



Assessing and managing the rising rhino population in Kaziranga (India)



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ABSTRACT

The greater one-horned rhinoceros (*Rhinoceros unicornis*) is a flagship species, and yet is poorly known unlike its African cousin. The species future is now under a growing threat, judging by the prospect of a legalization of the horn trade that has been the subject of recent debate, coupled with the fragmentation of the animal's habitat. In this study, we analyze the rhino habitat and assess its dynamics in the Kaziranga National Park (KNP), Assam, India. To compensate for the limited size of the data available, we use some numerical models and propose some original spatial analyses and indicators.

Our findings point to a healthy and increasing rhino population in a density-dependent scenario. An increase of at least 30% in the rhino population is expected in the coming twelve years, mainly as a result of the effective implementation of wildlife protection laws in the country. Kaziranga's grasslands have been quite stable in the past (7% between years, in average, and less than 19% at most), and are expected to remain so in the near future, especially in the core area of the KNP. In the absence of a detailed suitability map and known carrying-capacity values, we identified the areas most favoured by the rhinos, and developed a so-called “preference map”. We conclude by stressing the need to realistically combine the existing conservation strategies while increasing the monitoring effort on the species distribution.

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1. Introduction

Although all rhinoceros species are flagship species in their respective habitats, and are on the IUCN Red List (Talukdar et al., 2013), our understanding of the population ecology of this megafauna group is limited to some species only. While the African black (*Diceros bicornis*) and white rhinos (*Ceratotherium simum*) have been well studied in terms of demography and ecology (Ferreira et al., 2012; Tatman et al., 2000; Walpole et al., 2001, and references therein), the three Asian rhinos (*Dicerorhinus sumatrensis*, *Rhinoceros sondaicus*, and *Rhinoceros unicornis*) are still poorly known. Of these, the unicorn or greater one-horned rhino, the subject of this paper, lives in the northern part of India and neighbouring territory, and its demography, behaviour, and relationship with its habitat deserve much more attention than is apparent in available literature (Acevedo, 2005; Dinerstein, 2003;

Laurie, 1982; Srivastava, 2002). One may recall some African studies (Conway and Goodman, 1989; Harley et al., 2005), and in particular those touching on the poaching pressure for their horns (Poudyal et al., 2009). We discuss here the likely future of the unicorn rhino population living in the Kaziranga National Park (KNP), Assam, India, with a close look at its demography and habitat dynamics using original methods and indicators adapted to the meagre dataset available.

The KNP is a key protected area located in the Brahmaputra plains in north-eastern India, and is part of a rich biodiversity hotspot (Myers et al., 2000). Apart from the unicorn rhino (population estimated at 2329 individuals in the March 2013 census), Kaziranga is home to what is probably the densest tiger population in the world, and to a complex food web encompassing several wild species. It simultaneously provides ecosystem services for a large human population dependent on the KNP forests for their livelihood (Saikia, 2009; Srivastava, 2002). While the authorities have made efforts to protect the various fauna and their habitat, they would have had greater success if they were equipped with a better understanding of the rhino–habitat relationship and its direct implications for this species viability (Mathur et al., 2005b).

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As things stand, however, we still do not have adequate information about the species basic biology, specifically on the existence of a density-dependent effect, or the importance of territoriality (Brodie et al., 2011; Dinerstein, 2003; Garawad, 2009), and about how this mega-herbivore affects habitat quality and habitat availability when the population density increases (e.g. Fritz et al., 2002). While some studies of the unicorn rhino do exist for the Indian and Nepalese parks (Acevedo, 2005; Kushwaha et al., 2000; Mathur et al., 2005b; Subedi et al., 2013), they show deficiencies, such as a narrow geographical focus or remoteness in time, which diminish their usefulness in arriving at a generalization of the rhino's behaviour and its relationship with its habitat.

What will be its IUCN status in the years ahead, after its present-day *vulnerable* state? The direction of the rhino's future demography, and of the dynamics of its habitat (i.e. whether the habitat will shrink and/or change in composition), will be mainly shaped by the existing poaching pressure and other mainly anthropogenic threats. Conversely, even a small increase in the population would call for a careful management of its spatial distribution to ensure a stable local population with minimal inbreeding (Dinerstein and Mc Cracken, 1990; Mathur et al., 2005b). In parallel, the dynamics of its habitat, more specifically its possible reduction and simultaneous fragmentation, may have a considerable influence on the population's long-term viability. The methods we indicate of projecting useful information on the rhino's demography are such as could be utilized in the case of other mammal populations.

Developments in regard to the horn trade, illegal globally, and our ability to build robust networks of protected areas, will remain the major elements among human impacts on the rhino's future (Biggs et al., 2013; Collins et al., 2013; Litchfield, 2013). The rhino does not enjoy the protection that Indian tradition accords to the elephant and the tiger, while Assamese society does show a strong attachment to the animal. The recently observed increase in the pressure on the African species should serve to echo the risk to the present relatively safe situation of the Asian populations (Syangden et al., 2008). Sustainable management of these species may need some complementary and sometimes controversial decisions (van Aarde et al., 1999; Van Aarde and Jackson, 2007).

Our objective were threefold: (i) to develop a demographic model from the available census data to prefigure the most probable scenario in the KNP; (ii) to analyze the KNP landscape's dynamics using remote sensing data and generic multiscale methods (Gaucherel, 2010; Gaucherel et al., 2010); (iii) to discuss the future of the rhino population in the light of changes in the KNP's vegetation.

We hypothesized that the KNP's rhino population remained relatively stable or was slowly increasing, and would continue in that direction. We developed several population-dynamics models to simulate the species demography, basing them on the data from the censuses carried out in the KNP that covered approximately three-year periods. Another hypothesis was that the rhino habitat was decreasing in size, partly due to competition with other mega-herbivores of the KNP and to the Brahmaputra's erosion in past years (Mathur et al., 2005a). From the KNP land-cover maps, we developed spatial analyses to document the habitat structure in space, in time, and at various scales (Gaucherel, 2010; Gaucherel et al., 2010). These two hypotheses (i.e. a stable rhino population and a decreasing surface habitat) combine to give the intuitive idea that the rhino population in this site is vulnerable. We finally combined these analyses in a context of scarce data on the basis of a ranking index with the intention of capturing the focal species preferences (Johnson, 1980), and building a robust and coherent image of its probable future in the KNP and further away.

2. Materials and methods

The Kaziranga National Park is located in the north-eastern state of Assam in India, and covers approximately 430 km² (Fig. 1a, see Appendix A in Supplementary materials). The Brahmaputra river's dynamics generates floods that affect the KNP's unique landscape and its wet, alluvial plain ecosystem. The oldest protected area in India, the KNP was declared a reserve forest in 1908, and was notified as a World Heritage Site by UNESCO in 1985. The KNP's landscape is highly heterogeneous and mainly covered by scrublands (19.7%), grasslands (39.6%), and woodlands (32.6%), as shown by diachronic Landsat images (Hazarika and Saikia, 2005) (Fig. 1). Land-cover and vegetation types were retrieved from supervised and unsupervised classifications of these Landsat images (Appendix A). Available population data in KNP allowed us to compute averaged population parameters such as the fertility, mortality, and poaching rates, and the sex ratio despite their obvious variations in time (Table 1, Fig. 2). Detailed sighting events (i.e. occurrences transformed into frequencies) of rhino individuals in the various land covers were not available at KNP, and we used sightings of the Chitwan National Park (CNP) (DNPWC, 2009) to compute the rhino preferences. The CNP, which is approximately 800 km away from KNP, indeed is a relatively similar though more forested landscape than KNP (Shrestha and Dangol, 2006).

We developed Leslie-Matrix projection models to quantify the population dynamics of the rhino species in the KNP (Caswell, 1989; Poudyal et al., 2009). Instead of developing a detailed spatially explicit population model (Rétho et al., 2008), for which data were not available, we intended to build a preliminary model to estimate the main demographical rates within the park. In the absence of a clear demonstration of a regulation of the density-dependent population of the unicorn rhino (Brodie et al., 2011; Dinerstein, 2003; Laurie, 1982; Ripley, 1952), we developed two (density-independent (DI) and density-dependent (DD)) models for this population (Appendix B). Both the models were developed for females, and were based on a two-stage matrix *L* (for calf and adult classes), fed by the above estimated parameters, and calibrated with a trial-and-error procedure on the basis of observed abundances and root-mean-square-errors (RMSEs). Both models covered a time span of 200 years, starting with the census year 1966. The DD model was based on a somewhat natural and robust Ricker function to mimic the fertility rate according to the population abundance (Caswell, 1989; Ricker, 1954). In addition to a detailed sensitivity analysis to assess the impact of each model's parameter, we estimated and compared the rhino's growth rate λ in year 2013 in Kaziranga for both models.

We proposed detailed spatial analyses of the KNP's landscape dynamics to then relate them to the rhino's presence and habitat utilization (Appendix C). We first estimated the KNP's land-cover changes computed with Cohen's Kappa, bearing in mind the rhino's need for a habitat mosaic (Dinerstein and Price, 1991; Kushwaha et al., 2000). We then estimated the KNP's grassland dynamics through comparisons of grassland-density maps for all the available dates to identify the rhino's most favoured habitat for its short grasses and wallowing grounds (Garawad, 2009). All these spatial analyses were based on two methods that have been extensively described and applied to ecological questions (Gaucherel, 2007, 2010; Gaucherel et al., 2008, 2010). Both the methods (multiscale heterogeneity map (MHM) and comparison map and profile (CMP)) are based on the principle of a circular moving window simultaneously crossing the images to be analyzed (MHM uses a single image, Gaucherel et al., 2007) or compared (CMP compares two images), combined respectively with specific textural or similarity indices. They lead to local and quantitative analyses, which become multiscale when the number of the moving window sizes varies.

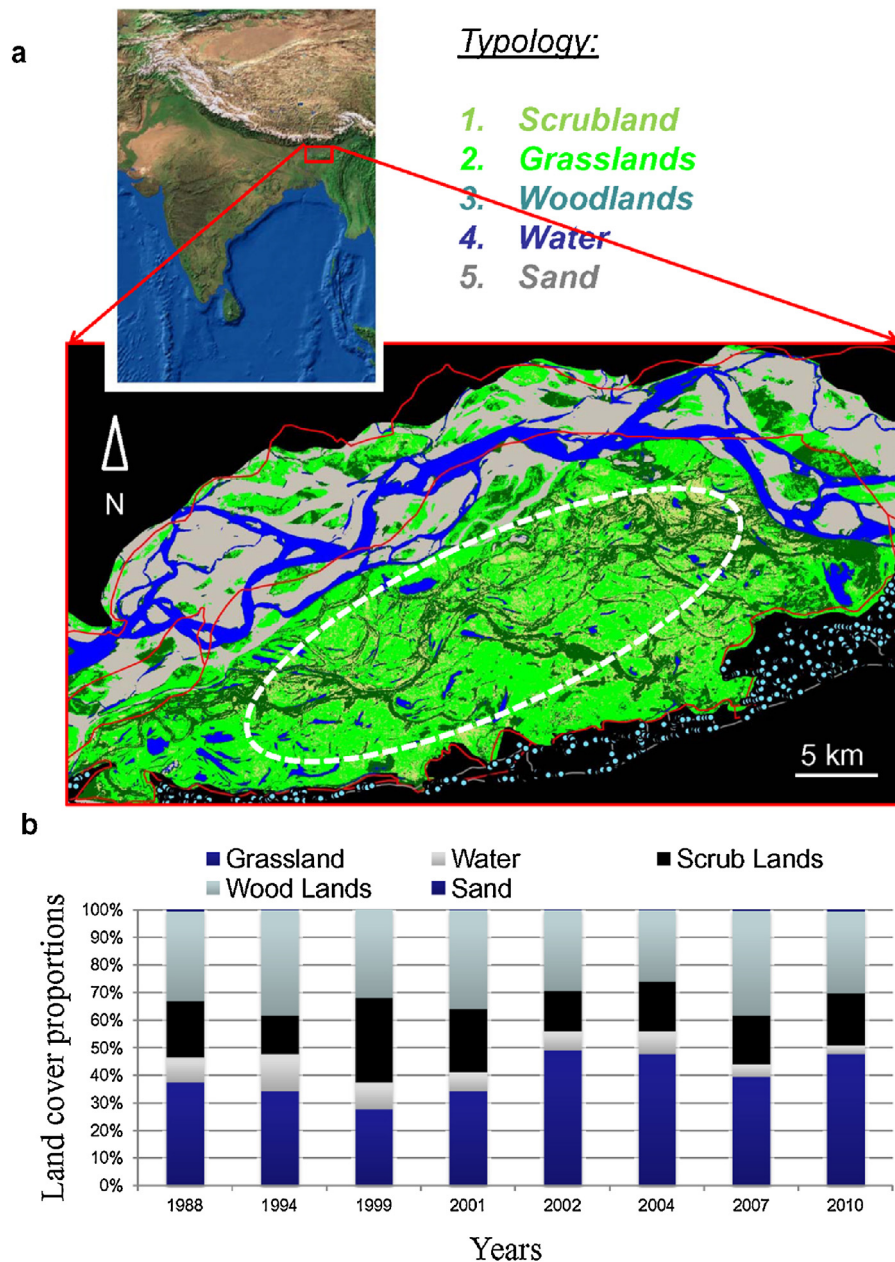


Fig. 1. Location (a) and landscape composition (b) of the study area: Kaziranga National Park (KNP). Located in Assam, north-eastern India, the KNP is mainly composed of scrublands, grasslands, woodlands, water bodies, and sands (a). The park boundaries, highlighting the Brahmaputra area, are displayed in red, while the blue dots in the southern part of the KNP are human settlements (a). Land-cover proportions (in %) of the KNP varied from 1988 to 2010, according to remote sensing data. The dashed ellipse (a, white) highlights the KNP core area. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Unfortunately, datasets to build habitat suitability maps of the focus species were not available in the KNP, even in the most recent rhino census (Syangden et al., 2008). To compensate this lack, we built a rhino 'preference map' (Appendix D) that could also serve to study other populations and species. Based on rhino occurrences in the Chitwan National Park, the land-cover classes were first ranked to calculate the relative preferences of the rhino species, following Johnson's Ranking Index that is positive for favourable places and negative otherwise (Johnson, 1980). Then, we weighted each land-cover density map (obtained by MHM) by their associated land-cover preference values, and finally averaged all of them at each available date, to take into account the land cover mosaic, and thus capture the complementation-supplementation processes. This way of weighting various land covers is commonly used in expert knowledge (Rathore et al., 2012), although

our proposition used more objective (i.e. observed) correlations between the species presences and landscape features (Johnson, 1980). Averaging these preference maps led to a final KNP rhino-preference map covering the 1966–2010 period, averaged in space (i.e. pixel by pixel), and to a preference-dynamic curve, averaged between dates.

3. Results

After calibrations (Fig. 3a), the growth rates of the two models increased sharply in the past two decades, with similar RMSE (last row, Table 1). For each model, we looked for the couple of parameters leading to the lowest RMSE and thus to the optimal parameter values (columns 3 and 4, Table 1, solid circles, Fig. 3a). The optimized demography rates were close to the empirical values, while

Table 1

Demography and model parameter values of the study. Fertility, calf–adult transition, and survival rates with their respective standard deviations, as well as b and (fertility) α Ricker function parameters of the KNP rhino population as computed from the available census data (first column), from calibration of the density-independent model (second column), and from the calibration of the density-dependent model (third column). Their respective parameter elasticities are shown (fourth column), depending on the concerned (deterministic) model. Finally, the lowest RMSE associated to each model at the end of the calibration process is shown (last line).

Parameters	Observed parameter values	Density-independent (DI) model	Density-dependent (DD) model	Parameter elasticities (according to the model)
Fertility rate	0.296 ± 0.091	0.292	–	43.56 (DI)
Transition rate	0.534 ± 0.157	0.353	0.353	38.61 (DI)
Survival rate	0.943 ± 0.032	0.943	0.943	4209.8 (DI)
b	0.00165	–	0.000124	61.67 (DD)
α	0.48	–	0.260	53.51 (DD)
RMSE	–	72.38	105.94	–

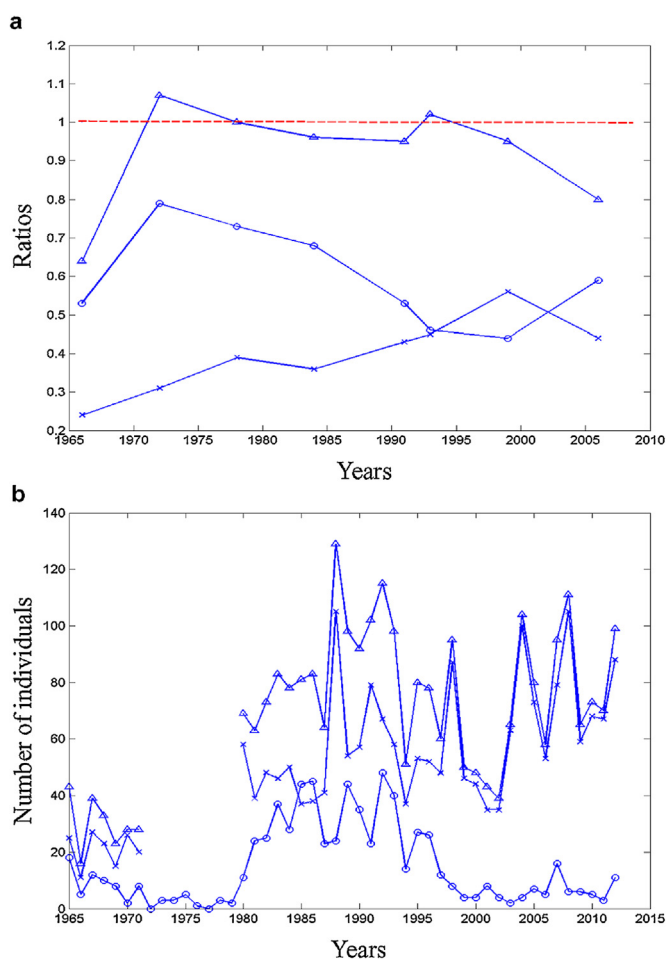


Fig. 2. Variations of demographic ratios (a) and mortality rates along time (b) for available years. The fertility (ratio of young females produced over reproducing females), calf–adult transition (number of calf females becoming adults) and sex (females/males) ratios are displayed in crosses, circles, and triangles respectively (a). The mortality rates (natural, poaching, and total (total number of rhino deaths observed in the KNP)) are displayed in crosses, circles, and triangles respectively (b).

the density-dependent parameters were slightly different from empirical values (columns 1, Table 1, empty circles, Fig. 3a). The estimated growth rates in Kaziranga, numerically computed on the basis of successive time steps, were those expected for such mammal populations: $\lambda = 1.0428$ (i.e. 4% population increase each year) for the density-independent (DI) model, and $\lambda = 1.0246$ for

density-dependent (DD) model in 2013. The DD growth rate underwent variations and gradually decreased to unity after the year 2150 approximately (Fig. 3b). The future population dynamics will likely stabilize between these two different (DD and DI) trends. Population uncertainties were estimated of about 150 individuals in average on the basis of the (approx. 10%) observed parameter variability and rapidly increased RMSEs (column 1, Table 1). The parameter elasticities (i.e. normalized sensitivities) have quite similar values, except for the survival rate parameter (approx. 100 times more sensitive, last column, Table 1). This is mainly due to the fact that this rate is close to unity, a value that would explode the population if increased. Hence, we fixed it to the observed value ($S_{\text{rate}} = 0.94 \pm 0.03$), assuming without additional information stable mortality and poaching rates.

The transition matrix between KNP land covers in different years revealed that at least 56% of the landscape remained unchanged in average (diagonal, Table 2), being probably an underestimated proportion considering that this was a local (pixel-based) computation. The other relatively high transitions were found between the grasslands and scrubland or forest areas (around 6–7%). As expected, we observed a slightly greater similarity between KNP landscapes at broader scales (Fig. 4a, insert), because images more likely differ at pixel scale. The couples of years 2001–2002 and 2002–2004 appeared to show the highest similarity in KNP landscapes, with averaged Kappa greater than the interpretable (usual) threshold equal to 0.4 (Fig. 4a). Except for these years, the KNP landscape as a whole appeared to be quite unstable. Landscape differences were not correlated to time differences ($R^2 = 0.18$, not shown). Locally, Kappa similarities were higher in the core area of the park (dashed ellipse, Fig. 4b), and showed many more changes near its boundaries, particularly in the southern and more anthropogenic area of the park.

A distance-based index computing local and multiscale similarities between grassland densities at successive dates led to relatively stable grassland areas, in average (Fig. 5). Firstly, we observed relatively higher grassland densities (i.e. in presence and connectivity) since year 2000 (Fig. 5a, insert, warm colours). Yet, differences between the successive grassland patterns remained quite low (around 3.16% variations, in average), and oscillated between positive and negative grassland changes, with a maximum increase (of about 34.9%) reached between the years 2001 and 2002. This latter observation concerned the shortest duration between dates and may be explained by the Brahmaputra's dynamics or by image misinterpretations. There is a significant yet weak trend ($R^2 = 0.25^*$) of grassland variations as a function of the time difference (not shown). The final averaged map of grassland distances showed changes that mainly occurred outside the park core, in particular in its southern part, and an increase of as much as 18.7% (Fig. 5b).

The map in Fig. 6 shows the location and rank in preference along a time scale of the most rhino-favoured areas in the KNP. The average value at each date indicated a relatively stable and positive preference in the park as a whole (Fig. 6a), despite quite high spatial variations. Yet, some years such as 1999 were clearly unfavourable to rhinos (negative preference), and the associated map showed that less favoured areas were often located in the southern part of the park (Fig. 6a, insert). The overall averaged preference map confirms the differential perception of the core and peripheral areas of the park, the latter being much less favoured by the rhino (Fig. 6b).

4. Discussion

4.1. The KNP rhino

This paper, to our knowledge, is the first-ever attempt at an in-depth study of the important unicorn rhino population (of the KNP

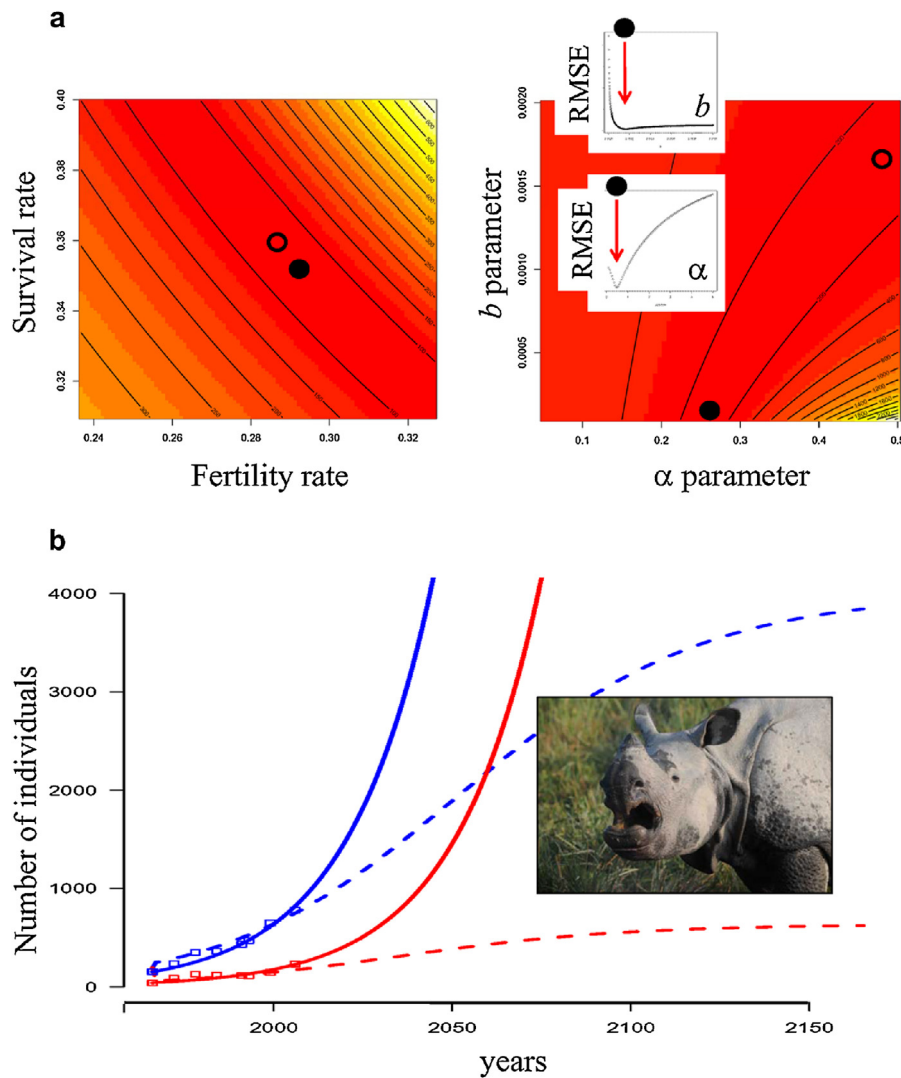


Fig. 3. Calibration figures (a) and population dynamics (b) of the KNP rhino models (b, calf in insert). The following simulations are results of calibration stages for the DI model (a, left) and the DD model (a, right). The DI model RMSE contour plot (in colours), as a function of fertility and transition rates, shows the initial observed values (empty circle), quite close to the final selected ones (solid circle) corresponding to the minimal RMSE value. The DD model RMSE contour plot (in colours), as a function of the b (strength of density dependence) and α (fertility factor), shows the initial observed values (empty circle), and the final selected ones (solid circle) corresponding to the minimal RMSE value. In insert are displayed the RMSE variations for b and α parameters to estimate their elasticities in the DD model, and the selected values (red arrows). Population simulations and projections (b) for the density-independent model (DI, plain lines) and density-dependent model (DD, dashed lines). Adult females (blue lines) and calf females (red lines) are superimposed (for clarity, uncertainties of ± 150 individuals in average were not added). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2

Transition matrix between the five land covers of the KNP, averaged over the seven couples of years available in the remote sensing data. Transitions (in %) are oriented from columns to lines (e.g. 6.04% of KNP pixels are shifting from Scrubland to Grassland). Hence, the matrix is not symmetrical, but all transitions sum to 100%. Dominant transitions (arbitrary fixed greater than 5%) have been highlighted in bold case, considering that for example changes from wood to water (1.54%) were not realistic (and that this threshold should thus be higher).

Land covers	Water	Wood	Scrubland	Grassland	Sand
Water	4.35	1.54	1.33	1.22	0.004
Wood	1.06	20.11	4.15	7.91	0.011
Scrubland	0.99	3.39	7.47	7.32	0.014
Grassland	1.18	7.91	6.04	23.91	0.013
Sand	0.016	0.014	0.013	0.02	0.004

in particular) with the help of population- and habitat-dynamic models. In our main result, we observed that the KNP's rhino population is increasing, and is unlikely to stabilize in the near future (i.e. before several decades, Fig. 3). We present the predicted state of the population based on the two scenarios of density-dependence

acting or not acting in the population. So far, both scenarios are equiprobable. In addition, the male demography is assumed to closely follow the female demography, although rescaled by the sex ratio (triangles, Fig. 2a). Following the observed demographic ratios (in the past 45 years) between the adult female and the other population classes, we thus predict a total rhino population (females + males + calves) at between 3076 and 3843 individuals in year 2025, for the DD and DI (deterministic) models respectively. These approximately 3500 individuals correspond to the $50 \pm 17\%$ variation from the 2329 individuals recorded in 2013. This prediction is likely to exceed the density of 8 individuals per km^2 (5 indiv./km^2 today), and demonstrates, contrary to our first hypothesis, a healthy and well-protected unicorn rhino population in this business-as-usual scenario.

The average annual mortality rate was estimated to be approximately equal to 6%, and was even lower for the past decade (Fig. 2b). The poaching rate was 1% on average, and rose to 3% in the year 1999. The comparatively low incidence of poaching deaths should be attributed to the efficient anti-poaching actions of the KNP

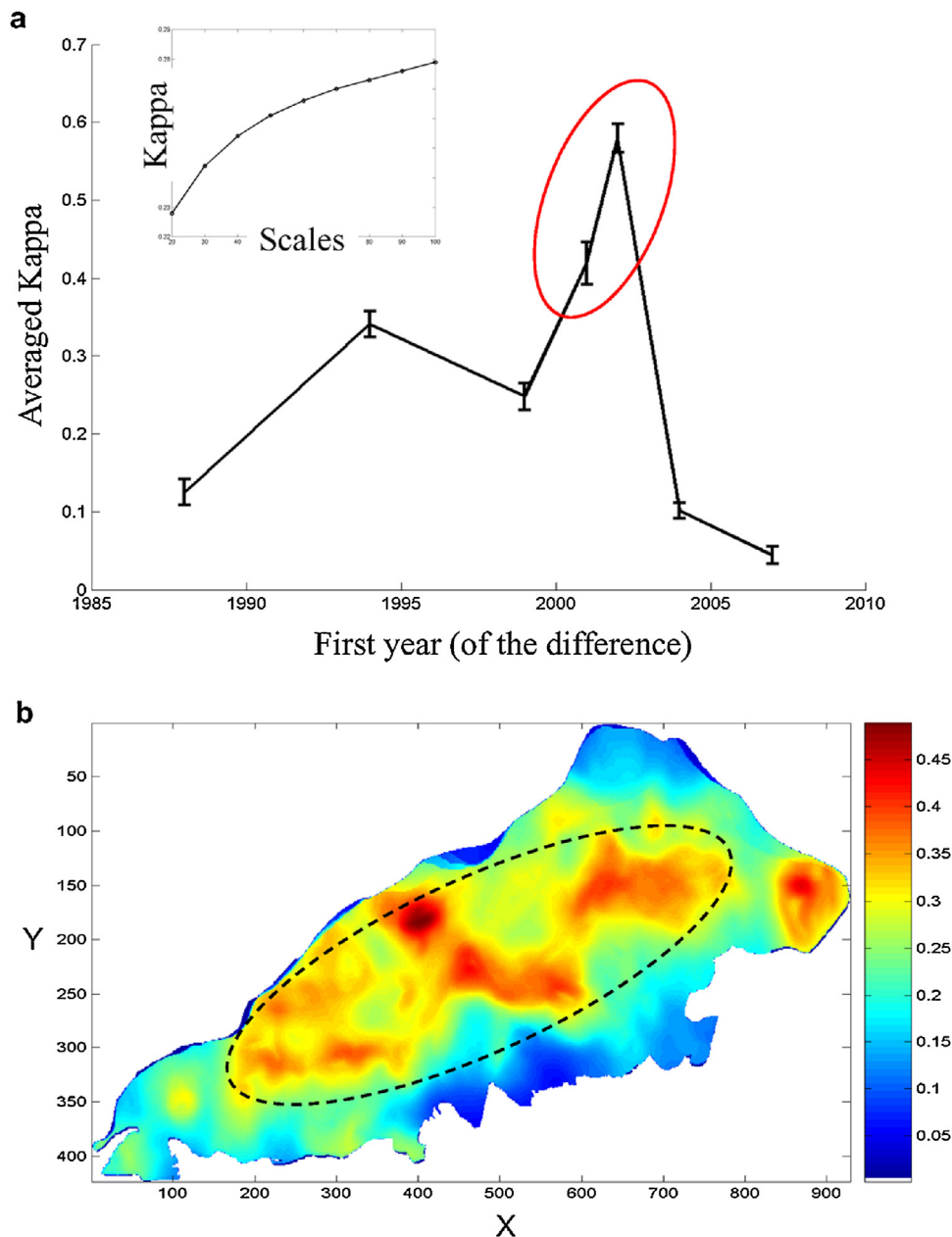


Fig. 4. Averaged CMP Kappa for KNP land-cover changes as a function of time (a) and mapped on the KNP area (b). The averaged Kappa variations along time are plotted as a function of the first year of compared successive dates (a) with their respective uncertainties, the highest values for years 2001–2002 being highlighted (a, red circle). Kappa test is appropriate for qualitative data comparison, and Kappa values are considered as: poor if <0.4 , fair if between 0.4 and 0.7, good if >0.7 . In insert is the averaged Kappa variation along scales over all the compared successive dates. The Kappa (in colour scale) is mapped in cartographic coordinates as an average over all compared successive dates (b). The highest Kappa values in the core area of the park showing quite similar landscapes across years are highlighted by the dashed ellipse. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

and Assam state authorities (Mathur et al., 2005b). However, it should be remembered that these statistics relate to poachings within the KNP's boundaries, and that several killings outside the park's area are reported every year, particularly those of males that stray beyond the park lands. While it may be unrealistic to lower the poaching rate, given the ineluctable pressure from a growing human population and road-building, it is to be hoped that the park's authorities will continue to act vigorously to control rhino mortality inside and outside the park (Mathur et al., 2005b; Srivastava, 2002).

The predicted population increase could be strongly limited by a decline in the extent of the rhino-preferred habitat, an outcome which, however, was not observed in our original

landscape-dynamic analysis. The local and multiscale analyses we performed on the KNP landscape revealed a relatively unstable landscape from year to year (differences often below the 0.4 Kappa threshold, Fig. 4). At the same time, we observed relatively stable grassland dynamics (low distances, Fig. 5), especially in the core area of the park. Grassland differences may be due to acts of management intervention, such as grassland burning, as well as to the coarse grain of our analysis, which may have blurred the distinction between short and tall grasses. Besides, our study suggests the potential of a quite stable carrying capacity of the KNP, but a greater vulnerability of land cover close to the boundaries. Indeed, it has been shown that these boundaries are largely affected by the Brahmaputra tributaries in the northern part and by human and

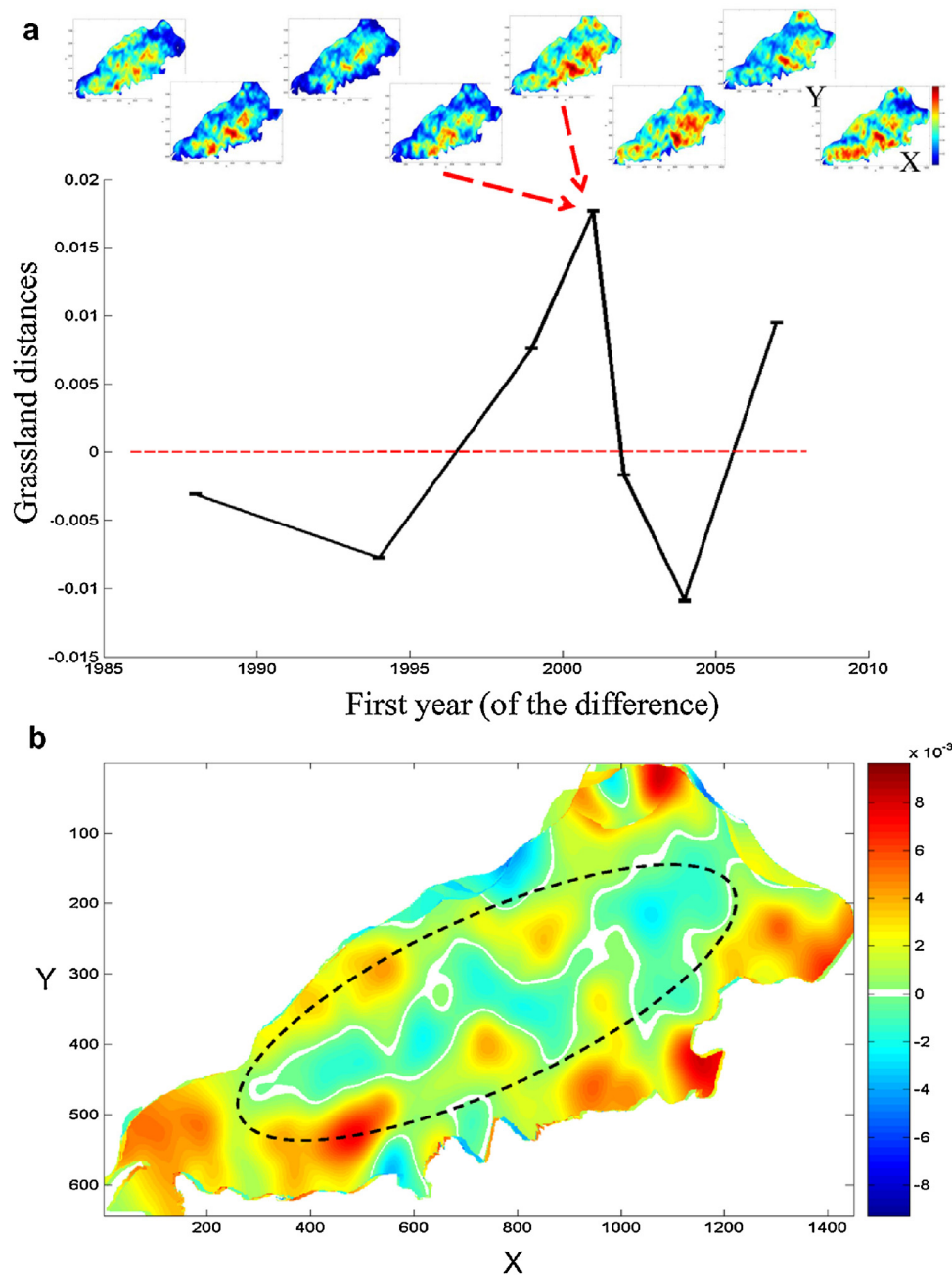


Fig. 5. KNP grassland differences between years, computed by the distance index (Appendix C), as a function of time (a) and mapped on the KNP area (b). The grassland distance variations along time are plotted as a function of the first year of compared available successive dates (a). In insert are shown the grassland density maps for each year (with the same colour scale), the highest difference (distance) being highlighted (a, red arrows) for the years 2001–2002. The red dashed line (a) shows the null distance, meaning no difference between the compared years. The grassland distances (in colour scale) are mapped in cartographic coordinates as an average over all compared successive dates (b). The lowest distance values (i.e. the lowest difference between grassland patterns) in the core area of the park are highlighted by the dashed ellipse. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

livestock pressures in the southern part of the park (Mathur et al., 2005b; Saikia, 2009; Srivastava, 2002).

Since, grasslands are not the only useful land cover for rhinos, we also computed local and multiscale rhino preferences for other land classes, to compensate for the lack of rigorous habitat-suitability maps (but see Kushwaha et al., 2000). This methodology can be applied to other sites and/or other species in instances where detailed observations are lacking. We tried to compensate the lack of data in the KNP by combining them with the CNP data and by computing multiscale and multirate maps with cutting-edge spatial analyses. It appeared that the overall KNP rhino preferences remained slightly positive (averaged value of about 0.05 ± 0.07 ,

whereas the grassland preference is set to 0.5) except for some infrequent years, mainly due to the relative land-cover stability in the core area of the park (Fig. 6). Although we were far from accurately estimating the carrying capacity of the KNP, our results from habitat dynamics suggest that the condition of the rhino habitat is likely to improve slightly, or at least to remain stable, in the coming years (Figs. 5a and 6). We would stress the need to frequently update such a preference map, and to compute it on the basis of successive spatially explicit surveys of rhinos (here, a single and stable survey has been supposed over the entire period under study) to detect trends in the use of the park's resources.

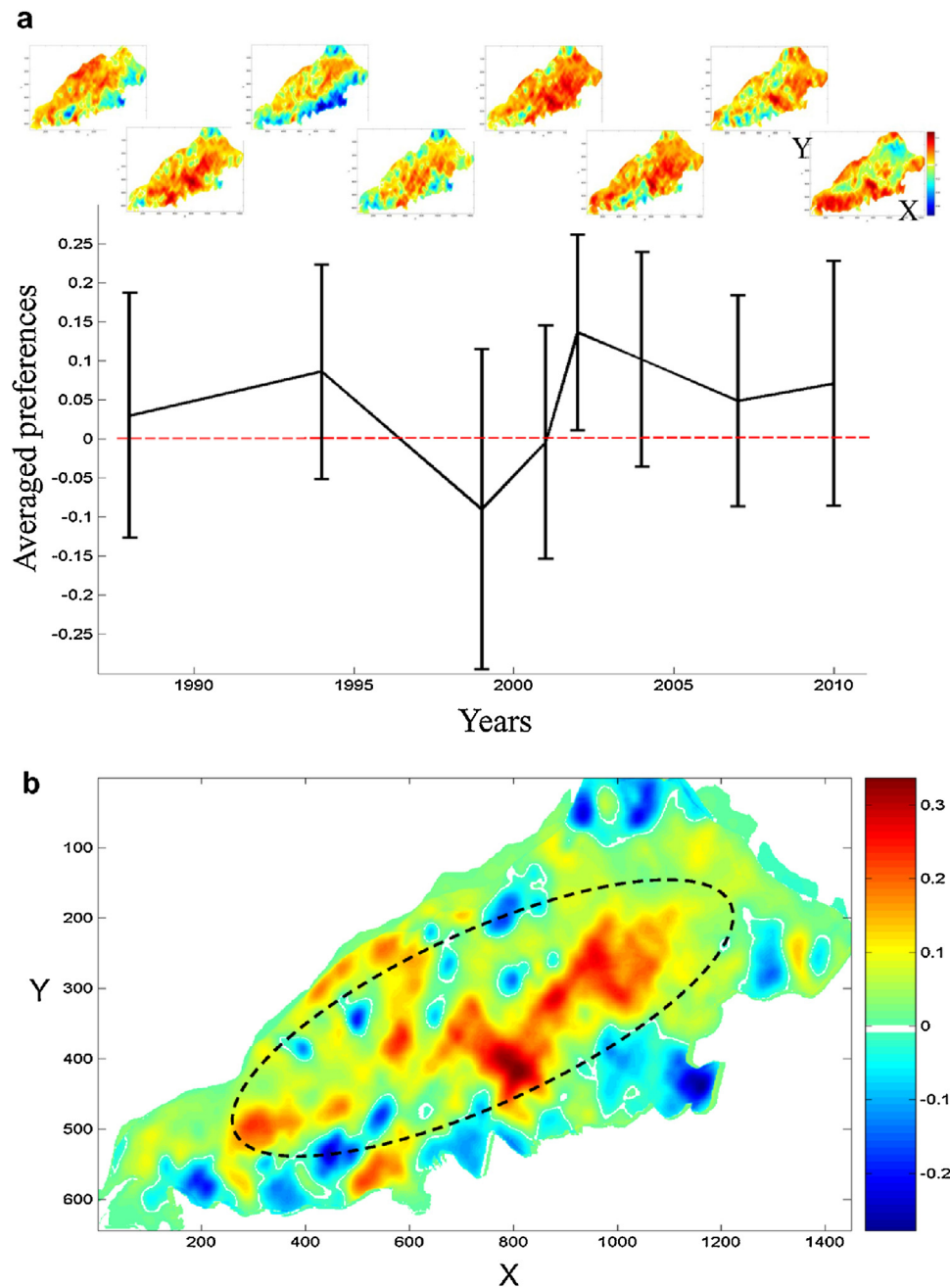


Fig. 6. KNP averaged preferences as a function of time (a) and mapped on the KNP area (b). The averaged preference variations along time are plotted as a function of years (a) with their respective uncertainties (Appendix D). In insert are shown the averaged preference maps for each year (with the same colour scale), the most detrimental pattern (with the lowest preference values) being highlighted (a, red arrow) for the year 1999. The red dashed line (a) shows the null preference, meaning that the KNP habitat pattern has no (positive nor negative) impact on the rhino population. The averaged preference (in colour scale) is mapped in cartographic coordinates as an average over all years (b). The highest preference values (i.e. the most favoured areas) in the core area of the park are highlighted by the dashed ellipse. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4.2. More data and more studies needed

This study, based on parsimonious but precious data, demonstrated the urgent need to collect additional data, as well as to study the unicorn rhino species and its habitat across its distribution. Even with some cutting-edge analytical tools (Gaucherel, 2010; Gaucherel et al., 2010) to hand, we hardly find ourselves in a position to make confident predictions about the rhino's future. A spatially explicit population model would certainly help in decision-making (Rétho et al., 2008). While analysis may be replaced with better methods, such as in this study, there cannot be a substitute for baseline data. We lacked high-resolution biological

data, for example data on demography and density-dependence (but see Ripley, 1952; Laurie, 1982). We lacked data on the ecology and behaviour of rhinos, particularly on their sex-specific territorial behaviour and on their feeding and habitat selection (but see Sarma et al., 2011; Subedi et al., 2013). Finally, we also lacked data on the rhino-landscape relationships within the KNP, information which would have allowed us to draw a rigorous habitat-suitability map (Ibanez et al., 2013; Sarma et al., 2011). Many studies have explored these parameters for the African rhinos (Biggs et al., 2013; Brodie et al., 2011; Conway and Goodman, 1989; Tatman et al., 2000), but the Asian rhino clearly lacks such detailed studies.

Several methods are today available to help us improve our understanding of rhino biology. The total count method in use at present in census operations is statistically unreliable, while mark-resight techniques or the 'distance sampling' method are more powerful methods recently proposed for proper understanding of mammal population dynamics (Thomas et al., 2006; Wegge and Storaas, 2009). If adopted in India, the latter methods could provide reliable figures on rhino densities on an annual basis. Another efficient method of value would be GPS collaring, which facilitates continuous recording of habitats selected by a few representative individuals (Benhamou, 2011; Gaucherel, 2011), and provides real-time preference data. This safe, non-invasive, and powerful technique, commonly used for the African rhinos, allows one to quantify individual movements and to associate their patterns with their landscape features.

4.3. The (unicorn) rhino conservation

With a predicted 50% increase in the KNP's rhino population in the coming twelve years (i.e. around a thousand more individuals) and a stable habitat (Figs. 4b and 5b), it becomes urgent to give serious thought to the question of the species management on a long-term basis and at broad spatial scales. The only possible converse to this projection would be the appearance of a much stronger density-dependence effect than the one detected in the declining trend of vital rates (Garawad, 2009). So far, we cannot discriminate between DD and DI models on the basis of observed data, but data in the coming years will likely fix this point. Here, we assume that the population growth rates have been correctly estimated and that they may be only marginally impacted by poaching and other threats. Parameter elasticities were relatively low (and thus robust) according to current-day data, but changing dynamics could rapidly impact them. In case no DD process is occurring soon, the park authority will face a huge challenge in terms of population management. India adopted, some years ago, a policy to regularly translocate some rhinos to other protected zones (Sale and Singh, 1987), but such a growing rhino population will require a vastly different mode of thinking. Translocations are costly, although possibly easier and more effective than previously thought for such a large, non-social mega-herbivore (Linklater et al., 2012).

A comparatively recent detailed study on some complementary and controversial management decisions (such as culling, sterilization, no action, etc.) for an increasing elephant population in southern Africa revealed that none of them seemed to be fully satisfactory (Van Aarde and Jackson, 2007). Some earlier authors had advocated a 'metapopulation approach' favouring individual migrations along corridors between protected areas, a management option also suggested for the black rhinoceros (Foose et al., 1993). A metapopulation results from the dynamics of a sub-population, through dispersal and recolonization between patches, some of which act as sources while the others act as sinks. Our study would be highly relevant for the growing rhino population in India, although it is not clear how a metapopulation approach would be successful (but see Thapa et al., 2013). However, this option presupposes a stable and well-planned 'landscape network', a quite unrealistic requirement given the extreme difficulty of monitoring rhino movements in riverine and swampy terrains. While hoping for a network of protected areas in the country, along the lines of that for tigers (Sharma et al., 2013), we have serious misgivings about the feasibility of such a project for rhinos, in the face of the poaching pressure in evidence up until now, of administrative difficulties, and of pressure resulting from the influx of people (Poudyal et al., 2009).

In the broader context, there is today an on-going debate on whether a legalized commercial exploitation of the rhino horn, however distasteful, might reduce the poaching pressure on these

endangered species (Collins et al., 2013; Litchfield, 2013). A sizeable increase in poaching on African rhinos has been recorded in recent years (Biggs et al., 2013), with a demand-and-supply imbalance that may later spread to Asian rhinos. Yet, while persistent rhino poaching in the KNP and in Assam in general cannot be ruled out altogether in the future, its impact may not affect the net size of the species projected population growth, if poaching roughly remains at the current 1% level.

What we have proposed in this paper is a generic methodology consisting of preference maps, and linking it to a demographic model of the rhino population. Our findings point to the potential usefulness of simultaneously combining the existing practices in rhino management, and in particular reinforcing and optimizing translocation, sterilization in target areas, and continual monitoring the species spatial distribution at both landscape and regional scales. A landscape approach that represents an alternative entails political synergies, cooperation of local people, additional funds, and ultimately a restructuring of the administrative machinery, even though it has produced some success in neighbouring areas (Thapa et al., 2013). There might be considerable benefits to the rhino metapopulation, and to the human population, if a multi-park think tank, or even a multi-country think tank, were to come into existence. A frequent audit of each strategy employed, possibly in combination with a spatially explicit model (Rétho et al., 2008), might help in suggesting relative weights to be assigned to the strategies.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolind.2016.01.023>.

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