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Greater one-horned rhino (*Rhinoceros unicornis*) mortality patterns in Nepal

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ARTICLE INFO

Keywords: Rhino Human-caused mortality Tiger attack Wildlife conservation Wildlife self-fighting Chitwan National Park Poaching

ABSTRACT

Nepal's lowland regions provide a rich habitat for greater one-horned rhino (Rhinoceros unicornis) populations. However, rhinos are facing human-caused and natural threats such as habitat loss and several other forms of anthropogenic pressure that cause mortality of greater one-horned rhinos (hereafter rhino) in Nepal. Understanding these patterns of mortality can provide important information for rhino conservation. In this study, we answered three important questions to aid in rhino conservation in Nepal:1)what was the pattern of rhino mortality (increased, decreased, or no change) during 2008-2018 in Nepal? 2) Does the pattern of rhino mortality vary by season, age, and gender? And, 3) what are the major causes of rhino mortality in Nepal? We collected rhino mortality data along with age, gender, and cause of death in the period between 2008 and 2018 in Nepal from secondary sources. We found that a total of 232 cases of rhino mortalities were observed during the 11-year period. Mortality of the rhino was associated with age and cause but not with gender and season. Among the nine categories of the causes of mortality, self-fighting, natural, tiger attacks, and poaching contributed about 80 % of total mortality. Mortality due to poaching of rhinos has decreased in recent years, while mortality due to self-fighting and tiger attacks have increased. We concluded that mortality causes associated with limited space and food, and tiger population growth are increasing in recent years. Therefore, habitat expansion, translocation to new suitable habitats, and multispecies conservation policy would contribute to long-term rhino conservation in Nepal.

1. Introduction

Wildlife mortality associated with anthropogenic pressures often contribute to a reduction in population size at regional as well as global scales (Adhikari et al., 2022; De Vos et al., 2015; Hernández and Margalida, 2009; Lee and Jetz, 2011; Petchey, 2000; Rodriguez and Delibes, 2004; StClair et al., 2020). Studies have predicted that more than 500 mammalian species will be extinct by the end of the 21st century if conservation efforts are not improved (Groombridge et al., 2002; Foreman, 2004; Collen et al., 2011; Bhandari et al., 2022). In particular, large mammals that have small or isolated population are more vulnerable to anthropogenic pressures such as habitat loss, road accidents, poaching, and hunting (Dale, 2001; Davies et al., 2000; Woinarski et al., 2015; Bhandari and Chalise,

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https://doi.org/10.1016/j.gecco.2022.e02189

Received 9 March 2022; Received in revised form 6 June 2022; Accepted 8 June 2022

Available online 10 June 2022

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2016; Schmidt et al., 2016; LaDue et al., 2021). If the mortality rate in small populations of such species continues to rise, those species may become extinct in the near future (Pimm et al., 1988; Cardillo et al., 2005; De Vos et al., 2015). For instance, large mammalian species such as West African Black Rhino (*Diceros bicornis longipes*) (Rookmaaker and Groves, 1978), Sicilian wolf (*Canis lupus cristaldii*) (Angelici and Rossi, 2018; Reale et al., 2019; Angelici et al., 2019), Tasmanian tiger (*Thylacinus cynocephalus*) (Mackness et al., 2002), and Caspian tiger (*Panthera tigrisvirgata*) (Kock, 1990) have become extinct in the past 100 years due to high human pressure. Furthermore, eastern black rhino (*Diceros bicornis michaeli*), southeastern black rhino (*Diceros bicornis minor*), and Javan Rhinoceros (*Rhinoceros sondaicus*) are critically endangered species according to the International Union for Conservation Nature (IUCN) red list status, requiring urgent and intensive protection.

A large mammal, the rhinoceros is an odd-toed ungulate that belongs to the family Rhinocerotodia and has five extant species; white rhino (*Ceratotherium simum*), black rhino (*Diceros bicornis*), greater one-horned rhino (*Rhinoceros unicornis*), Javan rhinoceros (*Rhinoceros sondaicus*), and Sumatran rhinoceros (*Dicerorhinus sumatrensis*) (Tougard et al., 2001; Orlando et al., 2003; Puranjit and Goswami, 2012; DNPWC, 2017; Schellhorn, 2018), all found in Asia or Africa (Tougard et al., 2001; Orlando et al., 2003; Jhala et al., 2021). Greater one-horned rhino (*Rhinoceros unicornis*) is distributed in the Indian subcontinent (India and Nepal) with a population of only ~ 3600 individuals (Subedi et al., 2013; Ellis and Talukdar, 2019; Das et al., 2015; Borthakur et al., 2016; Jhala et al., 2021). This species has become extirpated from Bangladesh and Bhutan with a continuous decrease in its populations within its current distribution range (DNPWC, 2017; Ellis and Talukdar, 2019; Jhala et al., 2021). Greater one-horned rhino (hereafter rhino) is in the Vulnerable category of the IUCN red list, as the population is fragmented and restricted to a small area of less than 20,000 km² (Ellis and Talukdar, 2019; Jhala et al., 2021). Gurrently, the Kaziranga National Park and Pobitora Wildlife Sanctuary in India, and the Chitwan National Park and Bardia National Park in Nepal are the major protected areas that maintain most greater one-horned rhino populations (Subedi et al., 2013; Ellis and Talukdar, 2019; Jhala et al., 2021). However, these populations are facing threats such as poaching, habitat loss, and other forms of anthropogenic pressure (Sinha et al., 2011; Talukdar, 2000; Ellis and Talukdar, 2019). To aid more effective rhino conservation, this study focused on their mortality pattern in recent years (2008–2018) and its underlying causes in Nepal.

Nepal's rhino population was at its most critical phase in 1966, when there were only 100 individuals. In recent years, an increasing trend in rhino population has been reported; its population increased to 409 in 2005 (DNPWC, 2009, 2017) due to the establishment of protected areas and implementation of conservation laws and regulations in Nepal (DNPWC, 2009, 2017). However, an increasing number of rhino causalities have also been reported (Subedi et al., 2013; DNPWC, 2017) due to anthropogenic and natural disasters (e. g., flooding) in recent years (DNPWC, 2005). Although historically poaching has been the major cause of rhino mortality in Nepal (DNPWC, 2017), mortality due to other anthropogenic causes such as electrocution and poisoning have also been frequently reported in recent years (DNPWC, 2017).

Individuals of different age and gender are often vulnerable to different threats and causes of mortality could be expected to differ across individuals within a population (e.g., Gaillard et al., 1998; leRoex and Ferreira, 2020). These age and gender differences in mortality is suggested for the rhino, as calves appear to be more vulnerable to flooding (DNPWC, 2017; Subedi et al., 2017) and attack by large carnivores (Laurie, 1982; DNPWC, 2017; Laurie, 1978). In contrast, poachers usually target adult rhinos rather than calves (Ferreira et al., 2012). Similarly, rhino mortality could be expected to change across seasons. For example, studies have shown high rhino mortality during droughts due to a scarcity of food and water resources (Ferreira et al., 2019, 2015; DNPWC, 2017; Subedi et al., 2017). Thus, rhino mortality causes can vary with gender, age, and season, but these patterns have not been systematically investigated for Nepal's threatened rhino populations.

Rhino habitats outside the protected areas are also decreasing due to anthropogenic pressure such as deforestation, and developmental activities (e.g., urbanization and farming) (DNPWC, 2017; Bhandari et al., 2022). Livestock grazing in the natural forests is creating additional pressure on rhino populations (DNPWC, 2017; Bhandari et al., 2022) causing them to be restricted entirely inside the protected areas. The restriction of rhino populations within a confined protected area increases intraspecific competition, resulting in fights for food, space and mating, and can cause direct or indirect mortality of individuals (Rachlow et al., 1998; DNPWC, 2017). On the other hand, increases in large carnivore populations such as tigers inside the protected areas can cause increased direct mortality on rhino calves as the tigers are forced to increase their prey diversity to ensure a sufficient food supply (Aryal et al., 2016). Similarly, the rhino populations in the buffer zone or close to human settlement areas are sometimes responsible for crop damage, resulting in human-rhino conflicts (Subedi et al., 2013; DNPWC, 2005).

We have very limited information available on rhino mortality patterns in Nepal in recent years (DNPWC, 2005, 2017) although rhino mortality is frequently being reported. For the conservation of rhino in Nepal, it is necessary to understand what are the major factors (e.g., death, effects of seasons, age and gender) linked to rhino mortality. We hypothesized that rhino mortality cases may be increasing over the years due to an increase in anthropogenic pressures. Furthermore, we hypothesized that these mortality patterns in rhino may vary by year, season, age, and gender. We attempted to answer three important questions in this study for rhino conservation in Nepal: 1) what was the pattern of rhino mortality (increased, decreased, or no change) during 2008–2018 in Nepal? 2) Does the pattern of rhino mortality vary by season, age, and gender? And, 3) what are the major causes of rhino mortality in Nepal?

2. Methods

In Nepal, rhino distribution is restricted to Nepal's lowland (< 1000 m) habitat in four National Parks (Parsa National Park, Chitwan National Park, Bardia National Park, and Suklaphanta National Park) (Fig. 1). Besides those protected areas, rhinos have also been reported from several community-managed and collaborative forests near those national parks (Fig. 1). The rhino habitats in Nepal are dominated by tropical, mixed broad-leaved forests such as Sal (*Shorea robusta*) forests (Bhandari et al., 2022). The average

temperature for these areas varies from ~ 12 °C in winter to ~ 40 °C in summer (Bhandari et al., 2022).

We gathered all the rhino mortality cases between the period 2008–2018 from secondary sources which are based on the publicly available sources such as annual reports, technical reports, newsletters and others (dissertation, annual bulletin and brochures) (Table SF1). We reviewed a total of 17 annual reports (DNPWC: 11; Bardia NP: 2 and Chitwan NP: 4), and three technical reports. We also monitored daily newspaper between Jan 2008 and Dec 2018. Two of the authors (SB and BA) were involved in monitoring newspaper data. All sources are listed in Table SF1. We compared our data with the annual reports released from the Department of National Park and Wildlife Conservation (DNPWC) to confirm the accuracy of our counts. Those records (mainly from newspapers and other printed forms) that lacked information on date of mortality, cause of mortality, gender, or age were cross checked with the national parks' press release statements (www.chitwannationalpark.org.np) or national parks' annual reports. The DNPWC, a government authority, conducts post mortems on dead rhinos in Nepal that are performed by a team of wildlife technicians and veterinarians (DNPWC, 2017). Annual reports have detailed information on each case, including estimated age, gender, cause of death, location and mortality date which were extracted for the analysis. In this way, for each mortality case, we recorded age, gender, date of mortality (year and month) and cause of death. We further categorized age into calf (< 6 years old) and adult (> 6 years old) (Subedi et al., 2017); gender into male and female; months were grouped according to four seasons: spring (March to May), summer (June to August), autumn (September to November), and winter (December to February) and cause of mortality into nine categories; poaching, tiger attack, disease/illness, electrocution, poisoning, natural disaster, natural death, self-fighting, and unknown (Table 1). Details on each mortality cause are provided in Table 1. Unknown mortality cause was assigned for the cases where postmortems were not possible on fresh caresses (DNPWC, 2017). Out of 232 cases of rhino mortality, there were 24 unknown cases, i.e., 10.3 % of the mortality data.

A linear regression model was used to examine the mortality pattern over the years (2008–2018), with year as the independent variable and number of mortalities as the dependent variable. Furthermore, since rhino poaching has been a major causes of rhino mortality (DNPWC, 2005, 2017), we also tested if rhino mortality due to poaching vs other causes differed linearly over the study period. We used chi-square contingency analysis to test the null hypothesis that there was no difference in causes of mortality between age groups (adult and calf) and gender (male and female). We used a one-way ANOVA (analysis of variance) to compare average mortality rates between months, seasons. Prior to using ANOVA, assumptions of normality and homogeneity of variance were tested by the Shapiro-Wilk's and Levene's tests, respectively (Razali and Wah, 2011; Ghasemi and Zahediasl, 2012). Results were considered

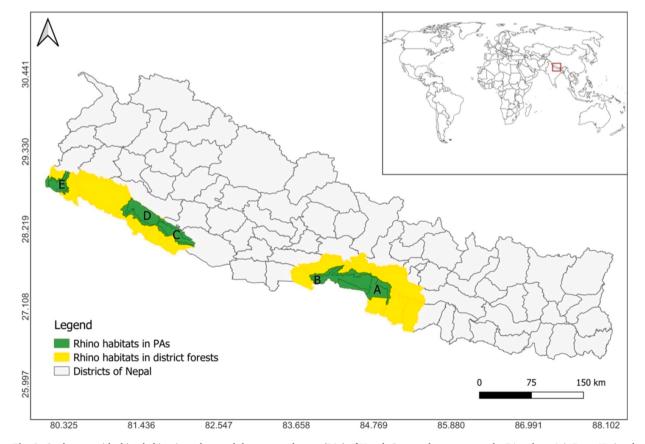


Fig. 1. Study area with rhino habitat in and around the protected areas (PAs) of Nepal. Green color represents the PAs where A is Parsa National Park, B is Chitwan National Park, C is Banke National Park, D is Bardia National Park, and E is Shuklaphanta National Park. Yellow color represents the community forests and collaborative forests serving as habitats for the rhinos in Nepal.

Table 1Nine different categories for cause of rhino mortality between 2008 and 2018 in Nepal.

Causes	Details
Natural death	For adults: mortality associated with old-aged rhinos.
	For calf: mortality associated with pregnancy complications and mortality after becoming an orphan
Poaching	Mortality due to killing of rhino for its body parts such as horn
Electrocution	Mortality associated with electric wires when farmers use electric wire to protect their crops from wildlife
Tiger attack	Mortality due to attack from tigers (Panthera tigris)
Illness	Mortality associated with diseases or illness
Poisoning	Mortality due to poisoning
Flooding	Mortality associated with flooding
Self-fighting	Mortality due to fighting with each other
Unknown	Mortality due to unknown causes or not reported due to lack of postmortems on fresh caresses

statistically significant at p-values less than 0.05. All the statistical analyses were performed in R version 4.1 (R Core Team, 2021).

3. Results

A total of 232 cases of rhino mortality were reported during 2008–2018. Among the nine mortality causes, self-fighting, natural, tiger attacks, and poaching, contributed about 80 % of total mortality in Nepal (Fig. 2). Mortality did not change significantly across the years during 2008–2018 (F (1, 9) = [1.18], P = 0.3). When mortality was analyzed separately for poaching vs non-poaching, linear regression results showed that mortality pattern due to poaching had significantly decreased over the years (Adj. R^2 =0.64, F (1, 9) = [18.81], P = 0.001, Fig. 3A), while mortality cases due to non-poaching causes had significantly increased (Adj. R^2 =0.47, F (1,9) = [9.87], P = 0.01, Fig. 3B). Mortality patterns due to self-fighting (Adj. R^2 =0.68, F (1, 9) = [22.78], P = 0.001, Fig. 3C) and tiger attack (Adj. R^2 =0.69, F (1, 9) = [22.82], P = 001, Fig. 3D) had both significantly increased during the study period. Mortality patterns due to other causes (i.e., natural, flooding, electrocution, illness, and poisoning) did not change (Fig. SF1).

We found that cause of mortalities differed among rhinos of different ages (adult, calf) (χ^2 (DF = 8, N = 190) = 32.3, P < 0.01), but not between genders (χ^2 (DF = 8, N = 199) = 5.7, P = 0.67). Calf mortalities were mainly associated with natural cause and tiger attack, but not by poisoning and poaching (Fig. 4).

We further investigated if number of mortalities per month was associated with season and month of the year. Our result showed that rhino mortality number did not vary significantly by season (N = 44, F (3, 40) = [0.93], P = 0.43). However, mortality number differed significantly among months (N = 132, F (11, 120) = [2.56], P = 0.006), with the highest average mortality in November (14.7 % \pm 7.5 % of annual mortality cases), followed by September, January, February, and December. While low mortality was observed in the months of August and October (4.76 % \pm 5.2 % and 3 % \pm 4.4 %) of annual mortality cases, respectively (Fig. 5).

4. Discussion

Our study showed that mortality of the greater one-horned rhino in Nepal due to poaching has decreased over a period of 11 years (2008–2011) while mortality due to tiger attacks and self-fighting has increased. Specifically, the rhino mortality cases seem to be increasing since 2011 in Nepal which is a matter of concern for rhino conservation (Fig. SF2). Our study found that four major causes

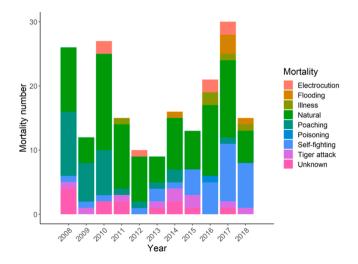


Fig. 2. Annual number of rhino mortality cases reported in Nepal from 2008 to 2018. In each year the different causes of mortality are represented by color.

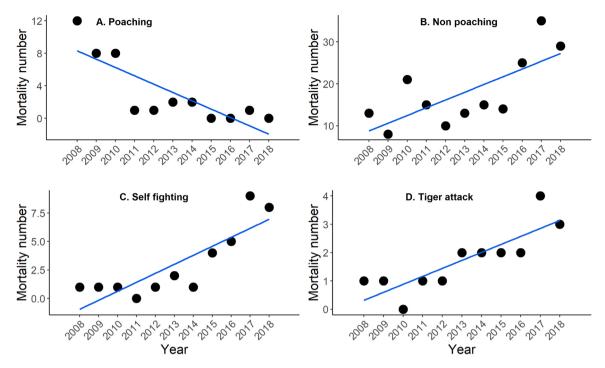


Fig. 3. Patterns of three major causal factors significantly changed from 2008 to 2018. Tiger attacks and self-fighting mortality significantly increased in recent years while mortality due to poaching significantly decreased.

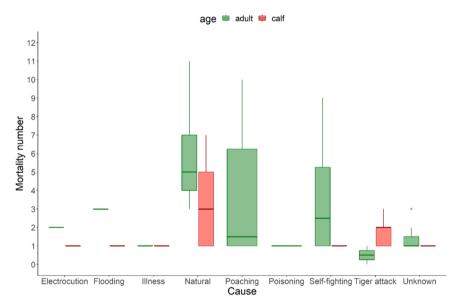


Fig. 4. Comparison of mortality causes between adult and calf rhinos in Nepal over the 11 years from 2008 to 2018.

(self-fighting, natural, tiger attacks, and poaching) contribute to the majority (\sim 80 %) of rhino mortality in Nepal. In addition, illness, flooding, electrocution and poisoning also caused some rhino deaths.

Poaching for the horn and other body parts is a major cause of the declining rhino numbers in Asia as well as in Africa (Subedi et al., 2017; Vigne and Martin, 1994). Poachers kill the rhino to extract and sell the horn which is of a high demand in the international market (Ferreira et al., 2015; Martin et al., 2009; Poudyal et al., 2009; Vigne and Martin, 1994), particularly in Asian countries such as Thailand, China, and Vietnam (Hanley et al., 2018; Shepherd et al., 2018; Eikelboom et al., 2020; Cheung et al., 2021). For instance, one kilogram of rhino horn can be sold for USD 50,000 (Haas and Ferreira, 2016; Stoner et al., 2019). However, trading rhino horns or any body parts is illegal in Nepal. With strict laws and their implementation, Nepal has celebrated zero rhino poaching years in 2015

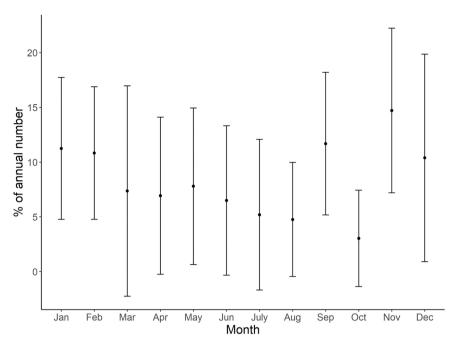


Fig. 5. Monthly mortality of rhino population in Nepal from 2008 to 2018, expressed as average annual percentages and standard error.

and 2016 (DNPWC, 2017), and poaching related mortality cases have been significantly reduced since 2011 owing to efficient conservation endeavors.

On the other hand, number of rhino mortality cases due to factors other than poaching, mainly tiger attacks and self-fighting, increased in recent years, and is one of the major concerns for sustaining rhino populations and their conservation. Mortalities due to tiger attacks may be attributed to a significant increase in tiger population in recent years (Karki et al., 2015; Aryal et al., 2016; Bhandari et al., 2019). Studies have reported rhino mortality cases by tiger attack in habitats with high tiger density in Chitwan National Park (Dinerstein and Price, 1991; DNPWC, 2017; Subedi et al., 2017). Frequently tiger related mortalities were inflicted upon rhino calves killed by tigers inside Chitwan National Park (Dinerstein and Price, 1991; DNPWC, 2017; Subedi et al., 2017) where tiger and rhino co-exist in similar habitats. Nevertheless, with the rapid increase in tiger density (~ 4.5 tigers/100 km²) (Karki et al., 2015; Aryal et al., 2016; Bhandari et al., 2019), rhino mortality due to tiger attacks could create a challenging environment for rhino calves in the near future. Therefore, as the populations of tiger and rhino increases in the same habitat, rhino mortality might increase due to tiger attacks, especially mortality of rhino calves. However, it may warrant long-term data to establish whether tiger attack could be the major threat for rhino conservation in Nepal.

Mortalities due to self-fighting have also increased significantly in recent times. This could be due to limited food availability and competition for territory and breeding access to females (Rachlow et al., 1998; Carlstead and Brown, 2005; DNPWC, 2009). For instance, Chitwan National Park which harbors around 600 rhinos in a 932 km² area (DNPWC, 2017), is facing a huge challenge to manage enough food and space for the existing rhino population (Subedi et al., 2013; Pant et al., 2021). Escalating anthropogenic pressure and shrinking natural habitat have limited the resources inside the protected areas where most of the regions outside the protected areas have become human settlements or have been converted to farmlands (Bhandari et al., 2022). Self-fighting mortalities may also be associated with territorial behavior of rhinos, especially in the breeding time (Rachlow et al., 1998). Studies have shown uneven gender ratios in rhino populations because of higher mortality in male rhinos while contending for the female (Rachlow et al., 1998; DNPWC, 2017; Subedi et al., 2017). Although we did not find significant differences in the causes of mortality between males and females, earlier studies within Nepal have reported significantly higher male rhino mortalities compared to the females (Rachlow et al., 1998; DNPWC, 2009; Subedi et al., 2017). As male rhinos were frequently targeted by poachers (Vigne and Martin, 1994; Martin et al., 2009) and poaching has been now reduced, the lack of a gender difference in our study might reflect the lower poaching risk. Future research on demographic data would be a valuable next step to understand whether overall risk of mortality differs between gender and age, and not just the causes of mortality.

Other mortality causes, electrocution and poisoning, which were primarily associated with human and rhino conflicts, were observed but there was no change in the pattern over the study period. When rhinos leave the protected areas to seek food in agriculture areas (Lahkar et al., 2011; Choudhury et al., 2016, Khadka, 2017), they may be killed through electrocution or poisoning traps (Sapkota et al., 2014; Subedi et al., 2017). The quality and quantity of food available inside the protected areas have also been an issue for sustaining existing rhino population, especially in Chitwan National Park, which harbors a majority of the rhino population. The recent concern with the invasion of plant species such as Mikania (*Mikania micrantha*) has significantly altered the native plant composition and has reduced the food availability (grasses) for the rhino population (Lahkar et al., 2011; Murphy et al., 2013; Khadka,

2017). With the continue increase in rhino population in current habitats, it will likely create more conflicts with the farmers, which may lead to increase rhino mortalities due to retaliatory killings through electrocution and poisoning. Our results also showed rhino mortality cases due to flooding. Due to heavy rain during monsoon period in the Terai region, some rhinos were found dead by drowning (Subedi et al., 2017; DNPWC, 2009), especially during June to September when rhino habitats become flooded. Similarly, some rhino mortalities were caused by diseases, wounds, and injuries, but these were a very small number suggesting these are not a major risk factor.

Although rhino mortality did not vary significantly with season, more rhino deaths were reported in September and from November to February, than in other months. The high mortality cases in December, January and February may be attributable to limited visibility due to the dense fog, shorter days, and lack of food availability inside protected areas, leading rhinos to wander in the agricultural lands or the buffer zone forest (DNPWC, 2009; Mihlbachler et al., 2018). Such events can increase human-caused mortalities to prevent crop raiding from the rhinos. On the other hand, the majority of rhino calf mortalities were observed during March and April which may be due to male rhinos often killing or separating the calf from mother during the mating time (Brett, 1998; Rachlow et al., 1998). Therefore, many calf mortalities due to orphanages i.e., natural death, were observed in our study. Similarly, tigers can attack or kill the rhino calves due to various other reasons such as limited visibility, scarcity of prey species for tiger (such as chital (Axis axis), wild boar (Sus scrofa), sambar deer (Rusa unicolor), etc.) with higher tiger density (DNPWC, 2017; Bhandari et al., 2019) during March and April months. In contrast, the lower rhino mortality in June, July, and August may be due to longer days for foraging, sufficient grass species, rain, and enough water sources (DNPWC, 2005). Furthermore, it is difficult to detect rhino mortalities during this period as it is the monsoon time when some habitats are flooded and tall grasslands reach above 4–7 m in height (Dinerstein and Price, 1991; Lehmkuhl, 1994; Peet et al., 1999; Murphy et al., 2013). In many instances, rhino mortalities in such situations cannot be detected until the rainy season ends i.e., September to November. Mortality causes of these rhino deaths cannot be confirmed when the carcasses are in decomposed state and were categorized as unknown. At the same time, such delayed reporting may affect monthly mortality number, i.e., underestimated the mortality number for June-August months while overestimated mortality cases for September-November.

5. Conclusion and implication for conservation

Although the rhino population is slightly increasing in Nepal (DNPWC, 2017; Subedi et al., 2017; Pant et al., 2020), their mortality continues at a high number. The significant decrease in poaching mortality has therefore revealed other challenges for rhino conservation within the limited habitat area. Our findings of new challenges for rhino conservation in Nepal, primarily rhino mortality due to tiger attacks, self-fighting and conflict with people are related to space and food availability. We acknowledge that continuing the zero-poaching policy in coming years will contribute to sustainable rhino conservation in Nepal. However, to minimize tiger attacks in Chitwan National Park with limited space and food for rhino, the habitat size requires expansion and other suitable areas such as Banke, Bardia and Shuklaphanta National Park in the west, and Koshi Tappu Wildlife Reserve and Parsa National Park in the east may be an option for relocating rhino population. As rhino populations in protected areas other than in Chitwan National Park are low, rhino translocation from the densely populated areas to Parsa National Park, Bardia National Park, and Suklaphanta National Park could be an effective way to reduce mortality and sustainably conserve rhinos in Nepal. On the other hand, low tiger density areas might be suitable for the rhino population growth. However, further study on habitat suitability by considering biotic interaction such as interactions with tiger populations (Jhala et al., 2021; Pant et al., 2021) could be important for rhino conservation in Nepal.

Rhino mortality due to poisoning and electrocution can be minimized by improving policy/management endeavors, and conducting public awareness programs at the root level. Similarly, rhino habitats outside the protected areas system could play an important role in long-term rhino conservation. Therefore, natural forests outside the protected areas are required to be managed as buffer zones for wildlife habitat, thereby reducing anthropogenic pressures such as intense farming, livestock grazing, logging and other forms of encroachment. These buffer zones could reduce rhino mortality and serve as a major potential habitat for the rhino in the future. Since rhinos share habitats with large mammals, a multispecies conservation policy would contribute to minimizing rhino mortality. In addition, conservation awareness programs and stricter implementation of wildlife conservation laws would also help to reduce human-caused rhino mortality in the future in Nepal.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability Statement

The data of this study are available from the corresponding author upon request.

Acknowledgements

We are thankful to the staff of the Department of National Park and Wildlife Conservation (DNPWC) and Chitwan National Park for helping in data collection and verification. We thank to Mr. Ana Nath Baral (Former Chief Conservation Officer of Chitwan National Park, Nepal) for technical help. We are thankful to editor and two anonymous reviewers for the valuable comments on the manuscript.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2022.e02189.

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