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(Fisher's exact test, $P = 0.01$), and kill rates (Fisher's exact test, $P < 0.001$) over the five-year period. Attack frequencies differed significantly among the seasons for elephants ($X^2 = 23.905$, $df = 3$, $P<0.001$), rhinoceros ($X^2 = 36.553$, $df = 3$, $P<0.001$) and others ($X^2 = 8.6$, $df = 3$, $P = 0.03$), with a higher frequency of attacks consistently occurring in winter. There were no significant seasonal variations in the frequency of attacks by tigers ($P = 0.08$), bears ($P = 0.68$) or leopards ($P = 0.60$) (Fig 5). However, the frequency of fatalities caused by leopards varied significantly with season ($X^2 = 13.4$, $df = 3$, $P = 0.003$), with a higher frequency of kills observed in autumn.

Attacks by wildlife differed significantly across the months (Fisher's exact test, $P<0.001$). Attacks by elephants were more frequent in December and less frequent in April and May (Fig 6b). Leopard attacks occurred mostly in April (Fig 6c), while tiger attacks occurred most often in January and May (Fig 6e). Rhinoceros in particular showed a distinct pattern, attacking humans more often in December and January (Fig 6d). The incidence of attacks by bears and others were not consistent throughout the year (Fig 6f). Generally, fatalities were significantly associated with month ($P = 0.02$), showing a higher frequency in September ($P = 0.04$) and October ($P = 0.02$).

Spatial pattern of the occurrence of human injuries and fatalities

Generally, attacks by wildlife were significantly associated with the location in which they occurred: home, farmland and forest (Fisher's exact test, $P<0.01$). We detected significantly different frequencies of attacks among the locations for elephants ($X^2 = 5.88$, $df = 2$, $P = 0.05$), tigers($X^2 = 43.13$, $df = 2$, $P <0.001$) and rhinoceros ($X^2 = 40.18$, $df = 2$, $P<0.001$). Attacks by elephants occurred more often in farmlands, followed by attacks at homes and in forests. Attack patterns of rhinoceros and tigers were consistently similar (Fisher's exact test, $P = 0.22$); they attacked more often in forests, followed by attacks in farmlands and homes. Bears and others showed a statistically consistent pattern (Fisher's exact test, $P = 0.13$), attacking mostly in farmlands, followed by attacks in forests and homes (Fig 7a).

The logistic regression analyses demonstrated a significant influence of location ($P<0.001$), season ($P<0.001$) and species($P<0.001$) on the likelihood of death resulting from an attack. (Table 2).The odds that a person would be killed in an attack were highest for elephants, followed by those for tigers (Table 2).

There were significant differences between the frequencies of attacks (or events) by wildlife inside and outside PAs ($X^2 = 130.56$, $df = 5$, $P <0.001$). Bears, rhinoceros, tigers, and others consistently attacked people inside Pas ($X^2 = 3.3$, $df = 3$, $P = 0.34$) (Fig 7b). However, elephants and leopards attacked people more often outside PAs, although there was a significantly different attack pattern between them (Fisher's exact test, $P<0.001$) (Fig 7b).

Discussion

Understanding patterns of human-wildlife conflict and identifying the underlying causes are an important component of conservation biology. Our results shed light on the spatiotemporal patterns of human death and injury caused by large mammals at the national level and provide insight into future conservation needs. Elephants, leopards and rhinoceros were the top three conflict species in terms of total attacks, followed by bears and then tigers. For the kill/injury ratio, elephants ranked the highest, followed by tigers, leopards and then rhinoceros. Both the incident prevalence and kill prevalence were the highest for elephants, followed by those for leopards, rhinoceros and tigers. Thus, our results suggest that human-elephant and human-leopard conflicts are the most serious human-wildlife conflict challenges in Nepal. Furthermore,

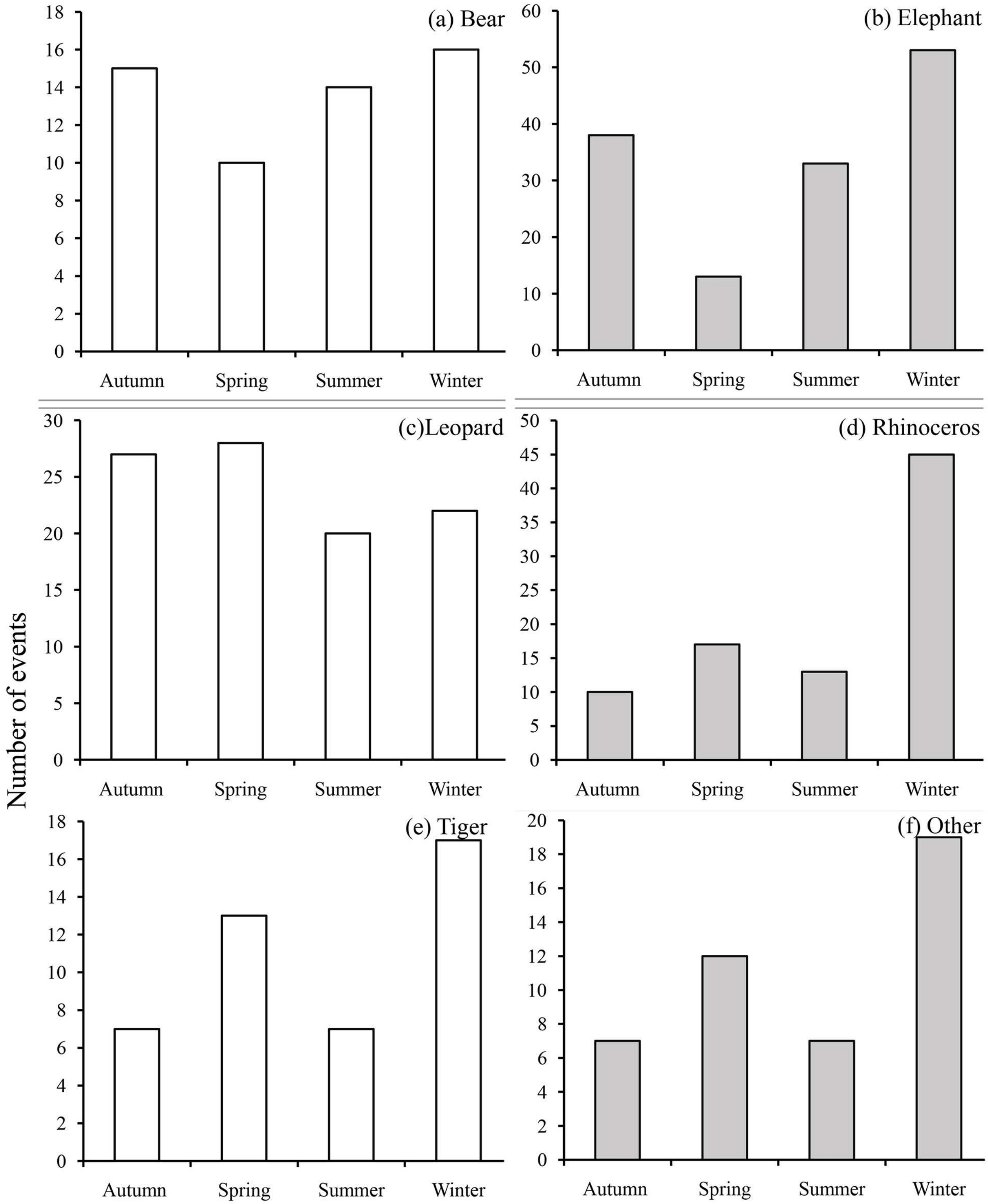

Fig 5. Frequency of attacks (both fatal and those causing injury) by bears, elephants, leopards, rhinoceros, tigers and others over the five-year period by season in Nepal:(a) autumn, (b) spring, (c) summer, (d) winter. Grey-filled bars indicate a statistically significant difference in the seasonal attack pattern.

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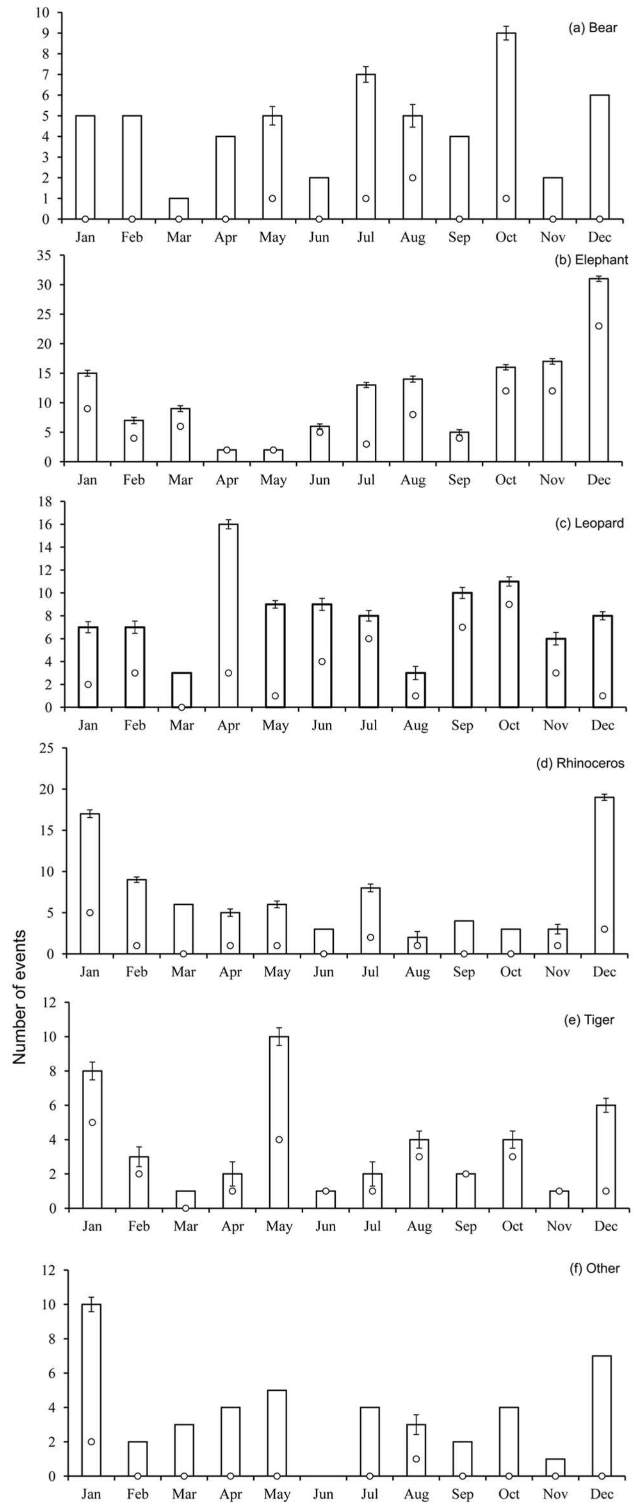

Fig 6. Frequency of attacks (fatal and those causing injury) by month over a five-year period (2010–2014) by (a) bears, (b) elephants, (c) leopards, (d) rhinoceros, (e) tigers, and (f) others. White circles indicate kill ratios. Error bars indicate the standard deviation of fatal events for the corresponding wildlife species and month.

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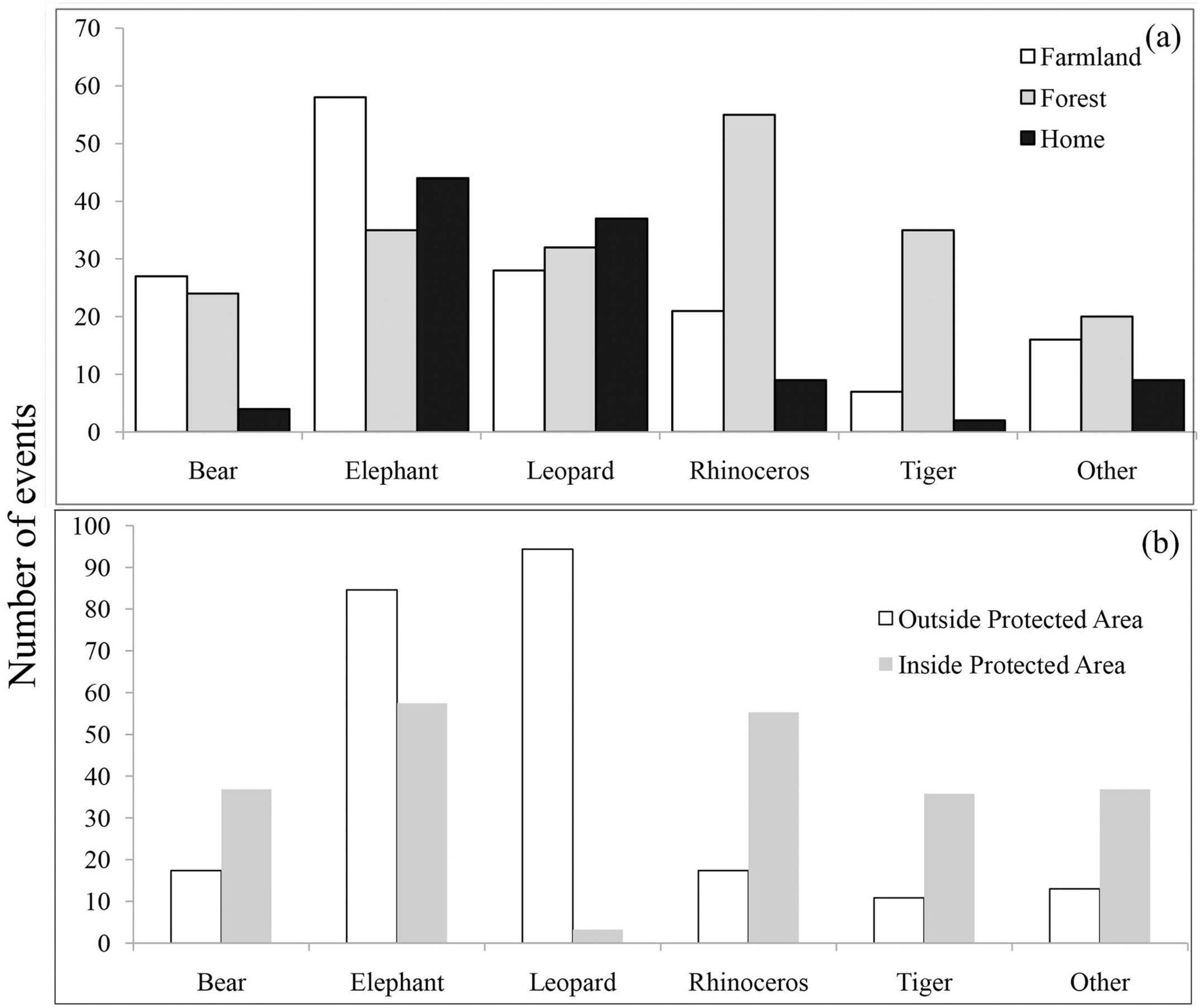

Fig 7. Spatial pattern of the occurrence of human injury and death caused by large mammal attacks in Nepal (a) in farmlands, forests, and homes, and (b) inside and outside protected areas.

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the preponderance of attacks occurred in human-dominated landscapes, which indicates the need for conservation management outside PAs.

Previous studies on human-elephant conflicts suggest that elephant attacks are common wherever elephants and people occupy the same space [16,29–32]. Elephants are the largest terrestrial mammal, and they roams vast areas while foraging for large quantities of food [33,34]. However, elephant habitats have been encroached upon to support the growing human population, resulting in the severe fragmentation of elephant populations and little to no interchange between them [34]. In Nepal, elephant populations are disjointed and confined to four small geographic clusters that were formerly part of an uninterrupted forest landscape that extended throughout southern Nepal and the adjoining region of northern India [35]. The pronounced occurrence of human-elephant conflicts may be attributed to (a) the loss of forests

Table 2. Results of the logistic regression analyses showing the effect of location, season and species on human fatalities.

	Estimate	Std. Error	z value	Pr(>|z|)	Odds ratio
(Intercept)	-1.96	0.51	-3.79	0.0001	
Location					
Forest	0.19	0.27	0.70	0.480	1.21
Home	0.96	0.30	3.17	0.001	2.63
Season					
Spring	-1.19	0.35	-3.34	<0.001	0.30
Summer	-0.55	0.33	-1.65	0.097	0.57
Winter	-0.71	0.30	-2.37	0.017	0.48
Wildlife					
Elephant	2.82	0.51	5.51	<0.001	16.85
Leopard	1.75	0.52	3.32	<0.001	5.80
Other	-0.38	0.77	-0.49	0.621	0.68
Rhinoceros	0.83	0.56	1.47	0.139	2.29
Tiger	2.66	0.57	4.62	<0.001	14.39

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along seasonal migratory routes [33,34,36], (b) the shrinkage of available forested areas [31,37] and (c) direct contact with human populations who are dependent on subsistence agriculture [11]. All of these factors are consistent with our findings, especially in eastern Nepal. This region of Nepal has historically been part of a seasonal migration route between Meghalaya in India and central Nepal [19]. Although a large swath of forest that previously connected with India and spread across the Siwalik foothills was destroyed for human settlements, elephants continue to use the same routes, resulting in their presence in human dominated landscapes. The high frequency of elephant-human conflicts in farmlands and homes in the dry season (December) (Fig 5c) is associated with the crop harvesting months. This finding is similar to those of other studies in Nepal and India [16,32,38]. In December, natural food sources are very limited in the forest, so paddy crops (e.g., rice) that are ready for harvest become a target for hungry elephants. Parker and Osborn [39] noted that the cultivation of unpalatable cash crops (e.g., *Capsicum annuum*) on private land has been shown to be effective in reducing human-elephant conflicts in Zimbabwe, and this may be a solution for Nepal. However, a mitigation plan focusing on the ecological needs of elephants is of prime importance. Forests along elephant migration routes are already very small and fragmented, and future development plans (e.g., roads, railways, and airports) will further disturb these routes. Hence, it is critical that a strategic environmental assessment is conducted in light of the complex infrastructure development planned in this region [40].

Human-felid conflicts have been recognized as one of the major impediments to the future conservation of some of these most endangered species [11,15]. Our results show a surprisingly distinct pattern of attacks by leopards and tigers. Leopards had the second highest incident frequency in terms of total attacks on people and fatalities of the wildlife species analyzed, and leopard attacks peaked in April, the driest time of the year. We argue that common leopards have made a comeback in their former habitats in Nepal's mid-hill mountains after the successful launch of the community forestry program. The program, administered by local residents at the community level, aims to meet local demands for fodder, firewood and timber; the biodiversity gains of community forestry are an unintended side effect [22,41]. Prey populations in community forests are likely to fluctuate due to shortages of food and water sources, especially in dry months [22,28,41]. Livestock are easy preys and their sheds are often poorly protected against leopard attacks. Therefore, people get attacked when leopards, particularly starving ones, resort to livestock depredation. The mid-hill mountain forests are generally not part of the PA system (this zone is very under-represented in Nepal's PA network), and most forest patches are close to human settlements [23]. Studies have shown that leopards can live in human-modified landscapes [42,43], and the extent of human-leopard conflicts is associated with the depletion of nature prey populations, the scarcity of water and livestock herding and guarding practices [44]. Therefore, effective conflict mitigation strategies should include the conservation of leopards' natural prey species in community forests (e.g., ban on wildlife hunting and habitat conservation and management) and the adoption of other measures (e.g., safe livestock enclosures, especially at night, and the herding of livestock outside of forests).

Tigers had a low attack prevalence compared with the four other major conflict species, and our findings suggest that attacks by tigers often occur in forested areas. Therefore, human disturbances in forests are the main reason for human-tiger conflicts. Similar to our results, Treves et al.[13] and Gurung et al. [14] reported that humans invading forests (e.g., pastoralists and fodder/firewood collectors) were often killed by tigers. Gurung et al. [14] found no seasonal pattern of attacks in Chitwan National Park, but attacks were spatially concentrated within the park boundaries, which is similar to our findings. Similar findings were also reported in Sumatra, where human-tiger conflicts are common in intermediate disturbance areas, such as multiple-use forests, where tigers and people coexist[45]. Carter et al.[46] found that tigers coexisted with people in disturbance areas by becoming nocturnal. Such findings suggest that tigers may be able to coexist with people, but it is reasonable to expect that human-tiger conflicts will increase in the future in Nepal for several reasons. Livestock constitute a large proportion (1–12%) of tigers' diets [47–49]. The availability of wild prey is therefore critical in determining the level of human-tiger conflict. Although core tiger habitats have not been expanded in Nepal, restoration campaigns driven by the landscape conservation program in the Terai Arc Landscape [50] have enlarged the areas of multiple-use forests, many of which are managed by local communities. Such multiple-use forests may became conflict hotspots, as Gurung et al. [14] documented in the buffer zone of Chitwan National Park. Therefore, establishing zones of core tiger habitat outside PAs, with a particular emphasis on maintaining viable prey populations, is critical for minimizing human-tiger conflicts. This is also important for achieving Nepal's commitment to the St. Petersburg Declaration, in whichthe government of Nepal committed to doubling its tiger population by 2025. This commitment is viewed differently by different experts; some find the targets of this plan highly ambitious [51], while others strongly support it [52]. We emphasize that improved habitat quality (e.g., increased prey populations and a reduced human footprint) is a pre-requisite for minimizing human-tiger conflicts and for gaining the support of communities for tiger conservation.

Rhinoceros occur in three locations in Nepal (Chitwan National Park, Bardia National Park, and Suklaphanta Wildlife Reserve); the latter two contain small, reintroduced populations. Rhinoceros were the species with the third highest prevalence of human-wildlife conflict at the national level. They attacked people primarily in the dry season (winter), and a large number of attacks took place in forests and farmlands. This was probably because of the geographical and temporal overlap that occurs between rhinoceros and people. Rhinoceros are active during the early morning [53] and wander into farmlands for opportunistic browsing, especially in the winter season when the quality and quantity of forage in forests are low [54]. Firewood and fodder collection, however, are major off-farm activities in the winter, and they take place in the early morning because of the short winter days. Our findings are in accordance with findings from Jnawali [55], who reported a high frequency of conflicts in farmlands and the adjoining forests. Our data suggest that there has been a decline in attacks by rhinoceros in recent years. This might be due to the increase in the use of electrified fences that separate rhinoceros populations from farmlands and settlements. Concurrently, tallgrass floodplain habitats and forage grass (e.g., *Saccharum spontaneum*), which are critical for rhinoceros [56], have been rapidly declining due to the succession of grasslands to woodlands (pers. observation) and the invasion of exotic plants such as *Mikania micrantha* [57]. Thus, habitat management within PAs needs to be urgently carried out to keep rhinoceros inside PAs and reduce the occurrence of crop-raiding in farmlands. This includes maintaining the environmental flows required to support high-quality grasslands, as mentioned above for tiger prey species. In addition, electric fences must be well maintained so that they continue to be effective.

Bears and other species (wild water buffalo, wild boar, and gaur) were less pronounced conflict species. Wild water buffalos in particular survive in an isolated and small reserve (Koshi Tappu Wildlife Reserve) in eastern Nepal where they frequently attack people. Plans are underway to translocate some of these animals to Chitwan National Park, which is unoccupied by people and contains high-quality habitat that is within the former geographic range of wild water buffalos. We suggest that these plans should include strategies to reduce human-buffalo conflict, as suggested by Heinen and Paudel [58]. Attacks by wild boar are not common, although this species poses a serious problem as a crop raider [26].

Our study demonstrates that human-dominated landscapes and not Pas are the major wildlife conflict hotspots in Nepal. The majority of these conflicts involved leopards and elephants, and people were more likely to be killed in their homesteads by these wildlife species (Table 2) than by other species. There was a decrease in conflict events in 2014 for elephants and leopards (Fig 4). Such a sharp decrease may be a combined result of technical measures used to mitigate human–wildlife conflict (e.g., electric fences and predator-proof corrals) and increased public awareness about animal behavior (e.g., avoiding making noises or engaging in other behaviors, such as human movement at night, that might provoke wildlife aggression). We emphasize that technical measures may not be the sole explanation for these reductions because (a) electric fences are confined mainly within the jurisdictions of parks and have not been effective due their poor quality (e.g., inadequate poles and wires), lack of a regular power supply and maintenance and the socio-economic conditions at the local level (e.g., people remove fences to allow free movement of their livestock into forests (park managers, pers. comm.). High winter rain levels in 2014 (50% above normal) compared with the previous four years [59], for example, may have also contributed to the avoidance of potential encounters by (a) providing wildlife with food/water in the forests and (b) limiting human activities within their villages. We argue that further research based on long-term data is necessary to ascertain whether such fluctuations are attributable to these factors.

Most victims (a) are frequent forest visitors, collecting firewood or fodder or grazing their livestock; (b) reside in small, poorly secured mud houses located adjacent to or near forests along with belongings that might attract wildlife (e.g., livestock, food-grain); and (c) attempt to chase off wildlife using rudimentary tools (e.g., locally made sound boxes and burning sticks). Thus, any conflict mitigation plan should focus on the socio-economic issues of local populations and the ecology of the wildlife involved to create non-overlapping resources for both groups [3,60,61].

Conclusions, Conservation Implications and Future Research

Nepal has eliminated the poaching of rhinoceros since 2011 (also known as zero poaching) [62]. Some reports even suggest that increases in the tiger and rhinoceros populations are occurring [47,63], and community forestry has been successful in restoring locally extirpated wildlife populations. However, these accomplishments may have been achieved at the cost of an increasing number of wildlife conflicts occurring outside PAs.

Our results suggest that elephants and leopards should be the main focus of management efforts to minimize injury and the loss of human life and mitigate human-wildlife conflicts. This is based on three major findings: attacks by these species were (a) the most frequent, (b) common outside Pas (spatial dimension), and (c) associated with a high human fatality rate. Earlier attempts to resolve conflicts were confined mainly within the jurisdiction of PAs and included, among other strategies,(1) the deployment of electric fences to prevent wildlife movement towards human settlements, (2) building predator-proof corrals to prevent livestock loss by predators at night, and (3) the planting of crops that are unpalatable to wildlife, such as peppermint. These mitigation strategies undoubtedly helped to reduce conflict. However, the efficacy of such measures at a national level is low because there is minimal infrastructure in places where it is urgently needed to address some of these issues. The widespread common leopard, for example, causes conservation conflicts along the entire mid-hill region of Nepal, far from PAs, but district forest offices have no institutional capacity to respond (e.g., capturing leopards, engaging in conservation planning and monitoring animals). The same is true for dealing with conflicts with elephants in lowland Nepal. Therefore, there is an urgent need to build the institutional capacity to address conflicts with these two species as part of the framework of overall conservation planning [3,61]. Here, we provide species-specific recommendations to guide future research and conservation activities in Nepal with the goal of reducing human-wildlife conflict (Table 3).

This study focused only on human injury and death; it did not look at the loss of livestock, crops and other human property. We recommend that future studies be conducted examining these aspects, which are likely to result in further recommendations for human-wildlife conflict mitigation.

Table 3. Ecological and conflict issues and management recommendations.

Wildlife	Ecological and conflict issues	Management recoqwmmendations
Elephant	—High frequency of attacks, with an extremely high kill ratio (67%)	—Restore corridors in critical areas along elephant migratory routes
	—Attacks occurred mostly in human-dominated landscapes (farmland and homes)	—Prepare a well-planned preventive mechanism (e.g., early warning system)
	—Attacks peaked in December	—Educate and train local residents about animal behavior
		—Protect villages with electric fences
Leopard	—Rapidly increasing rate of attacks	—Develop a network of community-based protected areas in the mid-hills and lower mountains
	—Almost all attacks occurred outside protected areas	
	—Attacks peaked in the dry months	—Incorporate wildlife management and conservation practices in community forestry programs (e.g., leopard-proof corrals)
		—Educate and train local residents about animal behavior
Tiger	—Attacks occurred mostly within protected areas and forests	—Maintain healthy prey populations
		—Maintain environmentally sustainable flows in critical rivers to maintain prey habitats
		—Reduce human dependence on forest resources
		—Identify and designate critical tiger habitats in protected areas and conservation landscapes, and prohibit human movement in such areas
Rhinoceros	—Attacks peaked in the dry season	—Restore grasslands and oxbow lakes to restore habitat in protected areas. Maintain these areas to ensure continued environmentally sustainable flows in critical rivers
	—Attacks occurred within protected areas	
		—Maintain and expand electrified fences to protect farmlands
		—Reduce human dependence on forest resources
		—Educate and train local residents about animal behavior

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Supporting Information

S1 File. Data collection strategies.
(DOCX)

S2 File. Descriptive statistics of variables.
(DOCX)

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Can forest fragmentation and configuration work as indicators of human–wildlife conflict? Evidences from human death and injury by wildlife attacks in Nepal

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A B S T R A C T

Fragmented forests and heterogeneous landscapes are likely to have less natural vegetation and smaller core areas, a low degree of landscape connectivity, high prevalence of anthropogenic edges, and high landscape heterogeneity, which may alter—at varying degrees—behavior of wildlife species such as attacks on humans. We evaluated whether or not forest fragmentation (e.g. shape, size and distribution of forest patches measured as landscape shape index, effective mesh size, and landscape heterogeneity), habitats (proportion of bush and grassland, distance to water sources), and human disturbances (human population density) have a significant relationship with frequencies of human deaths and injuries by Bengal tiger (*Panthera tigris tigris*), common leopard (*Panthera pardus*), one-horned rhinoceros (*Rhinoceros unicornis*) and Asiatic elephant (*Elephas maximus*). Data on human injury and death were obtained from a national survey over five years (2010–2014). The relationship between wildlife attacks and landscape attributes were investigated using a zero-inflated Poisson regression model. Attacks by tigers were significantly and positively associated with forest fragmentation (effective mesh size which is high in a landscape consisting of disconnected small patches). Attacks by common leopards were strongly positively related with landscape heterogeneity, and negatively related to the proportion of bush and grassland. Attacks by one-horned rhinoceros were positively significantly related to the distance to water sources, and proportion of bush and grassland in the landscape. Attacks by elephants were strongly and positively associated with the forest fragmentation (landscape shape index, which increases as patches in the landscapes becomes disaggregated). These results suggest that forest fragmentation is inevitably a critical driver of human–wildlife conflicts, although the extent of effects varies depending on species specific habitat requirements.

1. Introduction

Large mammals play important roles in the forest ecosystems mostly by maintaining prey populations and seed dispersal (Berger et al., 2001; Tanner, 1975). They are regarded as keystone species of ecosystems (Caro, 2010; Roberge and Angelstam, 2004; Williams et al., 2000). Forest fragmentation and deforestation lead to loss of core forest areas, disruption of dispersal ability of wildlife in their home ranges, and deterioration of quality habitats by different means such as frequent forest fire and invasion by alien flora and fauna, etc. (Bennett, 1990; Laurance et al., 2000; Lehmkuhl and Ruggiero, 1991). Furthermore, forest loss and degradation bring wildlife into human proximity and cause confrontation because both wildlife and humans compete for shared resources (Distefano, 2015; Woodroffe et al., 2005). Consequently, wildlife raid crops, damage property and kill humans. The subsequent aggressive actions by humans result in further escalation of conflict, including retaliatory killings of wildlife (Distefano, 2015; Michalski et al., 2006; Woodroffe et al., 2005).

Bengal tiger *Panthera tigris tigris* (Linnaeus, 1758), common leopard *Panthera pardus fusca* (Meyer, 1974), Asiatic one-horned rhinoceros *Rhinoceros unicornis* (Linnaeus, 1758) and Asiatic elephant *Elephas maximus* (Linnaeus, 1758) are top ranked conflict animals in Nepal in

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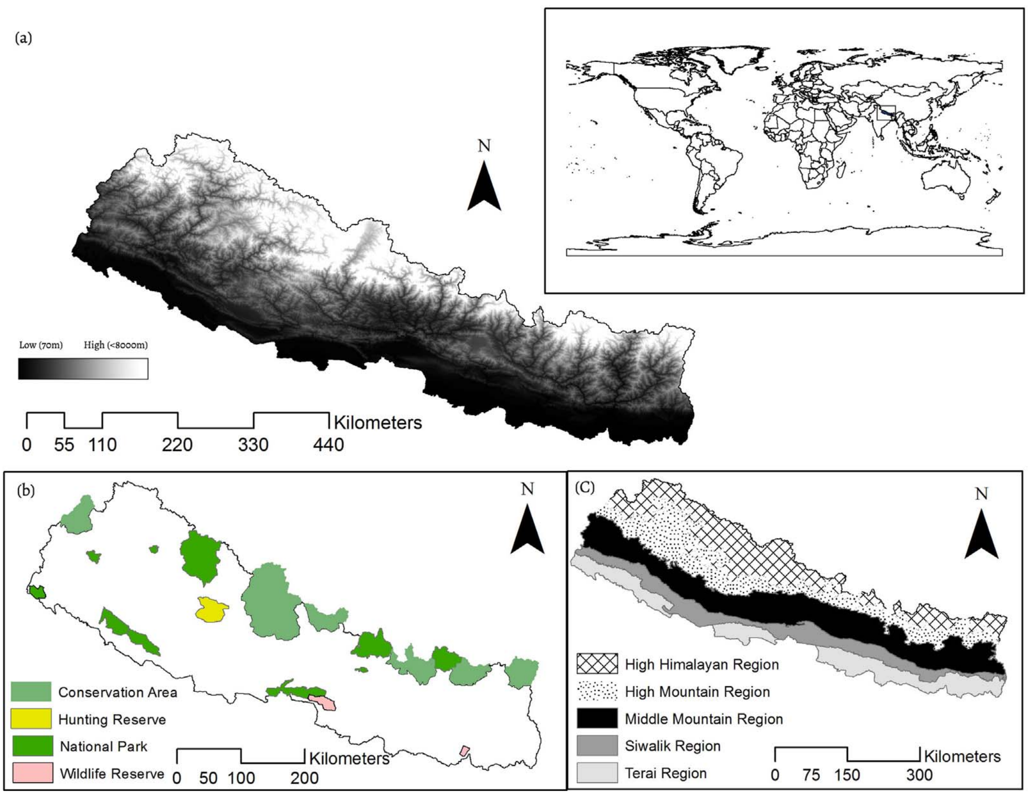

Fig. 1. Mountain landscapes of Nepal: (a) altitudinal gradient of Nepal, (b) protected areas of Nepal, and (c) physiographic division of Nepal (LRMP, 1986).

terms of fatalities and injuries of humans (Acharya et al., 2016). The first three, considered globally threatened mega-fauna, are now mostly restricted to a few protected areas of lowland Nepal and their adjoining forests due to rapid conversion of forests to agricultural lands and their fragmentation (Jnawali et al., 2011; Primack et al., 2013). Common leopards are widely distributed from the lowland to the midhills (Jnawali et al., 2011). The midhills forests have endured a long history of human influence as early settlers occupied these areas (Hagen, 1973). Both midhills and lowland forest are now fragmented forest in the human dominated landscape. As a result, human–wildlife conflict is common throughout Nepal (Acharya et al., 2016; Bhattarai and Fischer, 2014; Gurung et al., 2008; Jnawali, 1989; Pandey et al., 2015; Pant et al., 2015). The major types of conflict include death and injury of humans, crop damages, livestock depredation, property damage and retaliatory killing of wildlife and damages to their habitats. Conflict mitigation approaches include many traditional and new methods such as providing monetary compensation to victims (e.g. crop and livestock insurance schemes), construction of electric fences and trenches along forest borders to limit wildlife movement, and construction of predator-free corrals to minimize attacks on livestock (Acharya et al., 2016). Although these measures are critically important to mitigate conflict for the short term, there is a need for consideration of the long-term ecological requirements of the species in question (Distefano, 2015; Gore et al., 2008; Michalski et al., 2006; Treves et al., 2004).

Current strategies for biodiversity conservation in Nepal prioritize restoration of forested landscapes, with a particular emphasis on ecological corridors between protected areas, and reestablishment of connectivity along an attitudinal gradient of mountain landscapes (MFSC, 2010; MOFSC, 2015). Human–wildlife conflict is increasing in both frequency and severity throughout the country. Most of the studies on human–wildlife conflict are focused on quantifying the damage and species involved in the conflict. Few studies have been conducted to determine if, and to what extent, landscape fragmentation induces human–wildlife conflict, and whether habitat requirements outweigh the effects of fragmentation (Michalski et al., 2006; Treves et al., 2006).

Our ultimate goal was to evaluate the influence of forest fragmentation, human disturbance and landscape heterogeneity on conflict events, and determine whether forest fragmentation is a better explanatory variable than the others. We used data on the locations of conflicts associated with Bengal tiger, Asiatic one-horned rhinoceros, and Asiatic elephant collected between January 2011 and December 2014 to examine species specific responses to forest fragmentation (landscape shape index, effective mesh size and landscape heterogeneity). This assessment includes proportion of bush and grassland, distance to water sources, and human population density. Landscape shape index measures edges of forest patches and their aggregation, whereas effective mesh size measures probability that two randomly chosen pixels are not in the same patches, and thus characterizes subdivision of a landscape independently of its size. Landscape heterogeneity is defined by Shannon's diversity index which measures abundances of habitat types (McGarigal et al., 2002). Proportion of bush and grassland measures ratio of landscape occupied by bush and grassland. Distance to water sources measures shortest Euclidean distance between each pixel to its nearest water sources. Human population density measures numbers of people per unit area. We use our results to advise conservation planning in Nepal.

2. Material and methods

2.1. Study area

Nepal is disproportionately rich in biodiversity in terms of its surface area, mainly due to great variation in altitude (70–8848 m), precipitation, temperature and physiographic divisions (Paudel et al., 2012; Primack et al., 2013). The physiographic divisions of country include: (1) Tarai (flat land), (2) Siwaliks (the youngest Himalayan range composed of sedimentary rock and boulders), (3) middle mountain (a mountain range and intervening landscapes between 1500 m and 3000 m asl), (4) high mountain, and (5) high Himalaya (Fig. 1). The country's biodiversity is recognized for its high species richness, endemism, and high proportion of global fauna (Paudel and Heinen, 2015a; Primack et al., 2013). A network of 20 protected areas (PA), i.e. 24% of the country's total area, has been established for long-term biodiversity conservation. However, PAs are not systematically planned and are increasingly fragmented, which is mainly the result of rapidly growing human settlements (Paudel and Heinen, 2015b).

Nepal is a largely rural country, with 83% of the population living in rural areas. Nearly 85% of the population in these rural areas are actively engaged in agriculture, forestry and fishery (Government of Nepal, 2011). Forests provide basic and vital resources such as firewood, livestock fodder, medicinal herbs and timber to support people's livelihoods. Human–wildlife conflict is a major conservation challenge although the extents of problems vary across country (Acharya et al., 2016).

2.2. Data on human–wildlife conflict

We collected data on human fatalities and injuries from the Regional Forest Directorate (RFD) and the Department of National Parks and Wildlife Conservation (DNPWC). Both are agencies of the Ministry of Forest and Soil Conservation (MoFSC), Nepal. MoFSC implemented a guideline for monetary relief payments for wildlife related damages (e.g. human death and injury, crop and property damage, etc.) (see Appendix 1 in Acharya et al., 2016). Here, we systematically reviewed official records between January 1st 2010 and December 31st 2014 available at RFD and DNPWC. First, we contacted the responsible officers at RFD and DNPWC by telephone and email requesting scanned copies of official records of human fatalities and injuries by wildlife. We then organized all the incidents (human death or injury) according to (a) wildlife species (i.e. tiger, leopard, rhinoceros and elephant), (b) time of the incident (year and month), and (c) location of incident. The final database was rechecked for any computation errors and verified again with the original records.

2.3. Data on forest fragmentation habitat characteristics and human disturbances

We used six sets of variables to explain forest fragmentation, habitat characteristics and human disturbances (see Table 1 for detail). *Forest fragmentation* was described by three variables: (a) landscape shape index and (b) effective mesh size which indicate size and configuration of a forest patch in a landscape, and (c) landscape heterogeneity. Landscape heterogeneity was described by size and diversity of land cover types such as forest area, cultivated land, grassland, shrub land, wetland, water bodies, artificial surfaces, bare land, permanent snow and ice. *Habitat characteristics* were indicated by two variables: (a) proportion of bush and grassland in a landscape, and (b) distance to nearest water sources. *Human disturbance* was measured by the number of people per unit area (Table 1). The first three variables were derived from global land cover maps available at http://glc30.tianditu.com (Chen et al., 2015). The map is available at 30 m resolution and includes classes such as forest area, cultivated land, grassland, shrub land, wetland, water bodies, artificial surfaces, bare land, permanent snow and ice. We resampled the map to produce a map with a spatial resolution of 100 m, matching that of the water source map (Table 1).

We measured all three forest fragmentation indices (landscape shape index and effective mesh size) using landscape metric algorithms implemented in a spatial pattern analysis program, FRAGSTATS (McGarigal et al., 2002). First, we coded forest as 1 and other remaining land use classes as 0 and developed a binary map of forest and non-forest. This was done as forest cover and area are important habitat requirements for all considered wildlife species (Dinerstein, 2013; Odden and Wegge, 2005; Sukumar, 2006; Wikramanayake et al., 2004). Furthermore, aggregation reduces potential misclassification of pixels (e.g. shrub land and grassland can be cultivated land). Finally, we used a moving window sampling strategy to develop a continuous map of forest fragmentation in FRAGSTAT. We used a window size of 20 km^2 as a landscape unit to measure fragmentation metrics. This is equivalent to average home range of tigers (23 km^2, (see Thapa et al., 2015), common leopards (21.1 km^2)) (see Odden and Wegge, 2005) and rhinoceros (20.5 km^2 – male rhinoceros in Bardia National Park) (see Dinerstein, 2013). The home range of elephants have been reported from few to hundreds of square kilometers (e.g. 18–1000 km^2) depending on (a) availability of food and water, (b) local topography and climate, and (c) type of herd (e.g. resident or migratory) (Campos-Arceiz et al., 2008; Joshi and Singh, 2009; Sukumar, 2006). In our analysis we considered the smallest home range of Asiatic elephant (17 km^2 (see Joshi and Singh, 2009).

We then calculated the proportion of bush and grassland area in a landscape. We first classified each pixel (100 m) as bush and grassland (coded as 1) and others (coded as 0). We computed the proportion of bush and grassland in a landscape of 20 km^2 for each pixel by using a moving window algorithm, which is equivalent to the average of minimum home ranges of tigers, common leopards, rhinoceros, and elephants.

We also obtained a wetland map of Nepal (river, lakes, permanent

Table 1
List of variables used in the model.

Variable/code	Description
Landscape shape index (lsi) (McGarigal et al., 2002)	$\mathrm{lsi} = \frac{e_i}{\min e_i}$, where e_i = total length of edge (or perimeter) of class i (forest) in terms of number of cell surfaces; includes all landscape boundary and background edge segments involving class i (forest), and min e_i = minimum total length of edge (or perimeter) of class i (forest) in terms of number of cell surfaces. *Landscape shape index* provides a simple measure of class aggregation or clumpiness. The LSI values range between 1 and infinity. The LSI value is 1 when the landscape consists of a single square or maximally compact (i.e., almost square) patch of the corresponding type and LSI increases without limit as the patch type becomes more disaggregated.
Effective mesh size (mesh) (McGarigal et al., 2002)	$\mathrm{mesh} = \frac{\sum_{j=1}^{n} a_{ij}^2}{A}\left(\frac{1}{10{,}000}\right)$, where a_{ij} = area (m^2) of patch ij, and A = total landscape area (m^2). *The effective mesh size* (MESH) measures forest fragmentation. The lower limit of MESH is constrained by the ratio of cell size to landscape area and is achieved when the corresponding patch type consists of a single one pixel patch. MESH is maximum when the landscape consists of a single patch.
Landscape heterogeneity (div)	$\mathrm{SHDI} = -\sum_{i=1}^{m} P_i * (\ln P_i)$, where P_i = proportion of the landscape occupied by patch type (class) i. *Shannon Diversity Index of land use categories* is used as an index of landscape heterogeneity. It equals minus the sum, across all patch types, of the proportional abundance of each patch type multiplied by that proportion. It is 0 when the landscape contains only 1 patch (i.e., no diversity). The index increases as the number of different patch increases and/or the proportional distribution of area among patch types becomes more equitable.
Proportion of bush and grassland (bg)	Proportion of area occupied by bush and grassland in a landscape.
Distance to water sources (disw)	The distance to water sources measures Euclidean distance between each pixel of landscape to its nearest water sources.
Human population density (popden)	Number of people per unit area within an enumeration unit, ward, which is the smallest geopolitical entity of Nepal.

water streams, channels, etc.) from the topographic map of Nepal (1:25,000) from Department of Survey, Government of Nepal. We defined each pixel of the map based on its nearest Euclidian distance to water sources using the Spatial Analyst tool in ArcGIS. A human population density map was used as an index of human disturbance. Population count data was obtained from the Central Bureau of Statistics at ward level (the smallest administrative unit of Nepal) (CBS, 2012). We computed area of buildup and agricultural lands (inhabited region) of each ward, and calculated number of people per unit area within an inhabited region of ward. This is because human settlements in mountain regions are sparsely distributed throughout agricultural lands.

2.4. Data analysis

2.4.1. Sampling strategy

Our database included 247 attack records with information about (a) wildlife species involved in the attack, (b) type of attack (death or injury), (c) date of attack, and (d) location of attack. The locations of attacks were not recorded by geographical information system (GPS). We therefore considered the centroid of ward as the most approximate location of the conflict events based on two reasons. First, a ward is the smallest administrative entity (mean = 4.35 km^2) in Nepal and data are readily available at this level. Secondly, we evaluate the responses of wildlife to forest fragmentation and configuration metrics at landscape level (i.e. 20 km^2) and we found no significant difference between forest fragmentation metrics within a small spatial variation of the attack locations (~2 km). The data on attack events included tigers (n = 50), common leopards (n = 72), rhinoceros (n = 70) and elephants (n = 55) (Fig. 2). However, 47 attacks were in the same locations for individual species during our study period. This resulted 200 unique locations in our dataset: tiger (n = 45), leopard (n = 53), rhinoceros (n = 58) and elephant (n = 44). Thus, an attack location received at least one attack during five year period or it may have several attacks in a year for multiple years. Thirty seven locations had attacks from multiple species, which further reduced unique attack location to 163.

We assumed that once attack occurred in a location "A", it would be a potential conflict location at least once a year for a particular wildlife species during our study period. For example, if a tiger attacked a person in location "A" two times in 2011, three times in 2013, and nothing happened in 2010, 2012 and 2014, we assumed that location "A" had chances of wildlife attacks in 2010, 2012 and 2014. Thus, we coded wildlife attacks in location "A" by tigers as 0, 2, 0, 3 and 0 for the years 2010, 2011, 2012, 2013 and 2014 respectively.

Table 2
Variance inflation factor (VIF) of environmental variables of 163 unique attack locations by tiger, leopard, rhinoceros and elephant.

Variables	VIF
Landscape shape index	2.25
Effective mesh size	1.67
Landscape heterogeneity	1.96
Proportion of bush and grassland	2.14
Distance to water sources	1.35
Population density	1.12

We derived landscape indices (Table 1) for each conflict location. Before constructing models, we also examined multicollinearity in variables using vifcor function in R package (Naimi, 2014), which identifies a pair of variables with high correlation and excludes one of the correlated variables which has greater variance inflated factor (VIF). A VIF greater than 10 indicates a collinearity problem in the data (Chatterjee and Hadi, 2015). VIF suggested that no variable from the six input variables (Table 1) had a collinearity problem (Table 2). We computed average of environmental variables by frequency of attacks for all species and developed a graph representing the mean and standard error of mean of four individual wildlife species using ggplot2 package in R statistical software (Wickham, 2016).

2.5. Statistical model

We estimated relationship between attack events and predictor variables by using zero-inflated Poisson (ZIP) regression because our data included low counts with many zeros. Such data presents specific challenges to the statistical analyses as the data does not adequately fit standard distribution functions such as the Gaussian or Poisson (Zuur et al., 2009). Zero-inflated Poisson (ZIP) and zero-inflated negative binomial (ZINB) regression enable examination of the influences of explanatory variables simultaneously on count response and probability of zero count (Wenger and Freeman, 2008; Zuur et al., 2009).

Our analysis followed four steps. First, we developed two models (zero-inflated Poisson (ZIP) and zero inflated negative binomial) and determined appropriate distribution between these two models by using zeroinfl and vuong functions in the pscl package in R Studio Version 0.99.491 (R Core Team, 2015; Zeileis et al., 2008). Zero-inflated negative binomial models perform better than ZIP models for

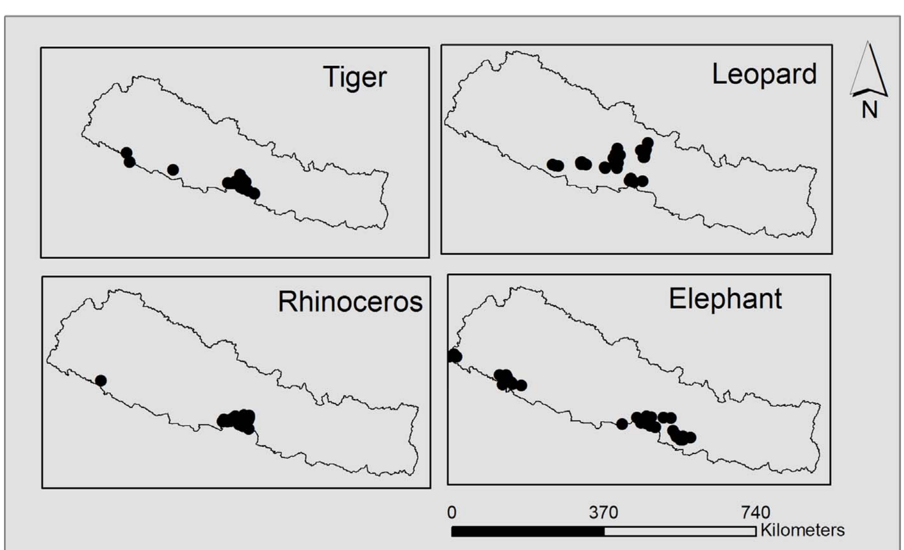

Fig. 2. Locations of attack event (death and injury of human) by wildlife (in clockwise: tiger, leopard, rhinoceros and elephant).

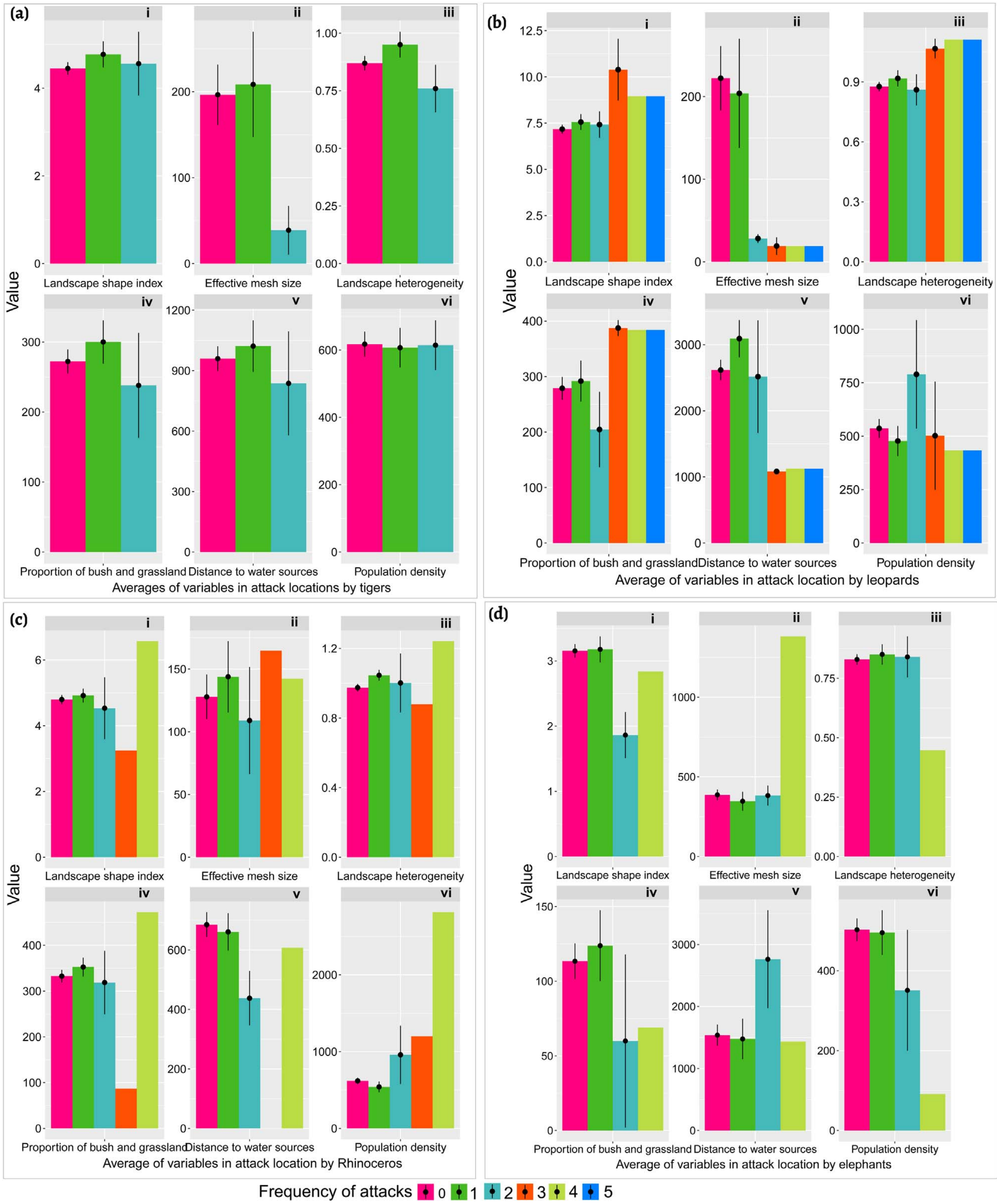

Fig. 3. Average of landscape attributes in an attack location categorized by frequency of attacks during a five year period (January 2011 and December 2014) for (a) tiger, (b) common leopard, (c) rhinoceros and (d) elephant.

over-dispersions, but this was not the case in our data. Second, we evaluated the parameter estimates of all independent variables. Third, we developed seven models (relevant combinations of predictor variables, including a null model) and compared AIC values to determine the most parsimonious model (AIC value closest to zero) among the candidate models using the multimodal inference package, MuMIn, in R (Bartoń, 2013). Fourth, we examined strength and direction of the relationship between predictors and frequency of attack events using the best model. The ZIP model has two components: a Poisson count model (count model) and the logit model for predicting excess zeros (zero model).

Table 3
Description of the candidate models used to investigate the relationship between frequency of attack cases and habitat fragmentation indices. Models for Bengal tiger, common leopard, one horned rhinoceros and Asiatic elephant were ranked on the basis of Akaike information criterion with small sample bias adjustment, AICc (see Table 1 for detail description of variables).

Model	logLik	AICc	ΔAIC	Weight
1. Bengal tiger *Panthera tigris tigris*				
mesh + popden + disw + div + lsi + bg	−165.08	358.7	0	0.76
mesh + popden + disw	−172.85	361.9	3.19	0.15
mesh + popden	−176.17	364.5	5.75	0.04
mesh + popden + disw + div	−172.25	364.8	6.09	0.03
mesh + popden + disw + div + lsi	−171.99	368.4	9.67	0
mesh	−188.96	386.0	27.27	0
Null model	−241.96	487.9	129.24	0
3. Common leopard *Panthera Pardus*				
div + lsi + bg + mesh + popden + disw	−174.927	416.3	0	0.99
div + lsi + bg + mesh	−185.811	416.6	13.52	0.001
div + lsi + bg	−187.901	420.0	3.68	0.001
div + lsi	−190.924	423.9	7.63	0
2. One horned rhinoceros *Rhinoceros unicornis*				
disw + bg + popden + lsi	−198	416.3	0	0.48
disw + bg + popden	−200	416.6	0.28	0.42
disw + bg + popden + lsi + mesh	−197.79	420.0	3.68	0.07
disw + bg + popden + lsi + mesh + div	−207.77	423.9	7.63	0.01
disw + bg	−219.07	427.6	11.35	0
disw	−188.96	446.2	29.92	0
Null model	−241.96	487.9	71.65	0
4. Asiatic elephant *Elephas maximus*				
lsi + mesh + bg + disw + div + popden	−152.32	333.2	0	0.66
lsi + mesh + bg + disw	−157.38	335.0	1.88	0.25
lsi + mesh + bg	−161.10	338.4	5.23	0.04
lsi + mesh + bg + disw + div	−157.60	339.6	6.43	0.02
lsi + mesh	−165.52	343.1	9.98	0
lsi	−169.88	347.8	14.65	0
Null model	−192.36	388.8	55.59	0

3. Results

3.1. Tiger

Of the total attack cases (n = 50), 45 attacks were in unique locations. Tigers predominately attacked once in a particular location (n = 40, 89%) during the study period (average attack = 1.11, min = 1, max = 2). Such locations were less fragmented than locations where recurrent attacks occurred (Fig. 3a ii). According to AIC values, the full model was the best model for predicting attacks by tigers (Table 3). Parameter estimates of the top model for tigers showed that effective mesh size and human population was negatively associated with counts of attacks by tigers (Table 4). Here, a 1-unit increase in average effective mesh size of forest was associated with a decrease in attacks by tigers by a factor of 0.99 ($e^{-0.001}$), so was human population density (Table 4). However, distance to water sources had a positive influence on the counts of attacks by tigers. We estimated that a 1-unit increase in distance to water sources increased counts of attacks by a factor of 1 ($e^{0.0006}$; see Table 4). However, it was not a significant predictor in the zero model.

Both effective mesh size and human population density also had a negative influence in the zero models. Parameter estimates suggested that a 1 unit increase in effective mesh size and human population decreased the probability of excess zeros (excess absences) by a factor of 0.72 ($e^{-0.32}$) and 0.55 ($e^{-0.58}$) respectively. There was, however, a highly significant increase in probability of excess zeros with increasing landscape heterogeneity (zero model) (Table 4).

3.2. Common leopard

Common leopards made 53 attacks in unique location, which included two attacks in 15% cases (n = 8), three attacks in 4% cases (n = 2), five attacks in 1.8% cases (n = 1) and six attacks in 1.8% cases (n = 1) (average attack = 1.38, min = 1, max = 5). All these high frequencies attack cases occurred progressively in the fragmented forest (Fig. 3b ii) and highly heterogeneous landscape (Fig. 3b iii). According to AIC values, the full model was the best model for common leopards (Table 3). The parameters estimate suggested that landscape heterogeneity had a significant positive effect on counts and zeros (Table 4). There was an increased probability of attacks by a factor of 87 ($e^{4.47}$) for a unit increase in average landscape heterogeneity. The proportion of bush and grassland had negative effect in the counts only. The landscape shape index had a strong negative effect in the zero model. We estimate that an increase of one unit of landscape shape index would increase odds of a zero count by a factor of 0.34 ($e^{-1.055}$) (Table 4).

3.3. Rhinoceros

Out of 58 unique attack locations by rhinoceros, nearly 84% of attacks (n = 49) by rhinoceros occurred once in a particular location during the study period. Furthermore, two attacks occurred in 12% of locations (n = 7), three attacks occurred in one location and four attacks occurred in another one location (average attack = 1.2, min = 1, max = 4). The frequent attack locations were near water sources and densely settled by human population (Fig. 3c v–vi). According to AIC values, the best model included distance to water sources, proportion of bush and grassland, human population density and landscape shape index (Table 3). All these variables except for landscape shape index were significant in the counts of attacks. Distance to water sources negatively affected only the counts. The proportion of bush and grassland negatively affected both counts and the zeros. Similarly, human population density had a strong positive effect both on counts and zeros. Landscape shape index had a strong positive effect in the zero model only. Parameter estimates suggested that each unit increases with average distance to water sources and was associated with a decrease in attacks by rhinoceros by a factor of 0.44 ($e^{-0.81}$). There was a strong increase in excess zeros with increasing landscape shape index by a factor of 2.2 ($e^{0.806}$).

3.4. Elephant

Elephants attacked people in 44 unique locations, which included two attacks in four locations and four attacks in one location (average attack = 1.15, min = 1, max = 4). These recurrent attacks occurred in the fragmented forest landscapes and away from by human settlements (Fig. 3d ii). According to AIC values, the full model was the best model for elephants (Table 3). The parameter estimates suggested that counts of elephants' attacks are positively associated with effective mesh size and proportion of bush and grassland, while negatively associated with landscape shape index (Table 4). Here we estimated an increase of 1-unit of landscape shape index reduced counts of elephant attacks by a factor of 0.41 ($e^{-0.89}$). Ranking wildlife based on the frequency of attacks, and by the average value of predictors associated with those attacks, suggests that elephant attacks often occurred in less fragmented forests, with rhinoceros, tiger, and common leopard attacks increasing in fragmented forests (Table 5).

4. Discussion

Forest and habitat loss and fragmentation are the major causes of decline in wildlife populations worldwide (Fahrig, 2003; Rochelle et al., 1999). As rapidly expanding human populations put pressure on the forested areas, fragmented forest landscapes are increasingly becoming

Table 4
Statistical significance of models explaining human wildlife conflict. The models (zero-inflated Poisson regression) include two parts (a) count model (Poisson with log link), (b) zero-inflation model (binomial with logit link). The mode for elephant is not zero-inflated (see Table 1 for detail description of variables).

Count model					Zero-inflation model			
Coefficient	Estimate	SD	*z*	*P*	Estimate	SD	*z*	*P*
1. Bengal tiger *Panthera tigris tigris*								
Intercept	−2.70	0.74	−3.62	< 0.01	−385.25	22.67	−16.99	< 0.01
mesh	−0.001	0.0005	−2.29	0.02	−0.32	0.06	−4.72	< 0.01
popden	−0.001	0.0003	−2.60	< 0.01	−0.58	0.08	−6.76	< 0.01
disw	0.0006	0.0001	3.23	< 0.01	0.17	–	–	–
div	0.05	0.73	0.06	0.94	407.28	22.10	18.42	< 0.01
lsi	0.005	0.107	0.04	0.96	−3.79	2.31	−1.64	0.10
bg	0.002	0.001	1.66	0.09	0.087	0.05	1.66	0.09
3. Common Leopard *Panthera pardus*								
Intercept	−3.41	1.01	−3.39	> 0.01	0.62	0.22	0.22	0.81
div	4.74	1.24	3.81	> 0.01	11.53	3.46	3.46	> 0.01
lsi	−0.02	0.09	−0.22	0.81	−1.055	−4.71	3.46	> 0.01
bg	−0.002	0.01	−1.96	0.04	−0.002	0.002	−4.71	0.31
mesh	0.0002	0.0007	0.33	0.74	−0.00001	0.001	−0.99	0.99
popden	−0.001	0.0003	−0.66	0.50	−0.001	0.0007	−1.69	0.09
disw	−0.0003	–	–	–	−0.001	0.0002	−4.93	> 0.01
2. One horned rhinoceros *Rhinoceros unicornis*								
Intercept	−0.58	0.52	−1.12	0.26	0.022	1.45	0.01	0.98
disw	−0.81	0.19	−1.79	0.04	0.00	0	1.42	0.15
bg	−0.003	0	−2.49	0.01	−0.02	0	−4.23	> 0.01
popden	0.001	0	6.33	> 0.01	0.01	0	1.88	0.05
lsi	0.050	0.15	0.31	0.75	0.806	0.43	1.85	0.06
Asian elephant *Elephas maximus*								
Intercept	0.50	0.91	0.55	0.57				
lsi	−0.89	0.16	−5.49	> 0.01				
mesh	0.0007	0.0003	2.12	0.03				
bg	0.002	0.001	2.11	0.03				
disw	−0.00006	–	–					
div	0.098	0.78	0.12	0.90				
popden	−0.0006	0.0004	−1.55	0.12				

conflict hotspots (Michalski et al., 2006; Sukumar, 2006). Our analysis provides insights on factors affecting human–wildlife conflict, and shows that fragmentation of landscapes has a great influence on human death and injury with the extent of influence differing among wildlife species (Table 5).

4.1. Human–tiger conflict: forest fragmentation

Our results showed that human–tiger conflict was positively associated with patchy forest landscapes. The zero model showed that probability of zero attack was strongly and positively associated with fragmented landscapes (poorly connected forest patches). Such patches may be small and disconnected forest patches that are not frequently occupied by tigers. Tigers need a large patch of undisturbed forest with a high density of prey base to support and maintain long-term genetic and demographic viability (Smith et al., 1999; Wikramanayake et al., 2004). Tigers are territorial and have a large home range (> 20 km^2), which depends on the density and availability of prey (Seidensticker and McDougal, 1993; Smith, 1993). Our results suggest that tigers attacks occurred in the less fragmented forests in comparison with leopards and rhinoceros (Table 5). These finding further suggest that sufficiently large patches of forests and their configuration are critical

Table 5
The average of predictors ranked by frequency of attacks by four wildlife species during period of 2010–2014.

Rank	Landscape shape index	Effective mesh size	Landscape heterogeneity	Proportion of bush and grassland	Distance to water sources	Population density
1	Elephant 2	Elephant 4	Elephant 4	Elephant 2	Rhino 2	Elephant 4
2	Elephant 4	Elephant 2	Tiger 2	Elephant 4	Rhino 3	Elephant 2
3	Elephant 1	Elephant 1	Elephant 2	Rhino 3	Rhino 4	Leopard 4
4	Rhino 3	Tiger 1	Elephant 1	Elephant 1	Rhino 1	Leopard 5
5	Rhino 2	Leopard 1	Leopard 2	Leopard 2	Tiger 2	Leopard 1
6	Tiger 2	Rhino 3	Rhino 3	Tiger 2	Tiger 1	Elephant 1
7	Tiger 1	Rhino 1	Leopard 1	Leopard 1	Leopard 3	Leopard 3
8	Rhino 1	Rhino 4	Tiger 1	Tiger 1	Leopard 4	Rhino 1
9	Rhino 4	Rhino 2	Rhino 2	Rhino 2	Leopard 5	Tiger 1
10	Leopard 2	Tiger 2	Rhino 1	Rhino 1	Elephant 4	Tiger 2
11	Leopard 1	Leopard 2	Leopard 3	Leopard 4	Elephant 1	Leopard 2
12	Leopard 4	Leopard 3	Leopard 4	Leopard 5	Leopard 2	Rhino 2
13	Leopard 5	Leopard 4	Leopard 5	Leopard 3	Elephant 2	Rhino 3
14	Leopard 3	Leopard 5	Rhino 4	Rhino 4	Leopard 1	Rhino 4

An increasing rank value of the landscape shape index indicates a high degree of disaggregated forest patches; an increasing rank value of the effective mesh size indicates an increasing disconnected forest patches in the landscape; an increasing rank value of proportion of bush and grassland indicates a high proportion of bush and grassland in the landscape; an increasing rank value of landscape heterogeneity indicates a high variability of land-use classes and their sizes; an increasing rank value of distance to water sources indicates a large distance to the nearest water sources; an increasing rank value of population density indicates a high human population density in the landscape. Please see Table 1 for a detailed description of predictors.

for tigers occupancy.

Tigers survive mainly in five protected areas in Nepal, which form three distinct sub-populations: (1) Chitwan National Park (CNP) and Parsa Wildlife Reserve (PWLR) in central Nepal, (2) Bardia National Park (BNP) and Banke National Park (BaNP) in mid-western Nepal, and (3) Suklaphanta National Park (SFNP) (Smith et al., 1999). Tiger habitats in Nepal have been expanded with the implementation of the Terai Arc Landscape Program (Gour and Reddy, 2015; MOFSC, 2015). We argue that expanded dispersal ranges are fragmented forests for tigers and risk lives of people there. This is because tigers dispersed into such small forest patches and/or fragments have a limited prey density and a high human disturbance (Barber-Meyer et al., 2013), and thus come into proximity to humans. Gurung et al. (2008) found a dramatic increase of human–tiger conflict after protection of forests surrounding CNP. Therefore we recommend expansion of core habitats of tigers for the species to thrive on high prey density and little human disturbance.

4.2. Human–leopard conflict: landscape heterogeneity

Although the best model for common leopard included all variables, only two variables, i.e. landscape fragmentation and proportion of bush and grassland, were significantly associated with the attacks on humans. Common leopard attacks were high in heterogeneous landscapes and in areas with a low proportion of bush and grassland. Furthermore, results suggested that more common leopards occupied the fragmented forests compared with tigers, rhinoceros and elephants (Table 5), and a high frequency of attacks were in highly fragmented and heterogeneous landscapes. Acharya et al. (2016) reported a growing incidence of common leopard attacks in Nepal, especially in the human dominated landscapes.

We suggest that the high incidences of common leopard attacks in Nepal is the result of past forest conservation practices. From the early 1990s, the government of Nepal encouraged local communities to conserve their forests by constituting a community forest user group, which is a group of local community members entrusted to protect public forests while meeting their needs of fodder, firewood and timber based on a government approved management plan (Acharya, 2002). Such a shift in forestry management proved to be highly successful in restoring forests, and contributed to the comeback of many wildlife species including common leopards to their former habitats (Acharya, 2002; Mikkola, 2002; Primack et al., 2013). Common leopards are adapted to a large range of habitats (Gavashelishvili and Lukarevskiy, 2008; Odden and Wegge, 2005), but they are largely territorial depending on the availability of prey species, human disturbances and competition with other cat species (e.g. tigers) (Odden et al., 2010). Common leopards in the human dominated forests of Nepal are likely to face a shortage of natural prey due to hunting by humans (Paudel, 2012), poor habitat quality, and frequent human disturbance (Paudel and Kindlmann, 2012). We suggest that future plans include conservation of large connected forest patches and a habitat management to support natural prey populations (Acharya et al., 2016).

4.3. Human–rhinoceros conflict: availability of water and grasslands

Distance to water sources, proportion of bush and grassland, human population density and landscape shape index were the most important variables explaining high human–rhinoceros conflict. Previous to this study we had expected that large mammals such as rhinoceros require large forest areas for foraging and browsing and therefore landscape fragmentation to be a significant variable explaining human–rhinoceros conflict. Our results however showed that human–rhinoceros conflict was high in either areas with high water sources or landscape with a high proportion of bush and grassland. Rhinoceros are habitat specialist (Dinerstein, 2013; Jnawali, 1995; Steinheim et al., 2005). They prefer tall grass floodplain habitat with dominant forage grass *S. spontaneum* (Steinheim et al., 2005) and frequently wallow in ox-bow lakes, rivers and temporary pools, especially between June and October (Laurie, 1982). Our findings perhaps suggest that critical habitats of rhinoceros are limited within protected area system, which may have forced them to move outside of protected areas.

Studies have shown a dramatic reduction of rhinoceros habitats within parks because of a rapid succession of grassland into forest and invasion of forests by *Mikania micrantha* and *Lantana camara* (Murphy et al., 2013). This might have caused rhinoceros to wander to nearby forests—most often community forests—that are protected by community people to meet their subsistence needs. Although we did not measure this in the current study, community forests are patchy (e.g. high edge density) and multiple used forests, which might have played a crucial role in the occurrence of conflicts. Thus, it is important to maintain critical rhinoceros habitats within parks, and reduce human movements inside protected forests.

4.4. Human–elephant conflict: forest fragmentation

The best model for human–elephant conflict included all variables considered in the model. Among them, variables describing higher habitat fragmentation (landscape shape index, effective mesh size, and proportion of bush and grassland) were significantly and positively associated with death and injury of humans. We noted that elephants are less resistant to the effects of habitat fragmentation than other wildlife species (Table 5). This is probably because elephants are one of the few remaining mega-herbivores and have a very large distribution range (Owen-Smith, 1992; Sukumar, 2006). This is true for elephants of Nepal. Historically, Nepal's alluvial lowland region, also known as Terai, had uninterrupted forests, also known as *Char Koshe Jhadi*, which were cleared for expansion of human settlements and farmlands and industrial developments (Hill, 1999). Terai forest were inhabited by a large elephant meta-population found across entire lowland Nepal adjoining the Nepal-India boarders(GoN/MoFSC, 2007; Sukumar, 2006). Today elephants are restricted to four small and fragmented subpopulations in Nepal: a eastern population (Jhapa district), (b) a central population (CNP, PWLR), (b) a western population (BNP, BaNP), and (c) a far-western population (SPWLR). These subpopulations are not well connected by corridors, and they face a shortage of good quality of habitats within parks (Choudhary, 2004; Pradhan et al., 2011).

In Nepal, elephants were recorded more often in tall grass floodplain, khair (*Bambax ceiba*)–sisso (*Dalbergia sisso*) forest and dense sal forest (with abundant *Mallotus phillippinensis*) (Pradhan and Wegge, 2007; Steinheim et al., 2005; Wegge et al., 2006). Such habitats may not be extensive within the protected area system today, and are degraded or/and fragmented outside of protected areas due to small core areas, high edge density and invasion by alien species (Peh, 2010). Choudhary (2004) noted a high chance of elephant attacks in the small forest pockets on elephant migration routes, especially in agricultural lands scattered over a large area of fields interspersed with forests. High human–elephant conflict in eastern Nepal has been linked to habitat fragmentation (Acharya et al., 2016; Pradhan et al., 2011). The eastern population includes of few resident elephants (~15) that move throughout fragmented forests along the Terai and Churia mountain range. Furthermore, a large number of migratory elephants (~100) from West Bengal of India move seasonally to the east-southern part of Nepal (e.g. Jhapa district of Nepal), but get restricted within a small portion of their historical seasonal movement route. Here elephants cause a massive damage on the property of people. Similarly, conflicts are frequently reported from the intermix areas of human settlements and forest patches near Chitwan National Park (Pant et al., 2015).

5. Conclusions

Our study demonstrates that large patches of forests are often critical for conserving large mammals in human dominated landscapes.

Tigers attacked most often in fragmented forest landscapes that are densely settled by humans. Elephant attacks were also high in the fragmented forests. These two large mammals showed preferences for very large patches of forests compared with common leopards and rhinoceros (Table 5). Rhinoceros showed a preference for large forests, but critical habitat requirements (e.g. water availably and grasslands) are also important. Common leopards attacked more often in the heterogeneous landscape and degraded forests areas in human dominated landscapes, which suggest that complex intervening landscapes (e.g. human settlements, agriculture lands, small patchy forest areas, and degraded forests such as bushes) are breeding ground of growing human–leopard conflict. Thus, future conservation plans should focus on increasing forest size and their connectivity in Nepal's mountains.

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Conservation and Population Recovery of Gharials (*Gavialis gangeticus*) in Nepal

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Abstract: The remnant populations of Gharials, *Gavialis gangeticus*, are now confined to the large, deep rivers of northern India and Nepal. In lowland Nepal, the populations are restricted to a few stretches of the Narayani–Rapti and Karnali–Babai river systems. Periodic censuses of the wild populations have been made over the past 12 yr. Here, we present population trends of Gharials in the Narayani, Rapti, and Babai rivers based on these surveys. The results indicate that the combined numbers of adults and subadults have been gradually increasing since 2005, but the numbers of adults are low and female biased, with very few males recorded from all study sites. In 1978, Nepal established a captive breeding center in Chitwan National Park, from which captive-bred animals have been periodically released 4–7 yr after hatching, at which time the animals are about 1.5 m total length. The detection of hatchlings and subadult classes that are smaller than these released animals in the rivers indicates that there is natural recruitment. Therefore, collecting all nests for ex-situ breeding might not be the best strategy until more rigorous field assessments are completed to determine the relative contributions of captive-bred versus natural recruitment. We suggest that more effort should be channeled toward field assessments, including mapping and monitoring habitat availability, habitat management to ensure necessary environmental flows to create sand banks and deep pools, and research to better understand the ecology and behavior of Gharials in Nepal's rivers.

Key words: Bardia; Chitwan; Climate change; Crocodylia; Himalayan rivers

Members of the only extant species in the genus *Gavialis*, *Gavialis gangeticus* (Gharials), live in deep, large rivers of the northern regions of the Indian subcontinent (Stevenson and Whitaker 2010). The historic range of Gharials included the Indus, Ganges, Mahanadi, and Brahmaputra river systems, and possibly the Irrawaddy River in Myanmar. Gharials have been extirpated from most of this range, however, and are now restricted to a few river stretches in India and Nepal (Groombridge 1987; Stevenson and Whitaker 2010). A very small sink population might exist in Bangladesh, populated by animals from India that washed over the Farakka Barrage (Sarker et al. 2008).

There was a range-wide decline of Gharials in the late 1970s (populations decreased by >90%), attributable to a number of causes, especially killing of adult males for the ghara (the rostral boss, used in indigenous medicines), and harvesting eggs for human consumption (Biswas 1970; Whitaker 1975; Choudhury et al. 2007; Katdare et al. 2011). Other threats to this species include (1) habitat changes and loss of prey caused by construction of dams, barrages, and irrigation canals that change instream flows and habitat; (2) sand and boulder mining and building embankments that change river courses and cause siltation; and (3) disruptive fishing techniques that decrease prey and kill Gharials that become entangled in nets (Choudhury et al. 2007; Stevenson 2015). In response to declines in populations of Gharials, the governments of both India and Nepal established ex-situ egg incubation and breeding programs to facilitate population recovery (de Vos 1984; Maskey et al. 2006; Stevenson 2015). Specifically, the government of Nepal initiated the Gharial Conservation Project with two ex-situ breeding centers, one in Chitwan National Park in 1978 and another in Bardia National Park in 1982 (Maskey et al. 2006). Eggs were collected from in-situ nests and transferred to the ex-situ breeding centers for incubation. Hatchlings were kept in the breeding centers for 4–7 yr, when they were about 1.5 m total length and considered to be safe from predation before they were released into the rivers (Maskey and Percival 1994). The first release from the Chitwan center occurred in 1981.

Nepal's wild populations of Gharials are now restricted to the Narayani–Rapti and Karnali–Babai river systems (Fig. 1). Although historically recorded from the Koshi River, Gharial are considered to be extirpated from this river system (Goit and Basnet 2011). In 2004, the total population of Gharials in Nepal's rivers was estimated at 93 individuals, but this included best-estimate numbers from Koshi, Karnali, and Babai that were not based on field surveys (Maskey et al. 2006). It is also not clear if the number comprised only adults or all age classes.

Since 2004 there have been periodic surveys of Gharials in the Narayani, Rapti, Karnali, and Babai rivers in lowland Nepal. Here, we analyze the survey results from 2005 onward to examine the population trends, especially in relation to the ex-situ conservation program for Gharials. While several sources have reported the results of the different surveys in these watersheds (Table 1), none have made critical assessments of the decade-long cumulative information that has been collected.

Materials and Methods

Study Area

The Narayani and Rapti rivers represent the western and northern boundaries, respectively, of Chitwan National Park

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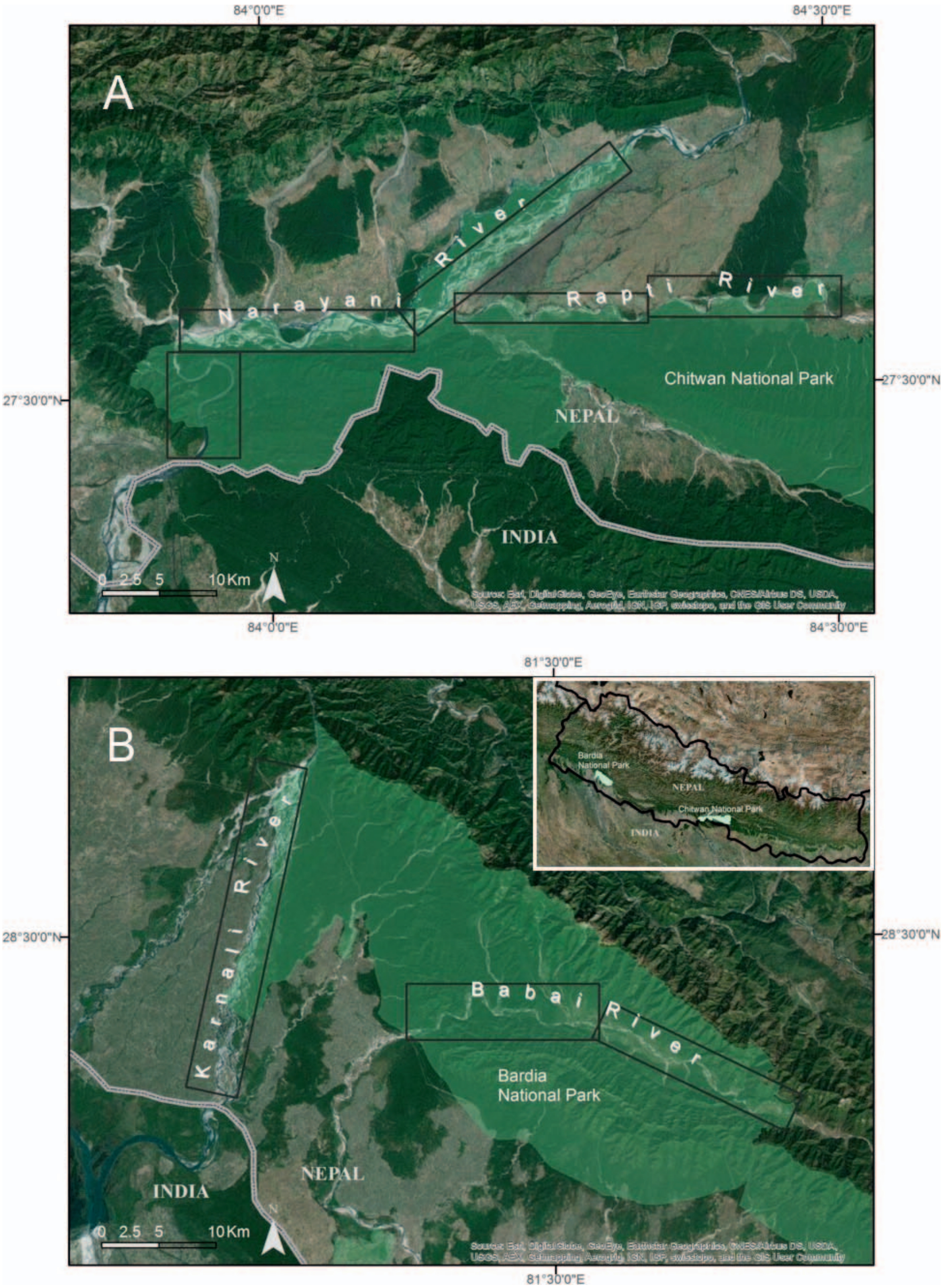

FIG. 1.—Study areas for *Gavialis gangeticus* surveys showing (A) Narayani and Rapti rivers in Chitwan National Park and (B) Karnali and Babai rivers in Bardia National Park. Note the wide, braided nature of the Narayani, relative to the Rapti River. The transect survey areas are indicated in black rectangles.

TABLE 1.—Results of *Gavialis gangeticus* surveys in four watersheds (Narayani and Rapti rivers in Chitwan National Park, and Babai and Karnali rivers in Bardia National Park) in Nepal, from 2004 to 2016.

Year	Males	Females	Total adults	Subadults	Hatchling/ immature	Not sexed	Total	Survey period	Reference
Narayani River									
1987/88							50		Maskey et al. 2006
2004							31		Maskey et al. 2006
2005	2	12	14	4	6		24	December	Ballouard and Cadi 2005
2006							22		Maskey et al. 2006
2008	2	9	11	14	9		34	January–February	Khadka et al. 2008
2010				22	1		23	November	Khadka 2011
2011	2	14	16	24	3	5	48	February–March	WWF Nepal 2011
2012			14	34	4		52	November	Khadka 2013b
2013	1	14	15	20	3		38	January	Rajbhandari and Acharya 2013
2014			12	47	1		60	February	Rajbhandari and Acharya 2013
2016	1	48	49	35			84	March	2016 survey data[a]
Rapti River									
2004							30		Maskey et al. 2006
2005	2	6	8	6	1		15	December	Ballouard and Cadi 2005
2006							25		Maskey et al. 2006
2008	2	19	21		2		23	February–April	Bhatta 2009
2010				23	3		26	November	Khadka 2011
2011		1	1	29		3	33	February–March	WWF Nepal 2011
2013			4	31			35	January	Rajbhandari and Acharya 2013
2016		20	20	52	5	5	82	March	2016 survey data[a]
Babai River									
2008	1	1	2	8			10		Khadka et al. 2008
2011	2	5	7	10			17	February–March	WWF Nepal 2011
2016	5	10	15	13		3	31	March	2016 survey data[a]
Karnali River									
2008							6		Khadka et al. 2008
2011	0	1	1	1	2	3	7	February–March	WWF Nepal 2011
2016	0	1	1				1	March	2016 survey data[a]

[a] Department of National Parks and Wildlife Conservation, Nepal.

(Fig. 1A). The Narayani is a large, snow-fed river originating in the Trans-Himalaya as the Kali Gandaki River. Six other rivers also originating in the high-elevation Himalayan ranges of northern Nepal are tributaries to the Kali Gandaki River, which eventually flows into the Narayani. Peak monsoon flows can be >4600 m^3/sec, whereas the dry season low flows can be <300 m^3/sec (Fig. 2). The river can be over 4 km wide at some points, with multiple braided channels and instream islands.

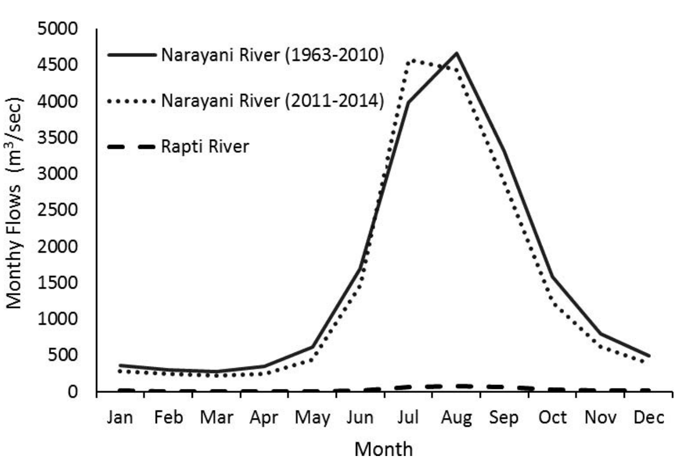

FIG. 2.—River flows (monthly averages, m^3/sec) from 1963 to 2010 in the Narayani and Rapti rivers of Chitwan National Park, Nepal. The two lines for Narayani River show a shift in peak flows between the two time periods. Data from the Department of Hydrology and Meteorology, Government of Nepal.

The Rapti River flows westward, along the northern border of Chitwan National Park, and joins the Narayani River near the northwestern corner of the park (Fig. 1A). This perennial river originates in the Mahabharat hills, which is a lower range of the Himalaya, and is fed from monsoon rains and spring water from the hills. The flows in the Rapti are much lower than the Narayani, with peak monsoon flows of around 77 m^3/sec and dry season flows of around 7 m^3/sec (Fig. 2).

Farther west, the Karnali River is a snow-fed river originating in the High Himalaya. The Karnali forms the western boundary of Bardia National Park, and eventually flows into India (Fig. 1B). The Babai River originates in the low-elevation Churia Range, the southernmost mountain range of the Himalaya in Nepal, and travels westward to join the Karnali River (Fig. 1B). For over 40 km, the Babai River flows within the core of Bardia National Park.

Field Surveys

Surveys were conducted along the Narayani and Rapti rivers over several years between 2004 and 2016, and along the Babai and Karnali rivers in 2008, 2011, and 2016 (Table 1). The rivers were divided into transects for the field surveys (mean ± 1 SD transect length = 22 ± 3.79 km; Fig. 1; Khadka et al. 2008; Bhatta 2009; Ballouard et al. 2010; Khadka and Thapaliya 2010; Khadka 2011; WWF Nepal 2011; Rajbhandari and Acharya 2013). Although the transect lengths were not consistent for surveys, all sections of the rivers with Gharials were covered during all surveys. In this analysis, data from all transects in the respective rivers were combined in the analysis for each year, and almost all of the

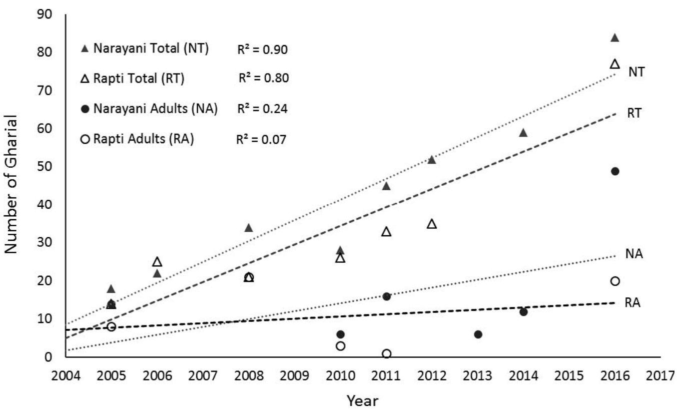

FIG. 3.—Numbers of Gharials (*Gavialis gangeticus*) recorded during surveys from 2005 to 2016 in the Narayani and Rapti rivers of Chitwan National Park, Nepal. The total number includes individuals from both adult and subadult age-classes. The regression lines indicate Narayani total (NT), Rapti total (RT), Narayani adults (NA), and Rapti adults (RA), based on data shown in Table 1.

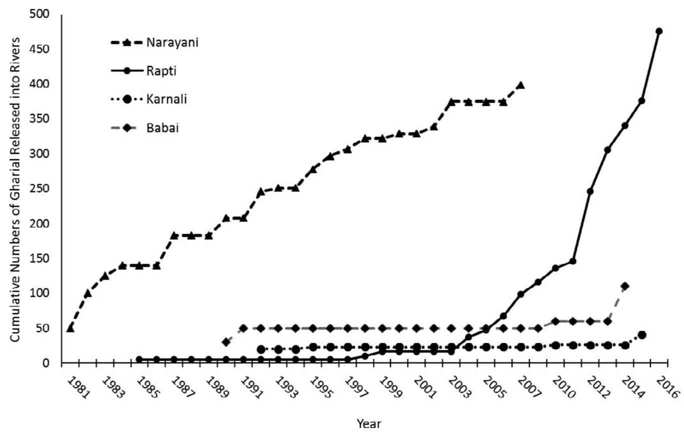

FIG. 4.—Cumulative numbers of Gharials (*Gavialis gangeticus*) released from ex-situ breeding facilities into four river systems in Nepal. See text for descriptions of each site.

river stretches with Gharials habitat were covered during all surveys of the respective rivers. Thus, we assume that the differences in transect lengths along a river stretch would not have an impact on the analysis of the total numbers of Gharials observed within the respective rivers across the years.

The surveys were conducted from November through March, when Gharials were most likely to be basking during the daytime. Survey efforts were timed to coincide with solar radiation available for Gharials' basking; thus, some surveys began soon after sunrise on clear days, while on foggy days, surveys were conducted from midmorning to midafternoon. Teams of observers used a boat to float along the river and scan the banks and water with binoculars for Gharials. When observed, Gharials were classified into the following age-classes based on estimated total length: adults, >280 cm; subadults, 280–220 cm; and juveniles, <220 cm (sensu Whitaker and Basu 1983). Individuals in the adult size class were sexed based the presence of the ghara in males (Stevenson and Whitaker 2010). Subadult males do not possess a ghara and cannot be sexed easily using morphological characters.

If replicate surveys were made along a transect during a particular sampling period, the data from the replicate with the highest number of individuals observed was used in this analysis. Individual counts included only direct sightings, whereas signs (e.g., tracks on river banks) were excluded.

Population Data Analysis

We collated the survey data from 2004 to 2016 in the Narayani, Rapti, Karnali, and Babai rivers (Table 1). For this analysis, we combined the subadult and juvenile age classes. We plotted the data for adults, as well as the combined numbers of adults and subadults for the Narayani and Rapti rivers. Hatchlings were not included because we considered it unlikley that most hatchlings would have been detected during these surveys. We did not analyze the trend data from the Babai and Karnali rivers because data were available for only 3 yr (Table 1). We also plotted the cumulative numbers of Gharials released from the ex-situ breeding center into each river to assess the population trends in relation to the stocking program.

RESULTS

When combining adult and subadult age classes, the number of individuals in both the Narayani and Rapti rivers increased over the survey period (R^2 = 0.90 and 0.80, respectively, for the two rivers; Fig. 3). There was also a positive relationship when considering only the adult age-class, but the R^2 values were lower (0.02 and 0.07 for Narayani and Rapti rivers, respectively). Both rivers experienced abrupt changes in population size. For example, the adult population in the Narayani experienced decreases in 2010 and 2013, but increases in 2011 and 2016 (Table 1; Fig. 3). Specific to 2016, 48 of 49 individuals accounting for the increase were females.

The adult population was consistently female-biased at all sites (Table 1). In the Narayani River, the male:female ratio ranged from 1:4 to 1:9 through the survey period. In 2016, only one adult male (with a ghara) was recorded. The range of sex ratios in the Rapti River was similar, from 1:3 in 2005 to 1:9 in 2008. No adult males were recorded at this site in 2016, although 20 adult females were recorded. The sex ratio of adult Gharials in the Babai River was also female biased, with values ranging from 1:2.5 in 2011 to 1:5 in 2016.

There were more adult Gharials in the populations of the Narayani and Rapti rivers in 2005, but from 2008 onward, there was a higher representation of subadults (Table 1). The population structure in the Babai River indicated a similar pattern, with more subadults in the population in 2008 and 2011; however, more adults were recorded in 2016 (Table 1). Between 1981 and 2006, 442 Gharials were released into Narayani and Rapti rivers from the ex-situ breeding center (Fig. 4).

DISCUSSION

Currently, the largest single population of Gharials occurs within the National Chambal Sanctuary in north-central India, with around 300 adults and subadults (Nair et al. 2012). The population of Gharials in Nepal's Chitwan National Park is considered to be the third largest across the range (Ballouard et al. 2010), an indication of the dire status of this species.

Trends in Population Structure and Growth

Field surveys conducted in Nepal's rivers from 2004 to 2016 reveal some broad trends that are useful to evaluate the status of Nepal's population of Gharials. The increasing trend for the populations found in the rivers of Chitwan National Park indicates that the population of Gharials is gradually recovering in those locations. The variation in numbers of Gharials detected through the years could be caused by detection biases, actual decreases (e.g., fatalities), behavior of Gharials, or a combination of all of these factors. It is also possible that some of the individuals classified as subadults (based on length estimates) could be reproductively mature, but stunted in growth as a result of being held in ex-situ breeding centers for up to 7 yr prior to being released (J. Lang, personal communication). Combining adult and subadult age-classes likely provided a more accurate population estimate at all of our study sites.

Since 2013, the surveys of Gharials were able to confirm the presence of only one adult male from the populations in the Chitwan National Park (Table 1). Data dating back to the 1980s also consistently revealed a female-biased sex ratio; Maskey (1989) reported a low of 1:9 in 1984 and a high of 1:6 males to females in 1987. Surveys of other crocodilans have also revealed highly skewed sex ratios attributed to sampling biases (Thorbjarnarson 1997). In Gharials, the skewed sex ratios could be partially attributable to behavior that make male individuals harder to detect. Adult Gharials form breeding aggregations from November to February (Whitaker and Basu 1983). During this time, males are territorial and maintain harems of several females. Most of the survey efforts analyzed in our study were conducted during this period; thus, the consistently skewed sex ratio favoring females could be the result of this behavior. As such, the sex ratios reported here might not reflect the actual sex ratio of the populations. It is also possible that some of the stunted adult males released from the breeding centers could have been misclassified as subadult females, compounding the bias. Whereas adult male Gharials used to be poached for their ghara, community surveys suggest that poaching is not a major threat in recent years (Bhatta 2009). Fatalities occur when Gharials become entangled in fishing nets or succumb to poisons used to kill fish (Bhatta 2009), but these deaths would not selectively remove adult males. However, given the consequences possible if adult males are not recruited into the populations, future surveys should be especially sensitive to accurately detecting this life-history stage.

The numbers of subadults in the rivers of Chitwan National Park, and in the Babai River, have increased since 2008 (Table 1; Fig. 3). Studies of other recovering crocodilan populations have also indicated a preponderance of individuals within the subadult age-class (Seijas and Chávez 2000; Fukuda et al. 2011). When considered together, the population trends and the age-class structure data indicate that the populations of Gharials in Chitwan's rivers have been increasing, albeit slowly, over the past decade.

The trend data for the Karnali and Babai rivers were not assessed because of fewer survey years, but the population age-class structure for the Babai River indicates a majority of individuals occupying the subadult classes, perhaps also indicative of a recovering population. The surveys in the Babai River have also recorded the presence of a few hatchlings. Because Gharials released from the ex-situ breeding center are beyond hatchling stage, the presence of hatchlings in the rivers indicate some in-situ nest success.

Release of Gharials from Ex-Situ Breeding Center

Had they all survived, the 442 Gharials released into Narayani and Rapti rivers from the ex-situ breeding facility between 1981 and 2006 would have reached the adult age-class by 2016. The minimum population of subadults and adults in these two rivers recorded in 2016 was 156. The population size of Gharials in these rivers when the breeding program was initiated is unknown, but is probably similar to the estimated population of 61 in 2004 (Maskey et al. 2006). Thus, the increase of about 95 animals between 2004 and 2016 represents about 21% of the Gharials released from the ex-situ center.

The Babai River flows through the core area of Bardia National Park and is relatively free from human disturbance. Surveys in this river in 2008 recorded eight subadults; but there had been no releases of captive-bred Gharials into the Babai River since the 1990–1991 season. A barrage at the lower end of the Babai River as it exits Bardia National Park prevents upstream movement of Gharials from downriver locations into the park, and no Gharials have been reported upriver, beyond the eastern boundary of the park. Thus, it is most likely that the subadults are products of in-situ breeding.

Despite the large numbers of captive-bred Gharials released into the Rapti and Narayani rivers, the population of Gharials remains low at these locations (Table 1). Only 19 of 273 captive-bred Gharials released into the Narayani River between 1980 and 1993 survived, leading Maskey and Percival (1994) to conclude that survival of head-started Gharials is only ~7% in the wild, and to question the viability of ex-situ breeding programs. Surveys in 2003 and 2004 that recorded the fate of marked captive-bred individuals found that 50% of the released animals disappeared after the first year, and only 20% were recorded in the second year (Ballouard et al. 2010). In India's National Chambal Sanctuary, Hussain (1999) estimated postmonsoon hatchling recruitment from in-situ nests to be 7.7%, and an egg-to-postmonsoon survivorship of 5.5%. Thus, if the survivorship of captive-bred animals in the wild in India can be considered a conservative benchmark for Nepal's rivers, the difference between ex-situ and in-situ survival rates and recruitment into the wild Gharial populations might not differ.

The ex-situ breeding program could become more relevant in the current context of climate change impacts. Climate models and projections indicate that future precipitation patterns could become erratic and the onset of the monsoon could become unpredictable in the Himalayan ranges (Xu et al. 2009; Ministry of Environment 2010; Shrestha et al. 2012). During the past 5 yr, the river flows in the Narayani River have peaked earlier, shifting from August to July (Fig. 2). Gharials lay eggs in nests dug into river banks, and located 1–6 m above the waterline and up to 10 m away from the water's edge (Whitaker and Basu 1983). Eggs laid during late March and early April, during the premonsoon dry season, hatch during June (Bustard

1980; Whitaker and Basu 1983). The light premonsoon rains may not affect nests and eggs, and are even considered necessary to prevent dessication, but heavy rainfall and floods that cause prolonged inundation can destroy nests and eggs (Khadka 2013a). Although the shift in peak flows to July over the past 5 yr does not necessarily reflect a climate-change-related trend, such changes in precipitation regimes can potentially affect nest survival and recruitment success. Therefore, we suggest that the ex-situ breeding program be continued as a preemptive strategy against possible climate-related changes to river flow regimes. We advocate, however, that the practice be changed to (1) retain nests that are above flood levels in situ, (2) move some in-situ nests above flood line or to ex-situ breeding centers where the incubation is closely monitored, (3) release most hatchlings soon after hatching instead of holding them in an ex-situ facility for 4–7 yr, and (4) hold ~30–40% of hatchlings in captivity until the postmonsoon season and then release them to increase the chances of surviving monsoon flows.

In-Situ Conservation Priorities

Gharials are a relatively long-lived species, with a breeding life of ~50 yr and a life span of 100 yr (Whitaker and Basu 1983). Studies have shown that Gharials prefer sandy banks and sand bars along rivers or in midriver for basking, with less preference for gravel or stony substrates, and avoid mud-covered banks (Rao and Singh 1987; Maskey et al. 1995; Hussain 2009). Adults prefer deeper pools with presence of larger fishes for foraging and as escape cover, while subadults and juveniles are usually found in shallower pools (Maskey et al. 1995; Hussain 2009; Ballouard et al. 2010). Suitable habitats in many of the river stretches have now been altered by dams and barrages (Maskey 1989). Sand and gravel mining in Nepal's rivers has caused river chanelization, resulting in fewer meanders and and less sand deposition to create sand banks. High silt loads from upstream erosion and instream mining cover sand banks with mud, creating less-preferred habitat. Thus, the extent of any population increase could be limited by decreased quality and quantity of habitat available for basking and foraging, and the territorial behavior of dominant males. Relatively little effort has been made to document these changes, or to reverse the pattern of habitat alteration.

A mark–recapture study in India's National Chambal Sanctuary revealed that actual numbers of Gharials were more than double the population numbers recorded from daytime boat-based surveys (Nair et al. 2012). The fluctuation of adults observed in successive years indicates that the population numbers recorded from Nepal's rivers based on direct observations could be attributable to sampling errors, given that an assumption of the surveys is that all adult animals will be basking during the surveys and all basking animals were counted. These assumptions also discount the fact that some animals might detect the boats and enter the water before being recorded. Thus, the numbers reported from the surveys analyzed in our study are likely underestimates, as suggested by values from 2016, when there was a sharp increase of 48 female Gharial detected from the Narayani River. We suggest that estimates of numbers and population structures of Gharials in Nepal's rivers can be rendered more accurate by including the use of mark–recapture methods or drone surveys that include counts of Gharials in a water channel.

Whereas hundreds of Gharials were reported from the lower reaches of the Narayani River in the early 1950s and 1960s (Maskey 1989), it is unlikley that any population of Gharials in Nepal will attain such historic levels because of the changes to habitat and food availability. Populations of Gharials at the sites analyzed in our study appear to be recovering, but there is no evidence to indicate that the recovery is attributable to restocking from ex-situ breeding programs. In fact, these data indicate that some recovery might be from natural recruitment. In the meantime, attention is being diverted from urgent actions necessary to address the threats to wild populations and increase the success of in-situ recruitment. These threats, ranging from harmful fishing practices, release of chemical pollutants from industries located along river banks, dry season sand and gravel mining in rivers, to seasonal agriculture on river banks have been highlighted for years (Andrews and McEachern 1994; Ballouard et al. 2010) but remain unchecked. Releasing large numbers of Gharials from ex-situ breeding facilities with the hope that some might survive is not an effective approach to conservation (Nair et al. 2012; Stevenson 2015). Thus, we recommend that the ex-situ breeding program be continued as a hedge against the projected impacts of climate change, but be informed by rigorous field surveys that assess and monitor the status of wild populations. We also recommend that more effort be chanelled toward mapping and monitoring habitat availability, managing environmental flows to create sand banks and deep pools, and research for improved understanding of the ecology and reproductive behavior of Gharials in Nepal's rivers.

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Personal contribution:

The published scientific papers that, together with the comprehensive summary, constitute this cumulative dissertation reflect a substantial part of my scientific research. They were selected under the premise that a high personal contribution is given. This is reflected formally by the lead-authorship for all presented articles. This includes the development of methodologies and statistical backgrounds for the articles, the writing and submission as well as the responsibility for the review process of each article. However, the contributions of the co-authors of the articles shall not be questioned.

Further research articles are listed in Annex II.

None of the scientific articles presented here have been or are currently part of another cumulative dissertation.

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