Original Research Article

Demography and viability of the largest population of greater one-horned rhinoceros in Nepal

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ABSTRACT

Megaherbivores are characterized by slow life history traits which when coupled with human exploitation makes them vulnerable to local extinctions. An understanding of key demographic parameters assists in guiding management interventions to ensure their recovery and persistence over the longer term. We monitored 110 (30 calves, 80 young and adults) individually known greater one-horned rhinoceros (*Rhinoceros unicornis*) for seven years in Chitwan National Park, Nepal (2009–15). Using known fate model with staggered entry design in program MARK we estimated annual calf survival at 0.765 ± 0.026 SE and that of remaining older age groups between 0.96 and 0.985. Both genders exhibited a typical Type I survivorship curve. The population consisted of 62% adults, 13% sub-adults and 26% juveniles and calves (dependent animals). The adult sex ratio (female: male) was 1.23 ± 0.09 SE and dependent: cow ratio was 0.636 ± 0.03 SE. Age at first calving was 7.91 years ± 0.31 SE. Shorter inter-calving intervals were observed for young adults compared to old adults. Overall inter-calving interval was 41.28 months ± 2.33 SE. Chitwan rhino population grew at a maximum realized rate of $r = 0.051 \pm 0.005$ SE. PHVA results showed that low level continuous poaching increased extinction probability compared to high but intermittent poaching episodes. An increase in annual poaching of over six females and 12 males over the current average of 5.5 rhinos per year, coupled with habitat degradation, caused by the alien invasive *Mikania micrantha* resulted in high extinction risks. Annually upto 13 rhinos (8 males and 5 females) from Chitwan can be used for reintroduction and supplementation of rhinoceros across their current and historic range.
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1. Introduction

The slow life history traits of megaherbivores makes them vulnerable to threats of habitat loss and poaching fuelled by illegal trade of their body parts across the world (Owen-Smith, 1992; Sukumar 1989; Moss, 2001). The greater one-horned rhinoceros (*Rhinoceros unicornis*, henceforth rhino) typifies the conservation problems faced by most megaherbivores. The global population of the rhino is estimated at 3300 with two major strongholds of the species (Talukdar, 2013). The largest

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population of ca. 2330 free ranging rhinos is in Kaziranga National Park Assam, India (Talukdar, 2013) and the second largest population of ca. 605 rhinos is in Chitwan National Park Nepal (DNPWC, 2015). The rhino is a habitat specialist inhabiting a mosaic of tall and short grasslands dominated by *Saccharum* spp. and riverine forests (Dinerstein and Price, 1991). These habitats in the Gangetic and Brahmaputra floodplains have almost entirely been lost to agriculture, now occurring only in a few isolated protected areas. Even in these remnant flood-plain habitats, the dynamic nature of floods, which ensured the successional habitats essential for rhinos, is now being obstructed because of human development and construction of flood control spurs and dykes along the river banks (Subedi et al., 2013). Though the rhino is considered vulnerable (Talukdar et al., 2008) and is protected by law, both in Nepal and India, the international illegal demand for rhino horn has made it one of the most difficult species to conserve in the wild (Leader-Williams, 2013). In addition, habitat degradation through rapid invasion of alien invasive plant *Mikania micrantha*, drying up of wetlands and oxbow lakes, and vegetation succession resulting in converting prime rhino habitats to less suitable habitats, has been observed to have negative impacts on rhino population in Chitwan (DNPWC, 2009; Murphy et al., 2013). The Sauraha subpopulation (east of Kasara) of Chitwan National Park seems to be most affected where there has been a 49% decline in the rhino population within the past 26 years (Subedi et al., 2013). *Mikania* was first recorded from Chitwan in 2000 and has been invading prime rhino habitats (floodplain grasslands and moist riverine forests) at a rate of ca. 2% per year (Subedi, 2012). These threats of poaching and habitat loss when combined with the slowlife history traits makes conservation and recovery of rhino populations a major challenge.

Rhino suffered a catastrophic decline in Nepal during 1960s, when the population was reduced to about 100 individuals and was confined to the Chitwan valley. The decline was attributed to hunting and loss of habitat that resulted during the conversion of *Terai* (lowland) grasslands and forests to agriculture following malaria eradication programs in 1950s and subsequent colonization by people (Laurie, 1979). During 1960s, 70% of the forests were cleared in Chitwan valley. After the establishment of Chitwan National Park in 1973 and strict law enforcement by the army since 1975, the rhino population gradually recovered to about 544 in 2000 (DNPWC, 2000; Dinerstein, 2003). During this period intensive protection and metapopulation management resulted in the establishment of populations in Bardia National Park of 67 (Karnali floodplain ca. 32 and Babai valley ca. 35 individuals) and in Suklaphnata Wildlife Reserve of 5 rhinos through reintroductions from Chitwan National Park. Subsequently, during the peak of the armed conflict (2000—2005), rhino conservation in Nepal was compromised and poaching became rampant, resulting in local extinction of the Babai valley population of Bardia, reduction of the Bardia Karnali population to 22 animals, the Suklaphanta population to four and the Chitwan population to 372 animals by 2005 (Thapa et al., 2013).

Subsequently, the democratic Government of Nepal invested significantly in rhino conservation and redeployed army personnel for anti-poaching (DNPWC, 2009). Recovery of rhino populations was a National concern. Therefore, there was a pertinent need for long-term monitoring of rhino population to gain an understanding of their demographic parameters for adaptive conservation management. To achieve this objective, an individual identity based (ID-based) intensive rhino monitoring system (Amin et al., 2006) is being implemented since June 2008. This monitoring system together with long-term data on rhino census (Subedi et al., 2013) and mortality records from Chitwan National Park (post-mortem reports) allowed us to estimate the demographic parameters of rhinos in Chitwan. Herein, we report the survival estimates of Chitwan rhinos obtained by intensive monitoring of 110 individually identified rhinos between 2009 and 2015. We also provide estimates on other demographic parameters such as realized population growth rates, age of first reproduction and calving interval. We compare the current demographic parameters with previous studies and subsequently, we use this information to parameterize a population habitat viability analysis in program VORTEX (Lacy, 1993). Given the high illegal demand in the international market for rhino horn, poaching is very difficult to stop and extremely resource demanding to control. Through the PHVA we assessed the probability of long-term persistence of the Chitwan rhino population under different scenarios of poaching, habitat degradation, the combined effect of both factors, and the possibility of harvesting of the population for reintroductions and supplementation elsewhere (Jnawali, 1995; Dinerstein, 2003). We use our results to guide conservation investment priorities by identifying critical threats and their thresholds. This would help in adaptive management and ensure the long-term survival of the Chitwan rhino population.

2. Materials and methods

2.1. Study area

The study was conducted between 2009 and 2015 in Chitwan National Park, declared as a world heritage site because of the assemblage of important populations of endangered species including tiger (*Panthera tigris*), greater one-horned rhinoceros, Asian wild elephant (*Elephas maximus*), gharial (*Gavialis gangeticus*) and Ganges river dolphin (*Platanista gangetica*). Chitwan National Park was established in 1973 as the first National Park in Nepal and is situated in a valley bounded by the Siwalik Hills. The Park includes a core area of 953 km^2 and an additional 729 km^2, surrounding the core area, set up as a buffer zone. The climate is subtropical monsoonal with three distinct seasons: monsoon (July—October), cool-dry (November—February) and hot-dry (March—June). Mean annual temperature range between 1980 and 2009 was 8 °C in January and 36 °C in April. Chitwan receives on average 2036 $\pm$ 64SE mm of rainfall per year, >80% of which falls in the monsoon (Subedi, 2012). The habitats can be broadly classed into Sal *Shorea robusta* forest, riverine and subtropical mixed broadleaved forests (e.g. *Trewia nudiflora*, *Bombax ceiba* and *Dalbergia sissoo*), tall grasslands (e.g. *Saccharum spontaneum*, *Narenga porphyracorma*, *Phragmites karka*), short grasslands (e.g. *Imperata cylindrica*), wetlands (including lakes) and shrub-lands (Laurie, 1982;

Dinerstein and Price, 1991; DNPWC, 2009). The riverine and subtropical mixed broad-leaved forests and grassland habitats tend to form a mosaic in the moist areas of the Park. Grasslands and riverine forests which are the prime habitats for rhino, account for only 25% of the Park.

2.2. Field method for identification and monitoring of rhinos

We implemented a standardized program of rhino monitoring based on individual identification (Amin et al., 2006) within 200 km^2 of typical rhino habitat in the Sauraha region of Chitwan National Park. Rhinos were identified from well recognized features such as horn shapes, body folds and marks (Laurie, 1982; Dinerstein and Price, 1991; Conway and Goodman, 1989; Kiwia, 1989; Walpole et al., 2001). Wildlife technicians and game-scouts were trained in ID-based rhino monitoring using the IUCN Asian Rhino Specialist Group accredited course (IUCN AsRSG, 2009). The trained rhino monitoring teams were equipped with digital cameras, binoculars, standardized field data sheets and trained riding elephants for surveying rhino habitats. A rhino identification photo catalogue was developed for the study area and copies provided to each rhino monitoring team for field identification. Each rhino encountered was photographed from different angles and its body characteristics noted on standardized figures. Where field identification was not possible, the recorded pictures and figures were compared with the computerized rhino database for accurate identification at the Park headquarters. At times field sighting of rhinos did not result in individual identification due to the context of the sighting such as dense vegetation, in a wallow, etc. Only sightings where identity could be confirmed were used for analysis. A total of 110 rhinos were monitored with a maximum sighting interval of two months to provide information on stage specific survival and reproduction.

2.3. Group composition and adult sex ratio

We used 553 rhino sightings obtained by systematic survey and opportunistic encounters across Chitwan National Park to deduce group composition and adult sex ratio. Majority of the dataset for this analysis was collected when researchers and park management personnel accompanied rhino patrols across Chitwan National Park. Each administrative block of Chitwan National Park with rhino habitat was sampled once annually by the research team. Within the intensive study area rhinos were individually identified and duplicate data on each rhino or groups was discarded from the analysis. Since surveys were done from elephant back even single rhinos from all age groups were easily detected. We do not believe that our sample was biased towards larger groups or sex or to specific rhinos. However, there was still some chance of sampling some groups and single rhinos more than once from across Chitwan National Park since rhinos could move between blocks or be encountered more than once on a survey or between years. We therefore used the sample survey with replacement model to compute the adult sex ratio and young: cow ratio (Skalski et al., 2005: section 3.2.2) and believe that the averages we report were accurate for the study period. We classified "young" rhinos as rhinos that were still dependent on their mothers and typically less than four year old (calf and juvenile category combined). We computed the average (averaged over observed groups) and typical group size (group size averaged over individuals) (Jarman, 1974) of rhinos.

2.4. Survival and annual mortality rate

Most individually known rhinos were located two or more times in a month. We could therefore determine the birth week of most calves with more intensive observations on pregnant females nearing parturition. We monitored radio-collared females on a daily basis and could observe birth and growth of their calves in more detail. Based on these observations and the experience of some of our field technicians who had been working with rhinos for over three decades, age of calves whose birth week was not known with certainty was determined using criteria of size relative to its mother, skin folds and texture, pigmentation, body hair, coordinated movements, suckling and foraging behaviour (Fig. S1). We checked the accuracy of our aging criteria on known aged calves and found that our team could accurately estimate birth date of calves less than two months old to a week. By the end of the study period, age of over 75% of the individually known rhinos was known since birth.

Due to intensive monitoring of the study area by the park staff, army personnel, and rhino monitoring teams we were reasonably certain that all mortalities of rhinos were detected within a couple of days. Post-mortem examinations were undertaken on all rhino carcasses by a veterinary officer. Adult and sub-adult rhino mortalities were categorized into natural, human caused and unknown causes. Calf mortality causes were categorized as tiger predation, infanticide, human caused and unknown. Mortality data from the study period was combined with mortality recorded since 1998 across Chitwan National Park for analyzing causes of death.

We used six stage categories (Dinerstein and Price, 1991; Kandel and Jhala, 2008) that were biologically meaningful in terms of rhino demography (Law and Linklater, 2014): calf (<1 year), juvenile (1–4 years), sub-adult (4–6 years), young adult (6–12 years), prime adult (12–20 years) and old adult (>20 years) since field aging all rhinos to exact years was unrealistic. We estimated stage-specific annual and span survival probability of rhino through known-fate models (Skalski et al., 2005) in program MARK (White and Burnham, 1999; Cooch and White, 2009) using the staggered entry design (Pollock et al., 1989; see Table S1 and Table S2). This technique can be used where the fate of an individually identified rhino is known with certainty and independently. We grouped encounter histories of rhinos into time intervals of six months and created a live-dead matrix where '10' meant the individual lived through the interval, '11' meant the individual died during the interval and '00' meant

censoring the individual for that specific interval (when unaware about the fate due to non-sighting; Cooch and White, 2009). Rhinos monitored before adulthood, and that lived sufficiently long to enter the next stage, were included in all appropriate stages with the assumption that survival rates in different stage class of an animal were independent. We assumed total life span of rhino as 35–40 years in the wild for span survival analysis based on the long-term records made in Chitwan National Park (Subedi, 2012). We estimated rhino survival by monitoring 80 adult and sub-adult rhinos (nine radio-collared and 71 non-collared but individually known), and calf survival by monitoring 30 rhinos (Tables S1 and S2). We tested for effect of stage groups and gender on survival rates in program MARK. During the course of our study factors likely affecting mortality were similar across years; no extraordinary events of flood, drought, or poaching occurred. We therefore, do not test the effect of individual time intervals on rhino survival and assume a constant survival rate within each gender for each stage across years. Also our sample size was relatively small for a meaningful analysis of complex models that included time and its interactions with sex and stage. We lumped the five stage groups (excluding calves) further when survival was similar between stages and gender for a more parsimonious and robust estimate of survival and compared models using AICc in MARK. Calve survival was estimated with time interval of months in a separate analysis. Models that included effect of sex and months on calf survival were compared using AICc. We report AICc weighted model averaged estimates of survival for all stages (Burnham et al., 2011) for biologically meaningful models whose likelihood estimates converged so as to provide robust estimates of survival. Annual, stage span and cumulative survival were reported.

2.5. Reproduction

We closely monitored seven known age sub-adult female rhinos within the intensive study area for a period of seven years (2009–2015) to determine age at first calving. Similarly, we monitored 21 known adult females over the same period to estimate inter-birth interval. We investigated seasonality of births from monitoring records from across Chitwan National Park wherein each young calf was aged and its birth date estimated to the closest two weeks. Births were subsequently pooled for three seasons, hot-dry (March–June), Monsoon (July–October) and cold-dry (November–February) seasons. After testing for normality of birth frequency data, seasonality in births was tested using Kruskal Wallis one way ANOVA (Zar, 2010).

2.6. Realized rate of growth

We used published data from the national rhino counts to compute the realized rate of growth (r) between 1966 and 2000 (increasing phase), 2001 and 2005 (decreasing phase), 2005 and 2015 (increasing phase). For the current increasing phase (2005–2015) we plotted four population estimates against years and fitted an exponential growth model to our data (Skalski et al., 2005). Natural log transformed population estimates were regressed against years to compute r (Caughley, 1977; Skalski et al., 2005) assuming exponential growth. Since rhino counts in Nepal are undertaken with a large effort covering all rhino habitats using the same methodology and were found to be comparable with statistically robust (mark-recapture) estimates (Subedi et al., 2013) we believe that use of total count data to compute trends and growth rates was justified. We computed finite rate of population change (lambda) by extrapolating population size between census years considering lambda to have remained constant between subsequent census years. Lambda was computed as population ratio between subsequent years (Caughley, 1977). We accounted for rhinos removed for translocation and those poached between 2005 and 2015 and recomputed r to evaluate the effect of these factors on population growth. We corrected for survival rates prior to adding poached and translocated individuals to the population estimates.

2.7. Population habitat viability analysis (PHVA)

We parameterized a PHVA based on rhino life history parameters obtained from the current study and published literature (Laurie, 1979; Dinerstein and Price, 1991; Dinerstein, 2003; see Table S3) in VORTEX 9.99 (Lacy et al., 2005). Poaching of rhinos for their horns due to a high demand in the illegal international market is the major limiting factor for free ranging rhino populations globally (Leader-Williams, 2013; Ferreira et al., 2015). Reliable rhino mortality records were available with the Department of National Parks and Wildlife Conservation (DNPWC) and the National Trust for Nature Conservation (NTNC) due to their intensive patrols and monitoring activity since 1998. In these 17 years (1998–2015) average annual loss of rhinos to poaching in Chitwan National Park was 10.05 ± 0.73 SE individuals. This average includes years of armed conflict (2000–2005) in Nepal when rhino poaching was highest. In the year 2002, a minimum of 36 rhinos were poached in Chitwan. The current illegal global demand for rhino horn could lead to Nepal rhinos facing similar levels of poaching as observed currently in South Africa (Ferreira et al., 2015; Leader-Williams, 2013). The current estimates of rhino survivorship include mortality caused by a low level of poaching that occurred during the study period (2009–2015). Thirty three rhinos were recorded poached during this period, giving an average rate of 5.5 rhinos per year. We built scenarios in VORTEX wherein poaching caused mortality was additive to current mortality estimates and occasionally included the extreme observed poaching rates of over 30 rhinos per year as scenarios.

A second factor that was likely to impact persistence of rhino population in Chitwan National Park was habitat degradation caused by the alien invasive plant *Mikania micrantha* (hereafter Mikania). Mikania was first reported from Chitwan National Park in 2000 and in a decade it has significantly (>40% cover) invaded 7% of the prime rhino habitat and another 70% is under various level of infestation (Subedi, 2012). The rate of conversion of rhino habitat to unsuitable habitat due to severe Mikania

infestation was estimated at 2% per year based on surveys conducted in 2008 and 2011 (Subedi, 2012; Murphy et al., 2013). Mikania invades open moist area that are occasionally disturbed (fire, flood, grass cutting, *etc.*). Such habitats that can support high cover of Mikania constitute ca. 50% of the current rhino habitat (Subedi, 2012; Murphy et al., 2013). The abundance and spread of Mikania are likely to decrease with time (Strayer et al., 2006; Holmes et al., 2009). Therefore, we built scenarios in VORTEX wherein 25–50% of the carrying capacity for rhinos decreased within 25 years. We used a value of 800 rhinos as the carrying capacity (K) of Chitwan National Park based on earlier estimates (Laurie, 1979; Dinerstein and Price, 1991; Dinerstein, 2003) and also varied K between the population estimate of 500 (Subedi et al., 2013) and a maximum of 800 rhinos to incorporate uncertainty in estimates of K.

Natural catastrophes affecting Chitwan rhinos have been rare. Past forty year records revealed no disease epidemics affecting the rhino population (Subedi, 2012). The worst flood affecting Chitwan in the recent history was reported in 1993 (Dhakal et al., 2011). Although actual loss of rhinos by this flood has not been documented, experienced senior wildlife technicians working in Chitwan suggest that such floods may likely result in mortality of about 5% of the rhino population (Subedi, 2012). We used this information to build a catastrophic event in VORTEX models that reduced survival of all age classes by 5% once in 25 years.

Using various combinations of levels of poaching, loss of carrying capacity, and catastrophes we simulated scenarios (Table 1) that mimicked realistic, extreme and moderate conditions that Chitwan rhinos were likely to face. The scenarios were setup to allow us to rate the relative significance of various limiting factors to the long-term persistence of rhinos in Chitwan National Park. Each scenario was run 1000 times for 100 years. Additionally, we altered the parameters in the model by 10% to evaluate the sensitivity of model outcomes to these parameters. Under the PHVA models, population persistence (probability of extinction), median and mean time to extinction, and stochastic rate of increase (r) were evaluated.

3. Results

3.1. Group size, adult sex ratio and inter-calving interval

Average group size computed from rhino sightings (n = 553) was 1.63 ± 0.03 SE, while typical group size was 1.98 ± 0.083 SE. Calves and juveniles constituted 26% of the population, sub-adults 13% and 62% were adults. The adult sex ratio (female: male) was 1.22 ± 0.084 SE. The young: cow ratio was 0.636 ± 0.03SE. Age at first calving (n = 7) ranged from 7 to 9 years with an average of 7.91 ± 0.31 SE years. Inter-calving interval ranged from 22 to 58 months (n = 21 intervals from 14 females) with an average interval of 41.28 ± 2.33 SE months. Shorter inter-calving intervals (24 ± 0.71 SE months) were observed for females (n = 5) that had lost their calf. Inter-calving interval was 45.35 ± 1.72 SE months for females that had not lost their calves (n = 16). Among females who did not loose their calves, the average inter-calving interval for young and prime adult females (n = 11) was 41 ± 0.95 SE months, while it was 52.66 ± 1.42 SE months for old adults (n = 5).

Table 1

Population Habitat Viability model results for greater one horned rhinoceros in Chitwan National Park, Nepal under various combinations of limiting factors. An average of 5.5 rhinos poached per year during the study period is incorporated in the parameterization of the PVA as mortality rates. The modeled loss by poaching is additional to the average annual loss. Mikania invasion was estimated at 2% per annum and would likely result in a maximum loss of 50% rhino habitat in 25 years.

Scenario	Scenario Details			Stoc-r	SD (r)	PE	N-extant	SD (Next)	Median TE	Mean TE
	Rhino Poaching	Carrying capacity (K) decline in 25 years	Flood caused losses							
Scenario 1	None	K = 800, no decline	Operating	0.025	0.022	0	795	12	0	0
Scenario 2	None	K = 800, 50% decline	Operating	0.025	0.024	0	395	9	0	0
Scenario 3	None	K = 500	Operating	0.025	0.023	0	495	9	0	0
Scenario 4	Yr1-6AF, 6AM	K = 800, no declines	Operating	0.008	0.025	0.01	760	97	–	89
Scenario 5	Yr1-6AF, 6AM	K = 800, 50% decline	Operating	−0.026	0.074	0.45	161	108	–	89
Scenario 6	Yr1-8AF, 8AM	K = 800, no decline	Operating	−0.035	0.094	0.61	417	280	88	75
Scenario 7	Yr1-18AM	K = 800, 50% decline	Operating	−0.013	0.042	0.28	789	48	–	55
Scenario 8	Yr1-10AF	K = 800, no decline	Operating	−0.032	0.04	1	0	0	48	49
Scenario 9	Yr1-8AF, 5AM	K = 800, no decline	Operating	−0.022	0.052	0.62	435	251	88	74
Scenario 10	Yr1-5AF, 5AM	K = 800, no decline	Operating	0.012	0.022	0	786	31	0	0
Scenario 11	Yr1-7AF, 7AM	K = 800, no decline	Operating	−0.004	0.049	0.135	613	233	–	82
Scenario 12	Yr1-6AF, 10AM	K = 800, no decline	Operating	−0.008	0.025	0.014	760	87	–	71
Scenario 13	Yr1-5AF, 5AM	K = 800, 50% decline	Operating	−0.004	0.039	0.05	267	105	–	92
Scenario 14	Yr1-5AF, 5AM	K = 800, 50% decline	None	0.003	0.025	0.01	335	75	–	96
Scenario 15	Yr1-5AF,10AM	K = 800, 50% decline	Operating	0.001	0.031	0.08	347	74	–	87
Scenario 16	5Yr-10AF, 20AM	K = 800, no decline	Operating	0.021	0.027	0	783	16	0	0
Scenario 17	5Yr-10AF, 20AM	K = 800, 50% decline	Operating	0.016	0.037	0	376	13	0	0
Scenario 18	2Yr-10AF, 20AM	K = 800, 50% decline	Operating	0.000	0.054	0.032	323	108	–	94
Scenario 19	5Yr-25AF, 35AM	K = 800, 50% decline	Operating	−0.001	0.079	0.014	263	92	–	96

Yr– yearly interval between poaching events, Stoc-r – stochastic growth rate, PE – probability of extinction, SD – standard deviation, Median TE– median time for extinction, Mean TE – mean time to extinction, K – carrying capacity, AF – adult female, AM – adult male), N-ext – Population size at year 100 for populations that did not go extinct. Deterministic r was 0.037 for all scenarios with environmental catastrophe and 0.04 without it.

3.2. Seasonality of births

Least number of births were recorded in March–April and October, while the months of January and August had the maximum number of births (Fig. 1.). There was no defined seasonality for births (n = 66, χ^2 = 4.58, df = 2, P = 0.1; Kruskal Wallis one-way ANOVA).

3.3. Mortality

A total of 374 rhino deaths were recorded in Chitwan National Park between 1998 and 2015, of which 49% were male, 35% female and 16% unsexed. Of the total mortalities 83% were adult, 4% sub-adult and 13% dependent young. Average annual recorded mortality was 21.83 ± 0.66 SE individuals of which poaching caused mortality was 10.05 ± 0.73 SE individuals and was the main cause of rhino mortality (Fig. 2.) in Chitwan National Park. Amongst the 47 calf deaths recorded, majority (29.8%) were due to tiger predation, disease was responsible for 10.6% of the deaths, while infanticide, natural calamities and unknown causes each contributed 19.1%, poaching of the mother and subsequent death of the calf accounted for only 2.13% of calf mortality. Natural calamities included floods, drowning in muddy swamps and death by tree fall.

3.4. Population growth rate

The rhino population and its finite rate of population growth (λ) fluctuated markedly over time in Chitwan National Park (Fig. 3.). The population increased at r = 0.05 ± 0.007 SE between 1966 and 2000 (R^2 = 0.92, P < 0.01). The population then declined with an r = - 0.076 between 2000 and 2005 due to poaching during insurgency. Subsequently, as a result of improved protection after insurgency, the population has been increasing again at r = 0.051 ± 0.005 SE (R^2 = 0.98, P < 0.01). The exponential population growth model: Population = $283.14e^{0.0506(year)}$ fit the data well for the recent increasing phase between 2005 and 2015 (R^2 = 0.98, P < 0.01). The realized population growth rate r after accounting for poached and translocated rhinos was r = 0.045 ± 0.004 SE (R^2 = 0.98, P = 0.009).

3.5. Survival

The null model with constant survival (no effect of time and gender) best explained calf survival, while model with survival differing with gender also had some support (Table S4). Annual model averaged calf survival was 0.764 (SE 0.02) (Table 2). Model that considered survival for juveniles and sub-adult stages to be similar for both sexes, while adult survival to be different between sexes was rated the best by AICc (Table S5). Model averaged survival rates were similar between sexes and but increased from calf to adult stage (Table 2). Survival rates, span survival and survivorship was similar between sexes (Table 2, Fig. 4). Both sexes conformed to a typical Type 1 survivorship curve (Fig. 4.).

3.6. Population habitat viability analysis (PHVA)

The extinction rates of the PHVA model were not sensitive to 10% changes in calf mortality, adult survival, and carrying capacity estimates. Loss of 50% rhino habitat to Mikania did not enhance extinction probability of the Chitwan population by
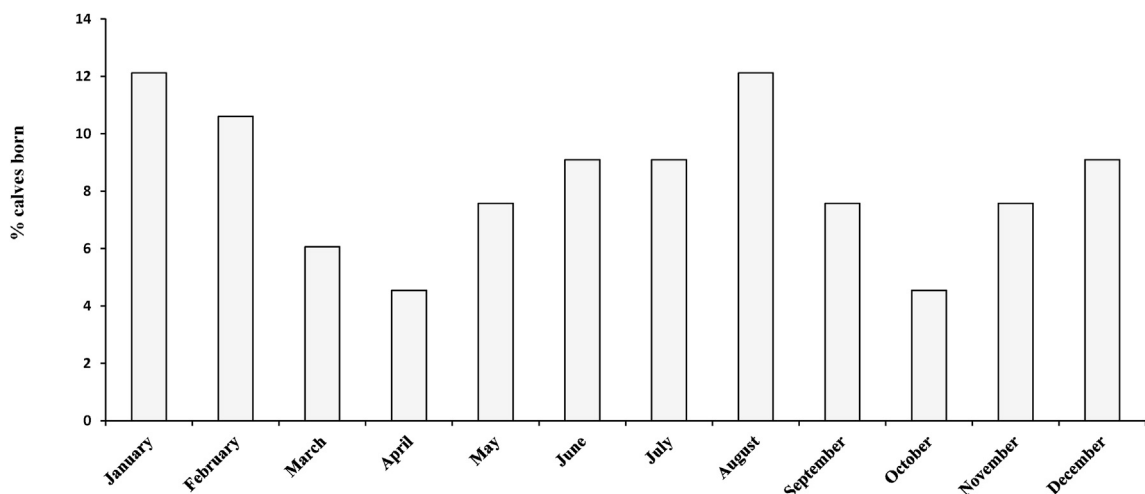

Fig. 1. Seasonality of rhino calving in Chitwan National Park recorded between 2008 and 2015 (n = 66 births).
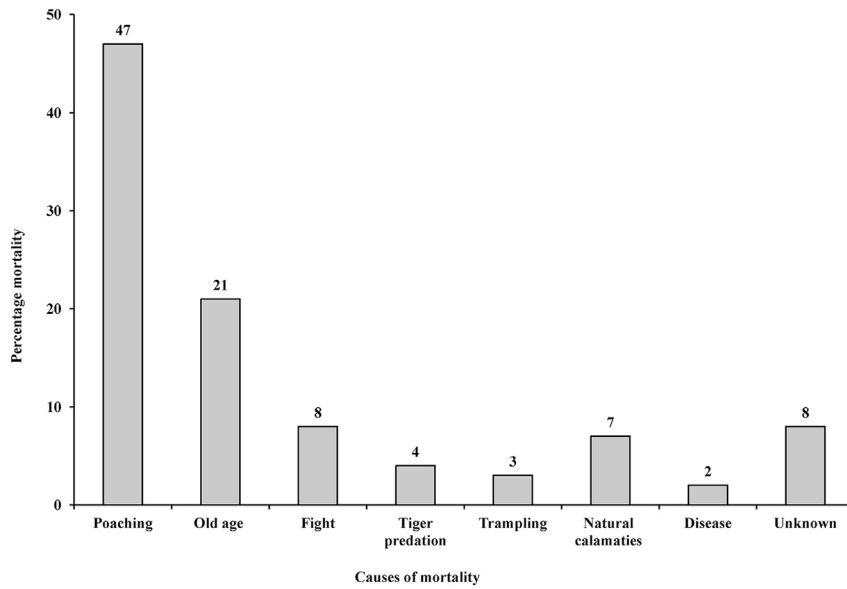
Fig. 2. Causes of greater one-horned rhinoceros mortalities in Chitwan National Park between 1988 and 2015 (n = 374).
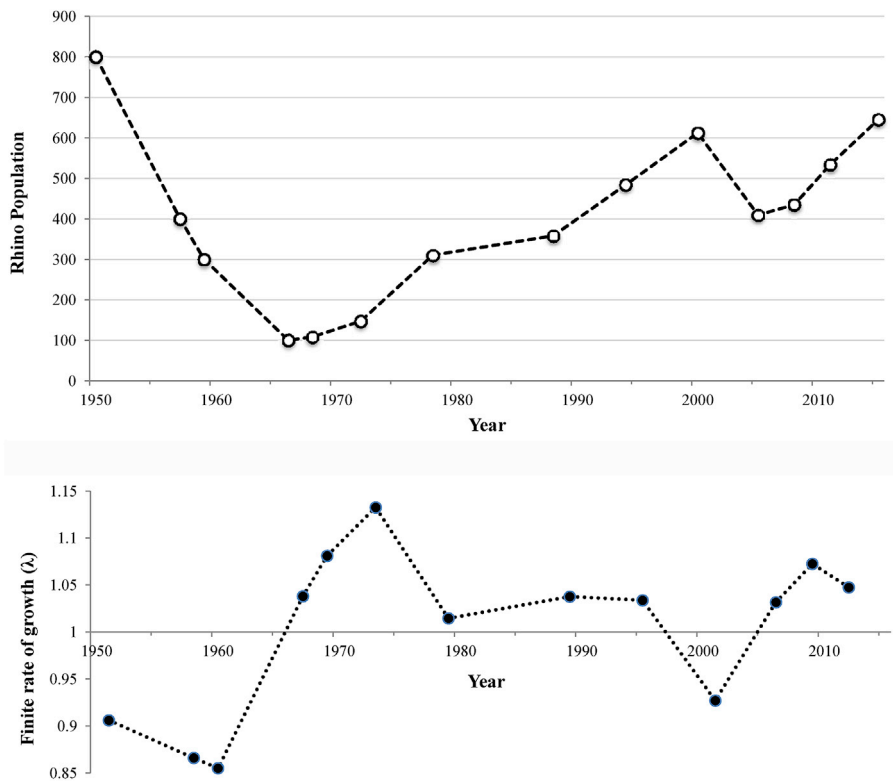

Fig. 3. Population trend of greater one-horned rhinoceros in Chitwan National Park, Nepal, between 1950 and 2015 (a) total population size by year; (b) finite rate of population growth (λ) per year.

itself. At K = 800 additional poaching losses of upto15 rhinos annually could be sustained before extinctions manifested. However, the population was more sensitive to loss of adult females and annual additional poaching of over six females increased extinction probability while removal of up to 10 additional adult males could be sustained annually. But when habitat was reduced to 50% by Mikania invasion, loss of even five additional adult females annually made the population

Table 2

Model averaged annual stage survival rates with standard errors (SE) and stage span survival for the greater one horned rhinoceros in Chitwan National Park, Nepal estimated from individually identified 110 rhinos monitored between 2009 and 2015 using known fate model in MARK.

| Age categories	Sample Size		Annual Survival Rate (SE)		Span Survival Rate (SE)	
	Female	Male	Female	Male	Female	Male
Calf (0—1 year)	14	16	0.761 (0.026)	0.771 (0.028)	0.761 (0.026)	0.771 (0.028)
Juvenile (1—4 year)	12	13	0.961 (0.012)	0.962 (0.01)	0.887 (0.02)	0.892 (0.017)
Sub-adult (4—6 year)	9	14	0.964 (0.01)	0.967 (0.01)	0.93 (0.014)	0.936 (0.014)
Young-adult (6—12 y)	13	16	0.984 (0.008)	0.985 (0.008)	0.91 (0.19)	0.916 (0.018)
Prime-adult (12—20 y)	17	17	0.985 (0.008)	0.985 (0.008)	0.889 (0.02)	0.889 (0.02)
Old-adult (>20 year)	19	12	0.985 (0.008)	0.983 (0.001)	0.745 (0.019)	0.712 (0.027)
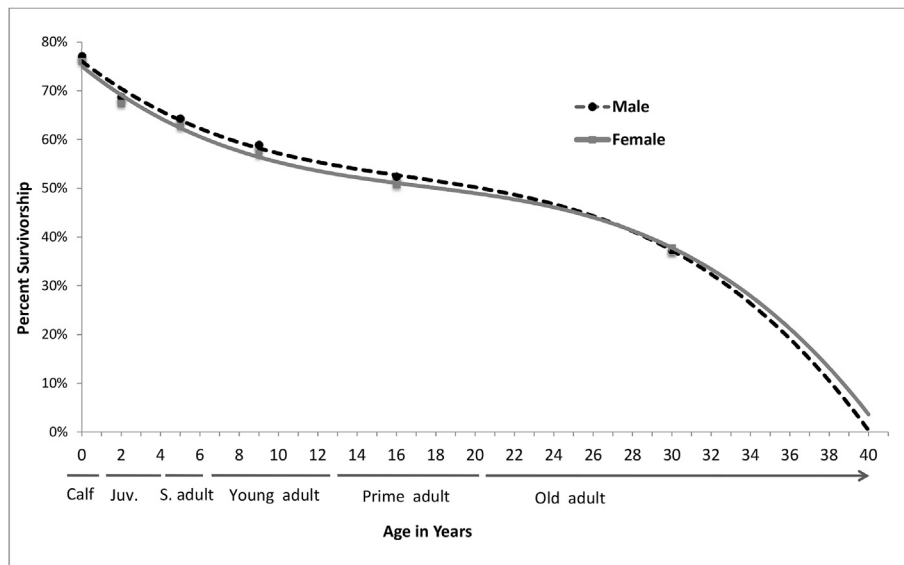
Fig. 4. Survivorship (cumulative survival) of greater one horned rhinoceros in Chitwan National Park, Nepal estimated from individually known 110 rhinos monitored between 2009 and 2015.

vulnerable to extinction events (Table 1). Periodic catastrophes like floods had no noticeable impacts by themselves. However, the synergistic effect of moderate increase in poaching, uncontrolled Mikania infestation and flood events resulted in population trajectories becoming extinct.

4. Discussion

Recovery of endangered species is best assessed and monitored from their demographic parameters (Owen-Smith, 1992; Moss, 2001; Trimble et al., 2009). Rhinos from across the world face a serious threat due to the illegal demand for their horn. The Chitwan rhino population is the second largest population of the greater one-horned rhinoceros and is often targeted by poachers, the last episode of intense poaching coinciding with the political unrest in Nepal (2000—2005). Fortunately, this recovering population has been the focus of earlier studies (Laurie, 1979, 1982; Dinerstein and Price, 1991; Dinerstein, 2003) which provided information on certain aspects of rhino demography that form a basis for comparison with the results from the current study. This study constitutes a large dataset of 110 individually known rhinos monitored over an eight year period to provide reliable insights into the population performance of Chitwan rhinos.

4.1. Sex ratio, young to cow ratio and inter-calving interval

Adult Sex ratio of Chitwan rhinos was skewed towards female as expected in most mega-herbivore populations (Owen-Smith, 1992; Moss, 2001). However, the proportion of males has marginally increased (Subedi et al., 2013) compared to previous studies (Laurie, 1982; Dinerstein and Price, 1991). Similar ratio of female: male (1.2) was reported from growing populations of black rhinoceros (*Dicerosbicornis*) (Walpole et al., 2001). Although theoretically, equal adult sex ratio is preferred for a larger effective population size (Lande and Barrowclough, 1987), populations with female biased adult sex ratio are often observed in polygynous systems and in areas with adequate food supply wereobserved to have higher growth rates in rhinos (Owen-Smith, 1992).

The dependent young to cow ratio of Chitwan rhinos (0.64) indicated that 36% of adult females were without calves at any given time. For a growing population of southern white rhinoceros, Owen-Smith (1992) reports a proportion of young to adult females of 85.5%. The proportion of unaccompaniedadult females would include those that have lost their calves, were in the final stages of pregnancy as well as very old senescent females. Yearling mortality recorded was 24% and juvenile mortality was 4.5%, this suggests that about 7.6% of adult females lost their calves while 28.4% of adult females did not have accompanying young for other reasons. These would include young unbred adults, senescent females and females in-between calves. Dinerstein (2003) reports percentage of adult females with dependent young as 59.8%, these proportions seem low for a megaherbivore and would result in reduced growth rate of the Chitwan population (Owen-Smith, 1992).

Owen-Smith (1992) suggests that amongst mega-herbivores it is the age of first birth followed by inter-birth intervals that respond to density dependent factors such as nutritional habitat quality compared to calf survival (Rachlow and Berger, 1998). Age at first birth (7.9 years) amongst Chitwan rhinos was slightly higher than previously reported by Laurie (1982; 7.2 years) and Dinerstein (2003; 7.5 years). Age at first birth in black and white rhinois between 5 and 9 years (Law et al., 2013; Walpole et al., 2001; Owen-Smith, 1992). In a low density white rhino population, mean age of first birth was 7.4 ± 0.4 years while in a high density population it was reported to be 10.1 ± 0.7 (Rachlow and Berger, 1998). The slight increase in age of first birth in Chitwan rhinos is suggestive of habitat quality decline (Reid et al., 2007) in the study area possibly induced by invasive Mikania or overstocking. However, the inter-calving interval recorded in this study (41.28 months) was slightly lower than that observed by Dinerstein (2003; 48 months) but similar to that reported by Laurie (1982; 42 months). Old adults were recorded to have about 12 months longer inter-birth interval compared to young and prime adults; this suggests reduced fecundity and/or poor nutritional condition associated with older rhinos (Robbins, 1993).

4.2. Seasonality of births

It would be beneficial to give birth in the most opportune season so as to ensure calf survival (Rutberg, 1987). High nutritional peaks coinciding with rains are known to induce estrous and mating in white rhinos (Owen-Smith, 1992). However, in the highly productive alluvial floodplain habitat, effects of seasonality are marginal on the nutritional ecology of rhinos (Subedi, 2012). The highest dry matter digestibility was recorded during early monsoon and early hot-dry season (Subedi, 2012) which coincides with fresh grass growth following rains and late winter burns. We observed a short birth peak in August similar to that reported by Laurie (1982). However, births occurred throughout the year. Due to the long gestation and lactation periods of rhinos timing births to coincide with these short nutrition peaks would have little adaptive advantage. Instead, it seems more likely that the nutritional status of individual female rhinos determines her estrous and conception (Robbins, 1993).

4.3. Mortality and population growth

Megaherbivores exhibit typical K-selected and slow life history traits (Owen-Smith, 1992). Calf mortality amongst mammals with high parental care is usually low. Rhino mothers are extremely protective of their calves and the only threat to their survival is from tiger predation, infanticidal males, catastrophic events like floods, and death of mother (Laurie, 1982; Dinerstein and Price, 1991). The estimates from this study are not directly comparable to Dinerstein (2003) since that study did not distinguish between yearling and juvenile age groups. However, after combining the survival estimates of yearling and juvenile rhinos, the estimates of this study are almost identical to those reported by Laurie (1982; 73% compared to 75% this study). It is interesting to note that rhino calves were most vulnerable during their first year of life (23% mortality), after which survival of even juvenile rhinos was high (94–98%). The variability associated with our estimate of survival across all age groups was small. Our mortality estimates included poaching which is additive to the natural mortality causes and primarily targets adults. Despite inclusion of poaching caused mortality Chitwan rhinos exhibited a Type I survivorship curve which suggests that current rate of poaching mortality of 5.5 rhinos per year was not a major cause of concern since it did not cause a linear decline in the survivorship curve (Type II curve). Over a longer term an average of 10 rhino deaths were attributed to human caused mortality, this is about 1.8% of the current rhino population (Subedi et al., 2013) and 47% of all recorded mortality. From 28 mortality events Dinerstein and Price (1991) estimated mortality due to poaching as 15%. Laurie (1982) recorded 27 rhino mortalities between 1972 and 1975 of which 30% were due to poaching. Currently poaching is responsible for nearly half of the total observed rhino mortality in Chitwan while other causes like intraspecific fight among males and floods had less impact.

With our limited data on population estimates during the current growth phase of the population we could not explicitly test between the exponential and logistic growth models. Nor could we check if age of first calving and inter-birth intervals were density dependent due to the small sample size collected during a limited range of rhino density. However, long-term population estimates and demographic data should be able to resolve the role of density dependence in Chitwan rhinos. Density dependent factors (Rachlow and Berger, 1998; Okita-Ouma et al., 2010) and poaching (Leader-Williams, 1988; Emslie and Brooks, 1999; Brodie et al., 2011) have been reported as limiting factors for black and white rhinos in Africa's Protected Areas. Lambda (λ) varied between a minimum of 0.77 and a maximum of 1.096 depending on the intensity of poaching and protection regime in the interim inter-census periods. In recent years (after 2008) despite low intensity poaching, Chitwan rhinos continue to exhibit recovery with λ varying between 1.03 to 1.067. During both population growth phases (1966—2000; 2006—2015) the realized rate of increase r remained constant at ca. 0.05. Growth rates (r) among recovering

black and white rhinos were reported to range between 0.05 to as high as 0.11 over short durations (Owen-Smith, 1992; Rachlow and Berger, 1998; Walpole et al., 2001; Okita-Ouma et al., 2010; Ferreira et al., 2011). The conservation management strategy for black rhinos recommends maintaining a minimal national population growth rate of 5% (Okita-Ouma et al., 2010). After accounting for translocated and poached rhinos the estimated growth rate was slightly lower. This suggests removals from Chitwan population (for reintroductions) are likely to increase the productivity of the Chitwan population. Eberhardt (2002) proposes that density dependence for long-lived species like rhinos operates first to reduce calf survival, followed by increase in age of first calving, subsequently with increased inter-calving intervals, and finally by increased adult mortality. Comparing observations from Laurie (1982) and Dinerstein (2003) with those recorded by this study suggests that these demographic parameters were comparable for Sauraha population and besides a decline in the growth rate (Fig. 3) despite drop in poaching rates, detectable influence of density dependent regulation on demographic parameters as proposed by Eberhardt (2002) was not supported by our data as the exponential growth fit the population estimates quite well. It is likely that with longer duration studies on this population, effect of density dependent regulation on demographic parameters could be documented, provided poaching related adult mortality is controlled.

4.4. Population habitat viability analysis (PHVA)

The results of the PHVA models largely depend on the reliability of demographic, habitat (carrying capacity) and threat parameters and the assumptions on which the models are based. The rhinos of Chitwan National Park have been well studied and reliable demographic parameters were available from the current and previous studies (Laurie, 1982; Dinerstein and Price, 1991; Dinerstein, 2003; Subedi et al., 2013). Demographic parameter estimates of the current study matched those reported by earlier researchers (Laurie, 1982; Dinerstein, 2003). Therefore, the parameterization and results of VORTEX simulations were likely robust. The assumptions made on carrying capacity decline, poaching trend and catastrophe were based on the real field data.

Our study showed that an increase in poaching over the current average of 5.5 per year by another six adult female rhinos per year can result in negative growth and extinction events especially when coupled with reduction in habitat quality and natural catastrophe. Without effective management control of Mikania, there is a significant risk to the long-term viability of the population in combination with moderate increase in poaching loss. Loss of female rhinos to poaching (or translocation) had a more severe impact compared to removal of males (Table 1). Poachers usually target male rhinos due to their larger horn size and this can act as a buffer against killing of demographically prised females. Sporadic highs of poaching take a large toll on a megaherbivore population which may take several years to recover, but moderate level of sustained poaching was more damaging and increased the probability of extinction substantially.

With effective protection and habitat management, the Chitwan rhino population could sustain removal of individuals on a set percentage. Eight male and five adult female rhinos from Chitwan could safely be used annually for reintroductions and supplementation of existing populations in Bardia, Shuklaphanta and elsewhere within the historical range of the *Rhinoceros unicornis*. Removal of rhinos for translocation should preferably be done from high density habitats like that of Sukibhar, Reu-Khoraimuhan, and Khoria-Temple tiger blocks (Subedi et al., 2013). A founder population of at least 20 rhinos in vacant suitable habitat and with sufficient carrying capacity for viable populations is recommended to achieve and maintain growth rates of at least 5%.

The impact of catastrophic events in our models was small (reduction of survival by 5%), however catastrophic events and their impacts on these ecosystems are likely to increase with climate change (Jentsch and Beierkuhnlein, 2008) in the form of localized cloud bursts and flash floods in the Terai and Himalayan region (Dimri et al., 2017; Gupta et al., 2013). If for some reason there is increase in the mortality of rhinos beyond the average figure of 5.5 per year due to poaching or other causes, then the number of rhinos removed for translocation should be adjusted accordingly.

The slow demographic parameters of the Chitwan rhino population were characteristic of those often observed in K selected mega-herbivore having low mortality, low growth rate and a typical Type I survivorship curve. The consistency of our parameter estimates with those estimated earlier along with low variability of these parameter estimates suggests that deterministic factors play a more important role in rhino life history strategies compared to stochastic factors.

A metapopulation management strategy focussing on optimising growth will also provide insurance against poaching outbreaks as those currently being experienced in African rhino range states. Along with poaching, habitat degradation driven primarily by the spread of invasive plant species is a serious issue. The park management needs to guard against poaching and invest in effective habitat management for controlling the invasive *Mikania*. With a high illegal demand for their horns, introduction of invasive aliens in their habitat and modification of natural forces like floods that are essential to create and maintain optimal habitat conditions, the greater one horned rhinoceros requires substantial conservation intervention for ensuring its long-term survival.

Author contributions

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Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.gecco.2017.11.008.

References

Amin, R., Okita-Ouma, B., Adcock, K., Emslie, R., Mulama, M., Pearce-Kelly, P., 2006. An integrated management strategy for the conservation of eastern black rhinoceros *diceros bicornis* michaeli in Kenya. Int. Zool. Year book. 40, 118—129.

Brodie, J., Muntifering, J., Hearn, M., Loutit, B., Loutit, K., Brell, B., Uri-Khob, S., Leader-Williams, N., Du Preez, P., 2011. Population recovery of black rhinoceros in north-west Namibia following poaching. Anim. Consev. 14, 354—262.

Burnham, K.P., Anderson, D.R., Huyvaert, K.P., 2011. AIC model selection and multi-model inference in behavioral ecology: some background, observations, and comparisons. Behav. Ecol. Sociobiol. 65, 23—35.

Caughley, G., 1977. Analysis of Vertebrate Populations. Blackburn press, New Jersey, USA.

Conway, A., Goodman, P., 1989. Population characteristics and management of black rhinoceros *Diceros bicornis minor* and white rhinoceros *Ceratotherium simum simum* in Ndumu game reserve, South Africa. Biol. Conserv. 47, 109—122.

Cooch, W., White, G., 2009. Program MARK: a Gentle Introduction, ninth ed. http://www.phidot.org/software/mark/docs/book/pdf/mark_book.zip. (Accessed 15 December 2016).

Dhakal, N.P., Nelson, K.C., Smith, J.D., 2011. Resident well-being in conservation resettlement: the case of padampur in the royal chitwan national park, Nepal. Soc. Nat. Resour. 24, 597—615.

Dimri, A.P., Chevuturi, A., Niyogi, D., Thayyen, R.J., Ray, K., Tripathi, S.N., Pandey, A.K., Mohanty, U.C., 2017. Cloudbursts in indian himalayas: a review. Earth-Science Rev. 168, 1—23.

Dinerstein, E., Price, L., 1991. Demography and habitat use by greater one-horned rhinoceros in Nepal. J. Wildl. Manage. 55, 401—411.

Dinerstein, E., 2003. The Return of the Unicorns: the Natural History and Conservation of the Greater One-horned Rhinoceros. Columbia Press, New York, 316 pp.

DNPWC [Department of National Parks and Wildlife Conservation], 2000. Rhino Count 2000 Initial Report. Department of National Parks and Wildlife Conservation, Kathmandu, Nepal.

DNPWC [Department of National Parks and Wildlife Conservation], 2009. The Status and Distribution of the Greater One-horned Rhino in Nepal. Department of National Parks and Wildlife Conservation, Kathmandu, Nepal.

DNPWC [Department of National Parks and Wildlife Conservation], 2015. Technical Report on National Rhino Count 2015 (April 7- May 05, 2015). Department of National Parks and Wildlife Conservation, Kathmandu, Nepal.

Eberhardt, L.L., 2002. A paradigm for population analysis of long-lived vertebrates. Ecology 83 (10), 2841—2854.

Emslie, R., Brooks, M., 1999. African Rhino: Status Survey and Action Plan. IUCN/SSC African rhino specialist group. IUCN, Gland, Switzerland.

Ferreira, S.M., Greaver, C., Knight, G.A., Knight, M.H., Smit, I.P., Pienaar, D., 2015. Disruption of rhino demography by poachers may lead to population declines in Kruger National Park, South Africa. PLoS One 10, e0127783.

Ferreira, S.M., Greaver, C.C., Knight, M.H., 2011. Assessing the population performance of the black rhinoceros in Kruger National Park. S. Afr. J. Wildl. Res. 41, 192—204.

Gupta, V., Dobhal, D., Vaideswaran, S., 2013. August 2012 cloudburst and subsequent flash flood in the Asi Ganga, a tributary of the Bhagirathi river, Garhwal Himalaya, India. Curr. Sci. 105 (2), 249—253.

Holmes, T.P., Aukema, J.E., Von Holle, B., Liebhold, A., Sills, E., 2009. Economic impacts of invasive species in forests. Ann. N. Y. Acad. Sci. 1162, 18—38.

IUCN AsRSG [IUCN Asian Rhino Specialist Group], 2009. The Greater One-horned Rhinoceros Monitoring Instructor's Training Manual. National Trust for Nature Conservation, Kathmandu, Nepal.

Jarman, P., 1974. The social organisation of antelope in relation to their ecology. Behaviour 48, 215—267.

Jentsch, A., Beierkuhnlein, C., 2008. Research frontiers in climate change: effects of extreme meteorological events on ecosystems. Comptes Rendus Geosci. 340 (9), 621—628. https://doi.org/10.1016/j.crte.2008.07.002.

Jnawali, S., 1995. Population Ecology of Greater One-horned Rhinoceros (Rhinoceros Unicornis) with Particular Emphasis on Habitat Preference, Food Ecology Andranging Behavior of a Reintroduced Population in Royal Bardia National Park in Lowland Nepal. Agricultural University of Norway, Aas, Norway, 129.

Kandel, R., Jhala, Y., 2008. Demographic structure activity patterns, habitat use and food habits of *Rhinoceros unicornis* in Chitwan National Park, Nepal. J. Bombay Nat. Hist. Soc. J. 105, 5—13.

Kiwia, H., 1989. Ranging patterns of the black rhinoceros (*Diceros bicornis* (l.)) in Ngorongoro Crater, Tanzania. Afr. J. Ecol. 27, 305—312.

Lacy, R., Borbat, M., Pollak, J., 2005. Vortex: a stochastic simulation of the extinction process. Chicago Zoological Society, Brookfield, IL.

Lacy, R.C., 1993. Vortex: a computer simulation model for population viability analysis. Wild. Res. 20 (1), 45—65.

Lande, R., Barrowclough, G.F., 1987. Effective population size, genetic variation, and their use in population management. Viable Popul. Conserv. 87—123.

Laurie, W.A., 1979. The Ecology and Behavior of the Greater One-horned Rhinoceros. Ph.D. dissertation. University of Cambridge, Cambridge, UK.

Laurie, A., 1982. Behavioural ecology of the greater one-horned rhinoceros (*Rhinoceros unicornis*). J. Zool. 196, 307—341.

Law, P.R., Fike, B., Lent, P.C., 2013. Mortality and female fecundity in an expanding black rhinoceros (*Diceros bicornis minor*) population. Eur. J.Wildl. Res. 59, 477—485.

Law, P.R., Linklater, W.L., 2014. Black rhinoceros demography should be stage, not age, based. Afr. J. Ecol. 52, 571—573.

Leader-Williams, N., 2013. Fate riding on their horns—and genes? Oryx 47, 311—313.

Leader-Williams, N., 1988. Patterns of depletion in a black rhinoceros population in luangwa valley, Zambia. Afr. J.Ecol. 26, 181—187.

Moss, C.J., 2001. The demography of an african elephant (*Loxodonta africana*) population in Amboseli, Kenya. J. Zool. 255, 145—156.

Murphy, S.T., Subedi, N., Jnawali, S.R., Lamichhane, B.R., Upadhyay, G.P., Kock, R., Amin, R., 2013. Invasive mikania in Chitwan National Park, Nepal: the threat to the greater one-horned rhinoceros *Rhinoceros unicornis* and factors driving the invasion. Oryx 47, 361—368.

Okita-Ouma, B., Amin, R., Van Langevelde, F., Leader-Williams, N., 2010. Density dependence and population dynamics of black rhinos (*Diceros bicornis michaeli*) in Kenya's rhino sanctuaries. Afr. J. Ecol. 48, 791–799.

Owen-Smith, R.N., 1992. Megaherbivores: the Influence of Very Large Body Size on Ecology. Cambridge university press.

Pollock, K.H., Winterstein, S.R., Bunck, C.M., Curtis, P.D., 1989. Survival analysis in telemetry studies: the staggered entry design. J. Wildl. Manage. 53, 7–15.

Reid, C., Slotow, R., Howison, O., Balfour, D., 2007. Habitat changes reduce the carrying capacity of Hluhluwe-Umfolozi Park, South Africa, for Critically Endangered black rhinoceros Diceros bicornis. Oryx 41, 247–254.

Rachlow, J.L., Berger, J., 1998. Reproduction and population density: trade-offs for the conservation of rhinos in-situ. Anim. Conserv. 1, 101–106.

Robbins, C., 1993. Wildlife Feeding and Nutrition. Academic press, California USA.

Rutberg, A.T., 1987. Adaptive hypotheses of birth synchrony in ruminants: an interspecific test. Am. Nat. 130, 692–710.

Skalski, J.R., Ryding, K.E., Millspaugh, J.J., 2005. Wildlife Demography: Analysis of Sex, Age, and Count Data. Elsevier Academic Press, Burlington, MA, USA.

Strayer, D.L., Eviner, V.T., Jeschke, J.M., Pace, M.L., 2006. Understanding the long-term effects of species invasions. Trends Ecol. Evol. 21, 645–651.

Subedi, N., 2012. Effect of Mikania Micrantha on the Demography, Habitat Use, and Nutrition of Greater One-horned Rhinoceros in Chitwan National Park, Nepal. PhD Thesis. Forest Research Institute University, Dehradun, Uttarakhand, 209pp.

Subedi, N., Jnawali, S.R., Dhakal, M., Pradhan, N.M., Lamichhane, B.R., Malla, S., Amin, R., Jhala, Y.V., 2013. Population status, structure and distribution of the greater one-horned rhinoceros *Rhinoceros unicornis* in Nepal. Oryx 47, 352–360.

Sukumar, R., 1989. The Asian Elephant: Ecology and Management. Cambridge University Press.

Talukdar, B.K., Emslie, R., Bist, S.S., Choudhury, A., Ellis, S., Bonal, B.S., Malakar, M.C., Talukdar, B.N., Barua, M., 2008. Rhinoceros unicornis. The IUCN Red List of Threatened Species 2008: e.T19496A8928657.

Talukdar, B.K., 2013. Asian rhino specialist group report. Pachyderm 53, 25–27.

Thapa, K., Nepal, S., Thapa, G., Bhatta, S.R., Wikramanayake, E., 2013. Past, present and future conservation of the greater one-horned rhinoceros *Rhinoceros unicornis* in Nepal. Oryx 47, 345–351.

Trimble, M., Ferreira, S., Van Aarde, R., 2009. Drivers of megaherbivore demographic fluctuations: inference from elephants. J. Zool. 279, 18–26.

Walpole, M.J., Morgan-Davies, M., Milledge, S., Bett, P., Leader-Williams, N., 2001. Population dynamics and future conservation of a free-ranging black rhinoceros (*Diceros bicornis*) population in Kenya. Biol. Conserv. 99, 237–243.

White, G.C., Burnham, K.P., 1999. Program MARK: survival estimation from populations of marked animals. Bird study 46, 120–138.

Zar, J.H., 2010. Biostatistical Analysis, fifth ed. Prentice Hall, New Jersey, USA.