RESEARCH

Population model for the greater one-horned rhinoceros (*Rhinoceros unicornis*) in Royal Chitwan National Park, Nepal

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Abstract

One of the largest wild populations of the highly endangered Indian rhinoceros (*Rhinoceros unicornis*) resides in and around Royal Chitwan National Park (RCNP) in Nepal. Unfortunately, rhino poaching in the park has increased dramatically since 1998. This paper presents a demographic model of the Royal Chitwan rhino population to describe the effect of poaching on the population, explore the validity of a decreasing carrying capacity in the park, and provide input to an overarching bioeconomic model. We used a simple, logistic-style model to describe the rhino population. Starting with values available from the literature, three sets of best-fit parameter values were chosen. We then used these three model variations to indicate the size the RCNP rhino population would have been had the extensive poaching between 1998 and 2003 not occurred. All three model variations suggested that the current rhino population was below the park's capacity and revealed the strong negative impact of poaching. These results supported the vital importance of continued anti-poaching efforts in Royal Chitwan.

Résumé

Une des plus grandes populations sauvages du très menacé rhinocéros d'Inde (*Rhinoceros unicornis*) réside dans le Parc National et Royal de Chitwan (RCNP) et dans ses environs, au Népal. Malheureusement, le braconnage des rhinos a terriblement augmenté dans le parc depuis 1998. Cet article présente un modèle démographique de la population de rhinos du Royal Chitwan pour décrire les effets du braconnage sur la population, étudier la validité d'une capacité de charge en diminution dans le parc et fournir un modèle bioéconomique général. Nous avons utilisé un modèle simple, style logistique, pour décrire la population de rhinos. En partant des valeurs disponibles dans la littérature, trois sets de paramètres les mieux adaptés ont été choisis. Nous avons alors utilisé ces trois modèles de variation pour indiquer quelle aurait été la taille de la population de rhinos du RCNP si le braconnage intense n'avait pas existé entre 1998 et 2003. Les trois variations modèles ont suggéré que la population actuelle de rhinos était en dessous de la capacité du parc et révélé le grave impact négatif du braconnage. Ces résultats insistent sur l'importance vitale de la poursuite des efforts antibraconnage à Royal Chitwan.

Introduction

One of the largest wild populations of the highly endangered (Zschokke et al. 2003) Indian rhinoceros (*Rhinoceros unicornis*) resides in and around the 932-km^2 Royal Chitwan National Park (RCNP) in Nepal. RCNP was established in 1973 and is Nepal's oldest national park. The park was designated a World Heritage Site in 1984 by the United Nations Educational, Scientific, and Cultural Organization (UNESCO) because of its rich flora and fauna and because it is one of the last refuges of both the greater one-horned rhinoceros and the Bengal tiger (*Panthera tigris*).

The greater one-horned rhinoceros is considered a flagship species of Nepal (Dhakal 2002) and conserving these animals is a major priority for the country. Unfortunately, rhino poaching in the park has increased dramatically (Martin 2004) since 1998 (fig. 1). Rhinos are poached for their nasal horn, which is highly valued in East Asia (Maskey 1998; Martin 2004). Approximate rhino population size estimates for RCNP are available for the years 1972, 1978, 1988, 1994 and 2000 (see Martin and Vigne 1996; Nepal 2000).

In 2003, an international and interdisciplinary team of researchers was formed to study the problem of rhino poaching in RCNP. The team is using surveys of local people, stakeholder analysis and modelling of the rhino population to yield a set of models that can be used to predict the outcome of various anti-poaching strategies. This research is a coordinated effort by personnel from Simon Fraser University, the Institute for Environmental Studies (Free University, Amsterdam), the Environmental Resource Institute (Forest Action, Nepal), the Ministry of Forests and Soil Conservation in Nepal, and several consultants.

In this paper, we present a demographic model of the RCNP rhino population. The purpose of this model is to 1) describe the effect that recent and future poaching has and could have on the population, 2) explore the validity of a decreasing carrying capacity in RCNP as a key influence on population change, and 3) provide annual population estimates between 1972 and 2003 (for years in which field counts are not available) as input to an overarching bioeconomic model. We used a simple, logistic-style model (Cromsigt et al. 2002) to describe the rhino population. Starting with values available from the literature, we chose three sets of best-fit parameter values by comparing the predicted population time trajectory according to

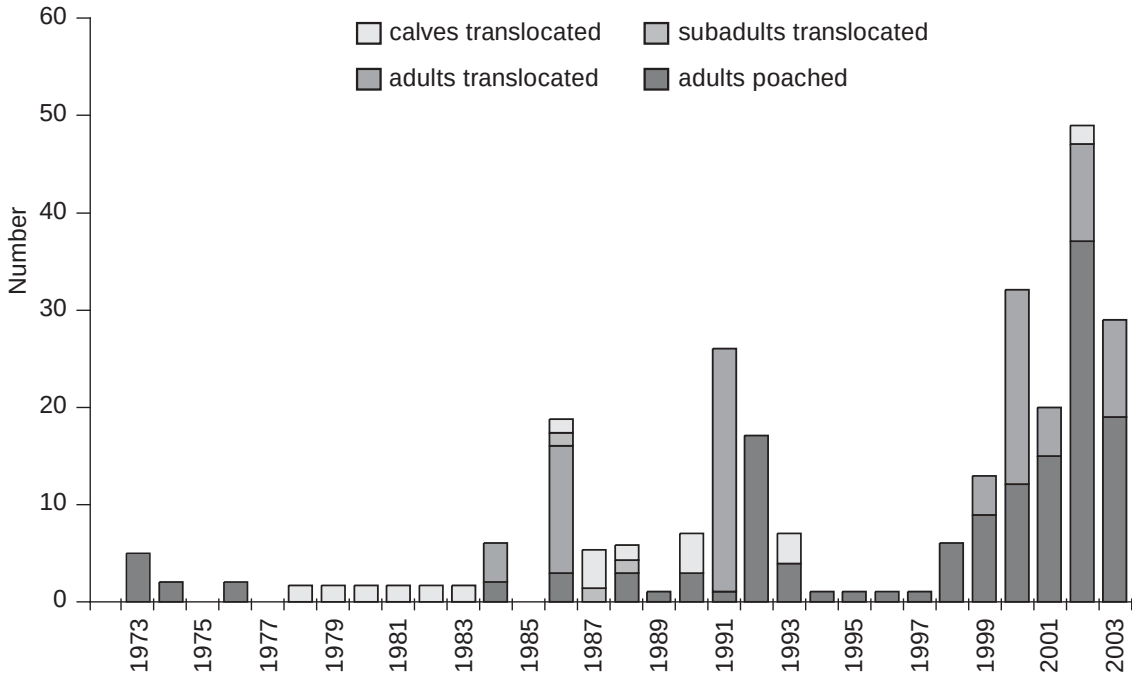

Figure 1. Rhinos translocated or poached from Royal Chitwan National Park, 1972–2003.

the model with actual field counts. We then used these three model variations to indicate what the size of the RCNP rhino population would have been had the extensive poaching between 1998 and 2003 not occurred.

Materials and methods

A discrete, stage-class population model with a one-year time step was used to represent the rhinos. The population was assumed to experience density-dependent regulation that can be described according to a logistic growth model. The animals were divided into three groups: 1) calves, including animals less than four years old, 2) subadults, which are between four and six years old, and 3) adults, which are seven years old or older. These distinctions are made because of the different mortality and reproductive rates experienced by rhinos in each group. Calves are highly vulnerable to tiger predation and do not reproduce. Subadults are relatively less vulnerable to tigers but are not yet reproductively active. Adults also are rarely subject to tiger predation and do reproduce. Adult males may die as a result of fights with other adult males (Dinerstein and Price 1991; Zschokke and Baur 2002). Adult males and females both have a nasal horn and may, therefore, be killed by poachers. Calves, subadults and adults have occasionally been translocated from their natal population (RCNP) to other national parks in Nepal for conservation purposes.

The specific model used can be described according to the following pseudocode:

$A_t = A_{t-1}$ + (maturing subadults – adult deaths – adults poached – adults translocated) * Δt

$SA_t = SA_{t-1}$ + (maturing calves – maturing subadults – subadult deaths – subadults translocated) * Δt

$C_t = C_{t-1}$ + (births – maturing calves – calf deaths – calves translocated) * Δt

adult deaths = $A_{t-1} * d_a$

subadult deaths = $SA_{t-1} * d_{sa}$

calf deaths = $C_{t-1} * d_c$

$T_{t-1} = A_{t-1} + SA_{t-1} + C_{t-1}$

births = $b * f * A_{t-1} * (1 - T_{t-1}/K)$

where A_t is the number of adults at time period t, SA_t is the number of subadults at time period t, C_t is the number of calves at time period t, d_a is the adult death rate, d_{sa} is the subadult death rate, d_c is the calf death rate, T_t is the total number of rhinos at time period t, b is the annual female reproductive rate, f is the percentage of adults in a population that are female, K is the equilibrium value of the RCNP rhino population where gains are exactly balanced by losses, and Δt is the time step (one year). Note that while K in our model refers only to RCNP rhinos, these animals may wander beyond the park boundaries so that the equilibrium value can be influenced by conditions both within and outside the park.

Three estimates of annual female reproductive rate b were tested in the model. The first two, 0.286 calves born per adult female per year (3.5-year intercalving interval) and 0.357 calves born per adult per female per year (2.8-year intercalving interval), are based on the overall birth rate per cow and the median intercalving interval, respectively, as reported by Laurie (1982). The third, 0.25 calves born per adult female per year (4-year intercalving interval), is based on figures reported by Dinerstein and Price (1991).

The first estimate of 57% for f, the percentage of adults in a population that are female, comes from the Dinerstein and Price (1991) description of the RCNP rhino population in 1988. The second, 59%, is based on 1994 survey data (Yonzon 1994). The third, 58%, is based on the 2000 survey (Nepal 2000). Laurie (1982) also reported adult male : female sex ratios but his definitions of the adult and subadult categories differ from those used in this analysis.

Three estimates are used for the equilibrium value K of the RCNP rhino population. The first, 800 rhinos, is the estimate of the 1950 Chitwan Valley population size reported by Martin and Vigne (1996) from Willan (1965) in Laurie (1978). The second, 1000 rhinos, is an estimate of RCNP population size in 1950 from Dinerstein and Price (1991). The third, 500 rhinos, is based on the loss of almost 60% of the original RCNP grassland areas favoured by rhinos (World Wildlife Fund pers. comm.).

Stage-specific annual natural mortality rates d_a, d_{sa}, and d_c come from the work by Dinerstein and Price (1991) on the Sauraha subpopulation of rhinos in RCNP: 2.8% for calves, 2.2% for subadults and 2.9% for adults. These rates include natural mortality events such as tiger predation, separation of calves from their mothers, floods, quicksand, or fights with conspecifics, they but do not include poaching.

Poaching data for kills made inside RCNP boundaries (fig. 1) are available for the years 1973 through 1993 where they are reported as ‘minimum number

poached' during a given year (Martin and Vigne 1996; Maskey 1998). Similar data were obtained for the years 1994 through 2000 from Dhakal (2002) and for the years 2001 through 2003 from the annual reports of the Department of National Parks and Wildlife Conservation (Nepal 2001–2003). Estimates of poaching from 1994 through 2000 are consistent with values from Martin (2001), who reports that the average number of rhinos killed in the entire Chitwan Valley (RCNP and surrounding areas) between 1994 and 1997 was under two a year and that 20 rhinos were illegally killed in 1998/1999 and 15 in 2000. It is assumed that all poached animals were adults.

Translocation data (fig. 1) are derived from the Department of National Parks and Wildlife Conservation annual reports (Nepal 1993–1994, 2001–2003), supplemented by values from Dinerstein and Price (1991) and Dhakal (2002). In several instances, the stage class from which animals were drawn or the exact year during which the translocation occurred is unknown. For these cases, total translocation numbers were evenly split between stage classes and over the time interval in question; hence some translocations are non-integer numbers.

The initial stage-class distribution for the starting population in 1972 was unknown and therefore set to the values observed by Dinerstein and Price (1991) in 1988. In that year, 21% of the rhinos were calves, 14% subadults, and 65% adults. This same age structure was observed by Laurie (1978) in 1975. The population in 1972 in RCNP (see Martin and Vigne 1996) was estimated, based on a helicopter survey, to consist of between 120 and 147 rhinos. However, the minimum estimated population size in 1978 was 270. This implies that at least 21 rhinos were added each year during this six-year interval, well above the 16.3 births per year recorded by Dinerstein and Price (1991) between 1984 and 1988 when the population was nearly three times as large. It is therefore likely that the 1972 survey underestimated the true number of rhinos. Instead, an initial 1972 population size of 216 animals was estimated by calculating the average net number of individuals (9 per year) added to the population between 1978 and 1988 (358 minus 270 divided by 10 years) and then back-calculating from 1978 to 1972 (six years).

The complete rhino population model was coded and run using the Stella 5.1.1 software package (High Performance Systems 1998). To begin the analysis, the model was used to predict 27 different population trajectories between 1972 and 2003 using all combinations of the three possible *f* (percentage of adult females), *b* (annual female reproductive rate), and *K* (equilibrium value) values. The validity of each parameter combination was assessed according to the differences between actual and predicted total rhino population size for the four years for which rhino count data are available.

Based on these 27 model runs, a smaller parameter space was explored to choose the three best parameter sets (combinations of *b*, *f*, and *K* that yielded a population trajectory that best fitted the field counts). The resultant best models were used to investigate the effect of recent poaching on the rhino population. For each model, the rhino population trajectory was first predicted including the poaching events between 1998 and 2003 and then a second time as if these poaching events had not occurred.

Results

None of the nine model runs for which the equilibrium value *K* was equal to 500 rhinos yielded population trajectories that were consistent with the field counts (fig. 2a). Instead, for these runs the model always underestimated the actual counts. This difference between predicted and actual rhino numbers became more exaggerated with time. For these nine runs, the only way that the model could be correct and the field data incorrect would be if there were continually increasing instances of double counting of rhinos during the field surveys, which is an unlikely scenario.

For the nine model runs where equilibrium value *K* was equal to 800 rhinos, the model always underestimated the 1994 and 2000 field counts (fig. 2b). For the three runs where the annual adult female reproductive rate *b* was equal to 0.250 the model always underestimated the actual counts. For the three runs where *b* was equal to 0.286 the model underestimated the actual counts in 1988, 1994 and 2000. For the three runs where *b* was equal to 0.357 the model overestimated the 1988 count but underestimated the counts in 1994 and 2000. The apparent 1988 overestimates could potentially be accurate (that is, the field count was an underestimate of the true population size) because the population estimate for this year came from a field study that focused on just one subpopulation of rhinos in RCNP (Dinerstein and Price 1991). However, the underestimates for all nine runs in 1994 and 2000 cast doubt on the validity of these parameter combinations because, as described

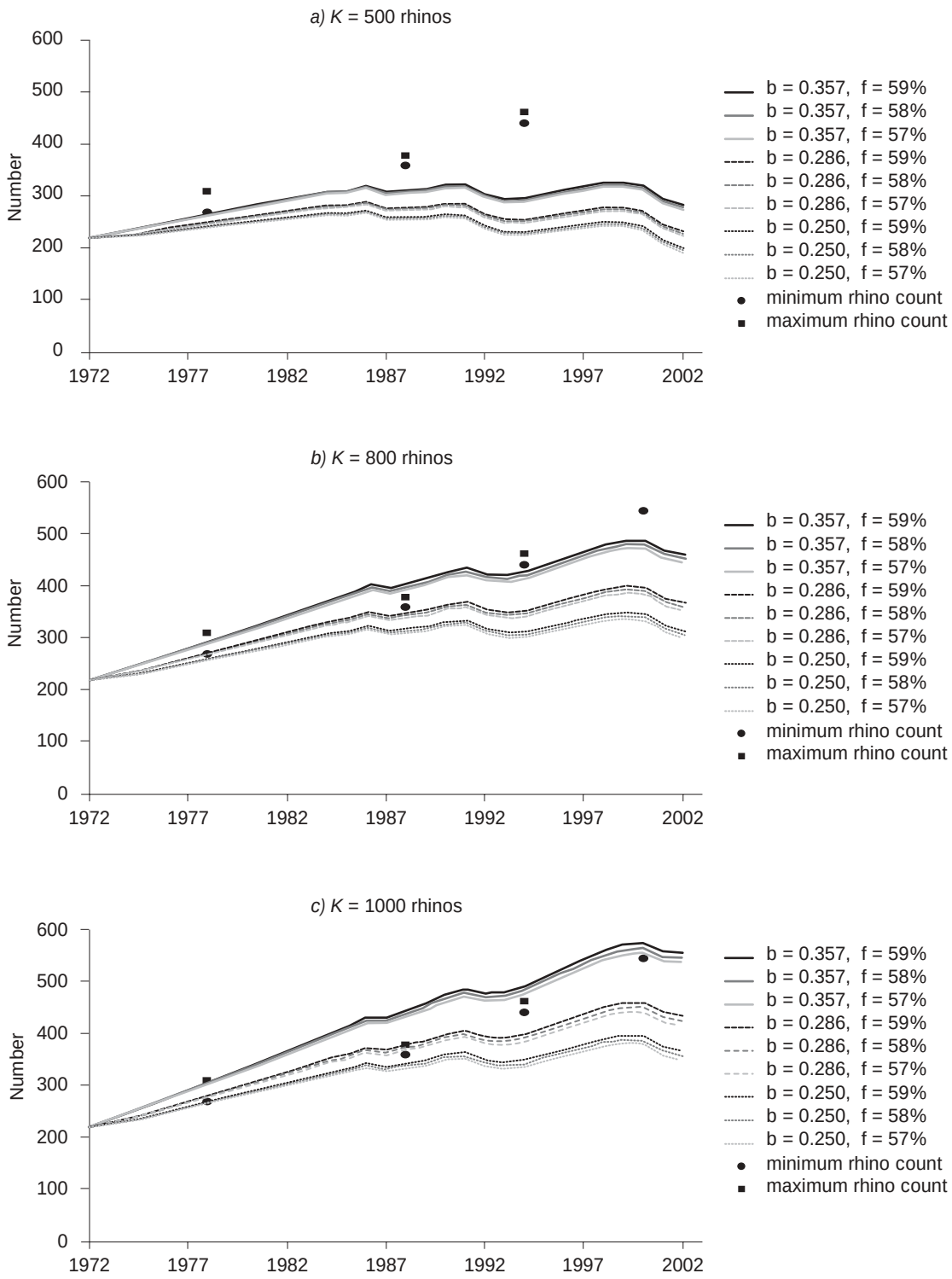

Figure 2. Population trajectories using three equilibrium values (*K*), in which *K* is *a)* 500, *b)* 800 and *c)* 1000 rhinos; *b* = annual female reproductive rate, *f* = percentage of adults in a population that are female.

above, they can be explained only by systematic double counting during the field surveys.

For the three model runs where equilibrium value *K* was equal to 1000 rhinos and the annual adult female reproductive rate *b* was equal to 0.250, the model always underestimated the actual counts (fig. 2c). For the three runs where *K* was equal to 1000 and *b* was equal to 0.286 the model underestimated the actual counts in 1994 and 2000. However, for the three runs where *K* was equal to 1000 and *b* was equal to 0.357 the model correctly predicted the number of rhinos within the range (between the minimum and the maximum) from the 1978 count, overestimated the 1998 count, but only slightly overestimated the 1994 and 2000 counts. For the run where the percentage of adults that were female *f* is equal to 57%, the overestimates were 14 rhinos in 1994 and 11 rhinos in 2000.

Based on these 27 runs, the parameter space was reduced and systematically explored. With *b* and *f* set to their maximum values, no model with *K* less than 840 predicted a population trajectory that passed between both the 1978 and the 1994 minimums and maximums so only *K* values between 840 and 1000 were considered. With *K* set to 1000 and *f* set to its maximum value, no model with *b* less than 0.320 predicted a population trajectory that passed between both the 1978 and the 1994 minimums and maximums so only *b* values between 0.320 and 0.357 were considered. Ultimately there was no single best model found because, while many parameter combinations yielded population trajectories that passed between both the 1978 and the 1994 minimums and maximums, parameter values that overestimated the 1988 population size (according to the field counts) underestimated the 2000 population size. Instead, three best models were chosen, where K = 1000. Model A, where b = 0.34 and f = 58%, minimized the underestimate of the 2000 count (fig. 3). Model B, where b = 0.34 and f = 57%, yielded a trade-off between overestimating the 1988 count and underestimating the 2000 count. Model C, where b = 0.32 and f = 59%, minimized the overestimate of the 1988 count.

The best models, A, B and C, all indicated that the RCNP rhino population is smaller now (in 2004) than

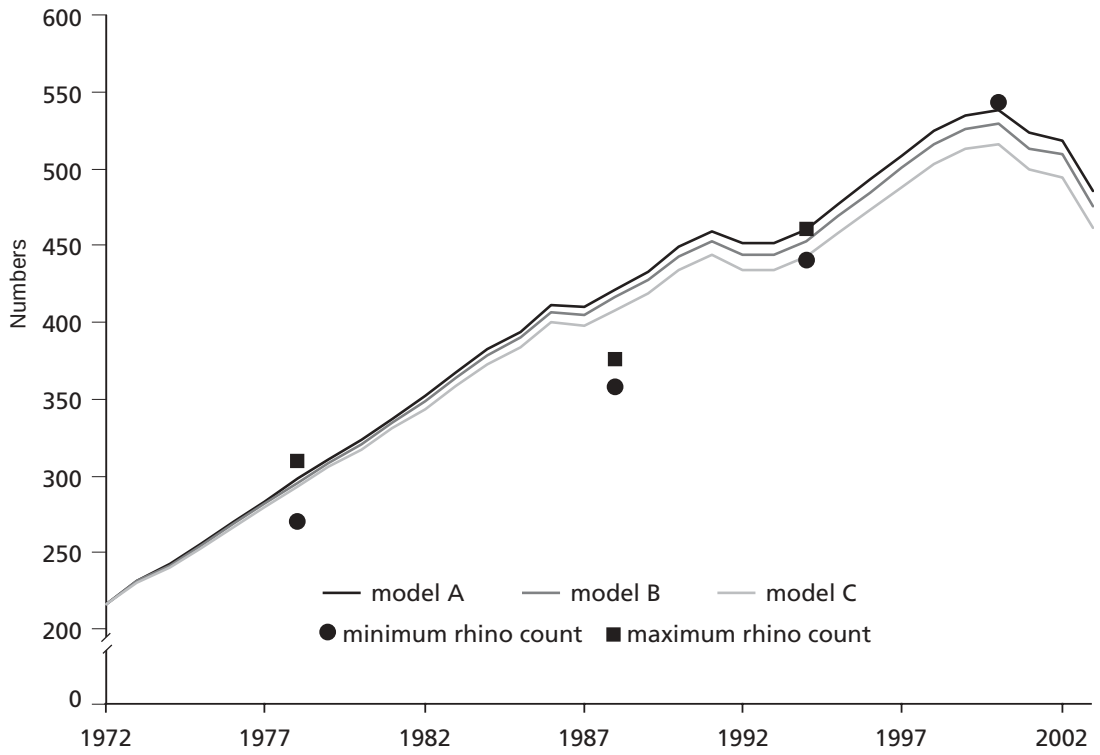

Figure 3. The three best models. In all three models equilibrium value K = 1000. In model A, *b,* the annual female reproductive rate = 0.34; *f,* the percentage of adults in a population that are female = 58%. In model B, again b = 0.34 but f = 57%. In model C, b = 0.32 and f = 59%.

it was in 2000 (fig. 3). All three models also showed that without the poaching losses between 1998 and 2003 the 2003 population would have been larger than the size estimated in 2003 (fig. 4). Models A and C indicate that in 2003 there were 79 rhinos fewer in the RCNP than there would have been had the poaching not occurred between 1998 and 2003. Model B indicates that in 2003 there were 78 fewer.

Discussion

Any of the three best-fit models may be used to provide annual RCNP rhino population estimates between 1972 and 2003 for years in which field counts are not available (objective 3). All three models yield estimates that fit the 1978 and 1994 counts. All three indicate a similar drop in the population size between 2000 and 2003. The major differences in these models are their overestimates of the 1988 count and underestimates of the 2000 count. Further information about these counts would be helpful in selecting a single best model. As described above, because the 1988 count was based on fieldwork focused on a single subpopulation within the park, it is plausible that individuals in the other subpopulations went unobserved and that this count is low. All parameter combinations that yielded a population trajectory fitting both the 1978 and the 1988 counts, as reported, underestimated the subsequent 1994 and 2000 counts. For example, even when K = 1000 and f = 59%, the model underestimated the 1994 count by 43 animals and the 2000 count by 86 animals (fig. 2c). However, without additional data it is difficult to estimate how low the 1988 count might have been. The 2000 rhino count, which recorded 544 animals, was conducted in the Chitwan Valley 'in and around the park' (Nepal 2004) and so is likely to be an overestimate of the number of rhinos in RCNP alone. Because this count is more recent, it may be possible to assemble extra information and approximate how many of these 544 rhinos were non-park animals.

A visual comparison of the predicted population trajectories (fig. 3) and the poaching data (fig. 1) suggests the strong negative impact poaching can have

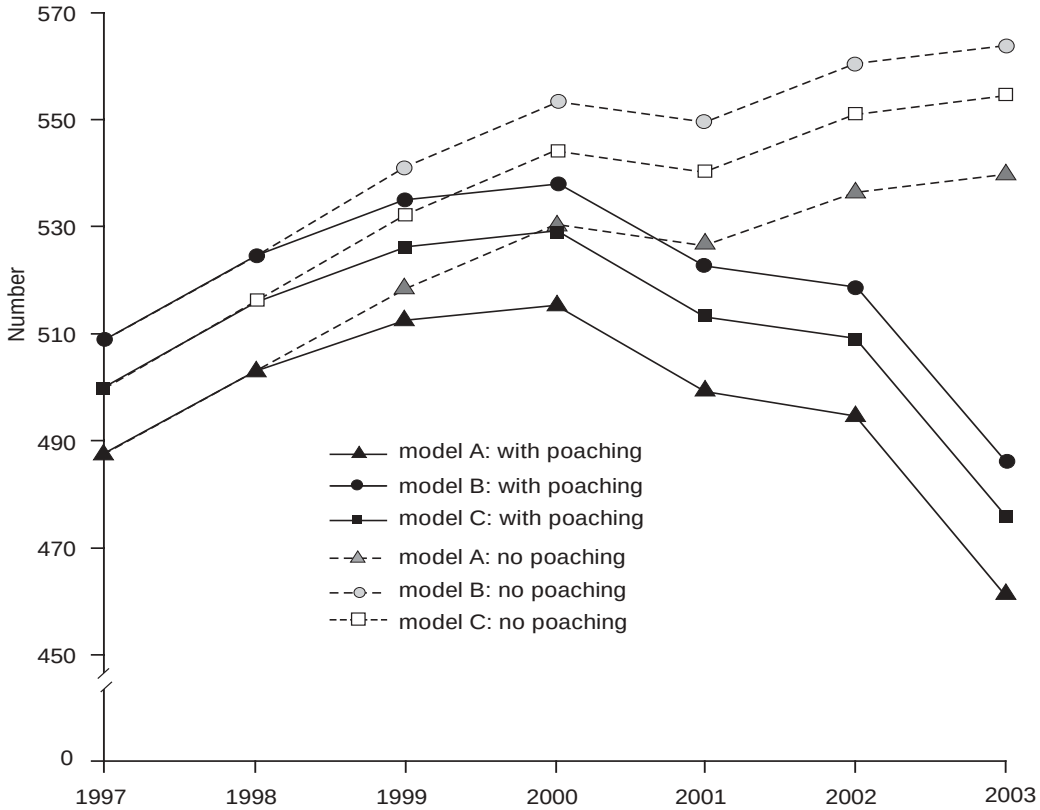

Figure 4. Modelled projections of what rhino populations are and what they would have been had the poaching in 2000–2003 not occurred.

on rhinos (objective 2). For example, the 17 poaching events in 1992 correspond to the predicted downturn in the rhino population size between 1991 and 1993. Similarly, the heavy poaching between 1998 and 2003 corresponds to a predicted drop in rhino numbers between 2000 and 2003. All three best-fit models indicate that if there had been no poaching between 1998 and 2003, the rhino population would have continued to rise (fig. 4).

Anti-poaching efforts such as those described by Martin and Vigne (1996) and promoted by the 2000 Anti-poaching Workshop conducted by the Department of National Parks and Wildlife Conservation and the World Wildlife Fund Nepal Program are critical to the recovery and persistence of rhino populations in RCNP and elsewhere (Martin 1998, 2001). In particular, actions that build support within local communities for conservation and create alternative income opportunities complement direct anti-poaching interventions. This process works by reducing social acceptability and the financial attractiveness of poaching (Milner-Gulland and Leader-Williams 1992). Much of the poaching in Nepal is thought to involve poor and marginal social groups who have few alternatives, and their activities may be tolerated by other groups who view rhinos negatively because of the damage caused to crop fields near the national park.

The significant loss of rhino habitat in and around RCNP and the increase in proximal human settlement (Martin and Vigne 1996) may have resulted in a reduction in the carrying capacity of the park (the density of rhinos sustainable over time; Dhondt 1988). Indeed if, as models A, B and C indicate, the current rhino count finds fewer rhinos now than in 2000, part of the cause may be a decrease in carrying capacity that has triggered density-dependent regulation via increased mortality rates, decreased birth rates, and increased emigration. However, it is important to note that models A, B and C indicate that a population decline will occur as a result of past poaching losses even if there has been no decrease in the equilibrium value *K* of RCNP. As described above, no model with *K* less than 840 showed a population trajectory that fit both the 1978 and the 1994 rhino counts. All three of the best-fit models use *K* equal to 1000. The model results suggest that the current rhino population is still considerably below an equilibrium value, and therefore natural (non-poaching) losses might equal or outpace gains and poaching cannot be viewed as a form of compensatory mortality. While it is logical that habitat loss and human settlement have had a negative effect on RCNP rhino population to some degree, this modelling exercise provides strong evidence that poaching has a major negative effect on rhino numbers (objective 1) and that the RCNP population size would be higher in the absence of poaching. This result again supports the importance of continued anti-poaching efforts.

As described above, the rhino population trajectory generated from demographic models described here is being used as input to an overarching bioeconomic model for natural, social and management systems for RCNP. One component of this larger modelling effort that makes direct use of the population trajectory is a retrospective econometric analysis of factors that may have influenced historical levels of rhino poaching. This analysis will indicate the effectiveness of current interventions and simulate the outcome of alternative policy options.

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