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Review paper

The catastrophic decline of the Sumatran rhino (*Dicerorhinus sumatrensis harrissoni*) in Sabah: Historic exploitation, reduced female reproductive performance and population viability

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HIGHLIGHTS

- The reason for the recent decline of the Sumatran rhino is poorly understood.
- The remaining small isolated rhino populations are deemed to go extinct.
- Historic exploitation led to low numbers of Sumatran rhinos on Borneo.
- PVA analyses identify the fertility of females as key factor for population growth.
- A resource selection study identifies habitat characteristics preferred by the rhinos in Sabah.

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ABSTRACT

The reasons for catastrophic declines of Sumatran rhinos are far from clear and data necessary to improve decisions for conservation management are often lacking. We reviewed literature and assembled a comprehensive data set on surveys of the Sumatran rhino subspecies (*Dicerorhinus sumatrensis harrissoni*) in the Malaysian state of Sabah on Borneo to chart the historical development of the population in Sabah and its exploitation until the present day. We fitted resource selection functions to identify habitat features preferred by a remnant population of rhinos living in the Tabin Wildlife Reserve in Sabah, and ran a series of population viability analyses (PVAs) to extract the key demographic parameters most likely to affect population dynamics. We show that as preferred habitat, the individuals in the reserve were most likely encountered in elevated areas away from roads, in close distance to mud-volcanoes, with a low presence of human trespassers and a wallow on site, and within a neighbourhood of dense forest and grassland patches

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preferably on Fluvisols and Acrisols. Our population viability analyses identified the percentage of breeding females and female lifetime reproductive period as the crucial parameters driving population dynamics, in combination with total protection even moderate improvements could elevate population viability substantially. The analysis also indicates that unrestrained hunting between 1930 and 1950 drastically reduced the historical rhino population in Sabah and that the remnant population could be rescued by combining the effort of total protection and stimulation of breeding activity. Based on our results, we recommend to translocate isolated reproductively healthy individuals to protected locations and to undertake measures to maximise conceptions, or running state-of-the-art reproductive management with assisted reproduction techniques. Our study demonstrates that a judicious combination of techniques can do much to illuminate causes of population declines, improve decision making for conservation management and possibly prevent similar developments in populations of other species of similar ecological standing.

Contents

1. Introduction

The conservation of highly endangered species is challenging. Basic data about their ecological needs and geographic distribution are often lacking (Funk and Richardson, 2002; Harris et al., 2009; Bland et al., 2015; Abram et al., 2015) and the question arises of how to use the limited and uncertain data to improve decisions for conservation management (Tear et al., 1995; Karanth et al., 2003; Huettmann, 2005). Conservation measures such as forest corridors connecting insular environments and the translocation of individual animals into protected areas have been proposed for endangered species suffering from habitat loss and fragmentation (Griffith et al., 1989; Bennett, 2003; Rayan and Linkie, 2015). These measures require an understanding which environmental variables, such as terrain, climate, substrate or land cover determine the distribution of a species (Ferrier et al., 2002; Rushton et al., 2004). The rise of habitat modelling techniques combined with Geographical Information Systems (GIS) has led to the development of new methods (Guisan and Zimmermann, 2000) to identify relevant habitat characteristics for the occurrence of a species. Habitat suitability models identify areas with the best resources for the conservation of the respective species and habitats (Leblond et al., 2014).

In addition to habitat loss and fragmentation, the size of a population, its vulnerability to demographic and environmental stochasticity and negative impacts of human activity also influence its viability (Mace and Lande, 1991; Melbourne and Hastings, 2008; Meek et al., 2015). Population viability analysis (PVA) methods help to identify factors important for the persistence or decline of a species. They improve decisions by reducing and quantifying uncertainty and thereby improve decision making for conservation efforts (Beissinger and McCullough, 2002; Robinson et al., 2015), or at least highlight the key gaps for which further scientific research should provide essential data.

The Sumatran rhino (*Dicerorhinus sumatrensis*) is a good example to illustrate the challenges in the conservation of a highly endangered species. The two still extant subspecies, *D.s. sumatrensis* in Sumatra, Indonesia, and *D.s. harrissoni* (hereafter called Borneo rhino), in Borneo in the states of Sabah, Malaysia, and Kalimantan, Indonesia, are split into very small and highly fragmented populations whose numbers are continuously decreasing. Around one hundred or so animals of the Sumatran subspecies are estimated to exist in three isolated populations in the wild whereas the Borneo rhino is nearly extinct (IUCN, 2015). Its disappearance occurred almost undetected and the reasons for its recent decline are little understood. The Sumatran rhino is an example of a large-bodied megaherbivore (Owen-Smith, 1988). It occurs in a tropical rainforest without any serious predators and may have always lived at low densities. Learning about the causes of the decline is an essential part in order to develop targeted conservation measures for its continued existence and that of its Sumatran sister subspecies. It may also be a model to understand similar past, current or future declines in species with a similar ecological position within tropical and subtropical habitats.

Several conservation strategies have been proposed to stop the decline and improve reproduction of the Sumatran rhino (Clements et al., 2010; Zafir et al., 2011; Nardelli, 2014). In terms of ecological approaches, translocation of individual animals into a small designated area to increase the chance of breeding encounters and to support natural breeding with artificial reproduction techniques is one key measure. However data suitable and relevant for such measures, such as the habitat requirements of the Sumatran rhino, hardly exist, as demonstrated by a comprehensive literature review of the last 20 years (Rookmaaker, 2014, see Appendix A).

This study reports and analyses an extensive data set from the yearly and monthly rhino surveys (SOS Rhino and BORA between 2000–2013, unpublished survey reports) in the Tabin Wildlife Reserve (TWR) in Sabah, Malaysia. We use a use-versus-availability approach (Boyce et al., 2002; Johnson et al., 2006) in order to assess resource selection of the population in this reserve. With the help of high-resolution remote sensing data, several environmental predictors were derived which indicate vegetation density at different scales. Additionally, we conducted a literature search to identify the main factors responsible for the decline of the Borneo rhino since 1874. We combine all information in a novel way with a PVA analysis to assess the probability of extinction for a hypothetical rhino population in Sabah in the 20th century, as well as for a locally restricted population in the TWR.

2. Methods

2.1. Study area

The Tabin Wildlife Reserve (TWR), at 5° 15′–5° 10′N, 118°30′–118°45′E, is a medium-sized (1205 km^2) protected area in the eastern part of the Malaysian State of Sabah (Fig. 1(A)). It consists mainly of lowland forest (*Dipterocarpus sp.*) and is surrounded by palm oil (*Elaeis guineensis*) plantations (Dawson, 1993). More than 80% of the reserve has been selectively logged between 1960 and 1984 (Sabah Government, 2014). Only the so-called "core area" in the centre and several virgin jungle reserves remain unlogged. Logging activities outside the reserve continued until 1989 (Sabah Government, 2014). The TWR holds several natural mineral sources, including four mud volcanoes and small patches of grassland which developed mainly as a consequence of logging between 1960 and 1984. It has tropical climate with temperatures ranging between 22° C and 32° C (Dawson, 1993). The annual rainfall amounts up to 3000 mm; the wettest period is between October and March (WWF-Malaysia, 1986, cited in Dawson, 1993). The topography of the area is characterised by steep hills and deep valleys which covers an altitudinal range from sea level to about 500 m. Tabin is well drained by a number of seasonal and perennial streams which originate in the hills and form the five major rivers of the area (Dawson, 1993).

2.2. Data collection

Data on rhino occurrence in the TWR were gathered from unpublished reports kindly provided by SOS Rhino and the Borneo Rhino Alliance, and by conducting a systematic camera trap study at the end of the study period. Both organisations conducted regular surveys on foot between October 2000 and February 2013. The surveys were mainly concentrated in the western and central area of the TWR (Fig. 1(B)) and lasted on average up to 8 days (Table A1). Rhino presence was either detected by direct sightings or more frequently by indirect signs such as footprints, scratch-marks, feeding-marks, faeces and wallows. Indirect signs such as wallows were often created by other animals and were therefore only used in combination with footprints in order to avoid false-positive detection. Individual animals could not be identified with this method. The location of rhinos as well as the position of human footprints, cartridge cases or tree logs, used to identify trespassers and disturbance, was measured with a portable Geographical Positioning System (GPS). In case of low GPS coverage, which occurred more frequently between 2000 and 2005, the location of rhino presence indicators was either estimated from a nearby area with better GPS coverage, such as rivers, clearings or hills, or estimated with the help of a topographic map. The estimated error of non-GPS locations averaged approximately 250 m.

During the surveys, GPS locations of the survey route were collected sporadically between October 2000 and July 2010 and systematically between June 2012 and February 2013 at intervals of 100 m, as part of an intensive survey accompanying the camera trap study (see below).

Between 2003 and 2005, the time and the position when and where the survey started, ended or interrupted was noted. This enabled us to sum up the time spent walking and the distance walked per survey (Table A1). For the years 2000 until 2002, information on survey length and duration was lacking, for the years from 2006 until 2008 this information

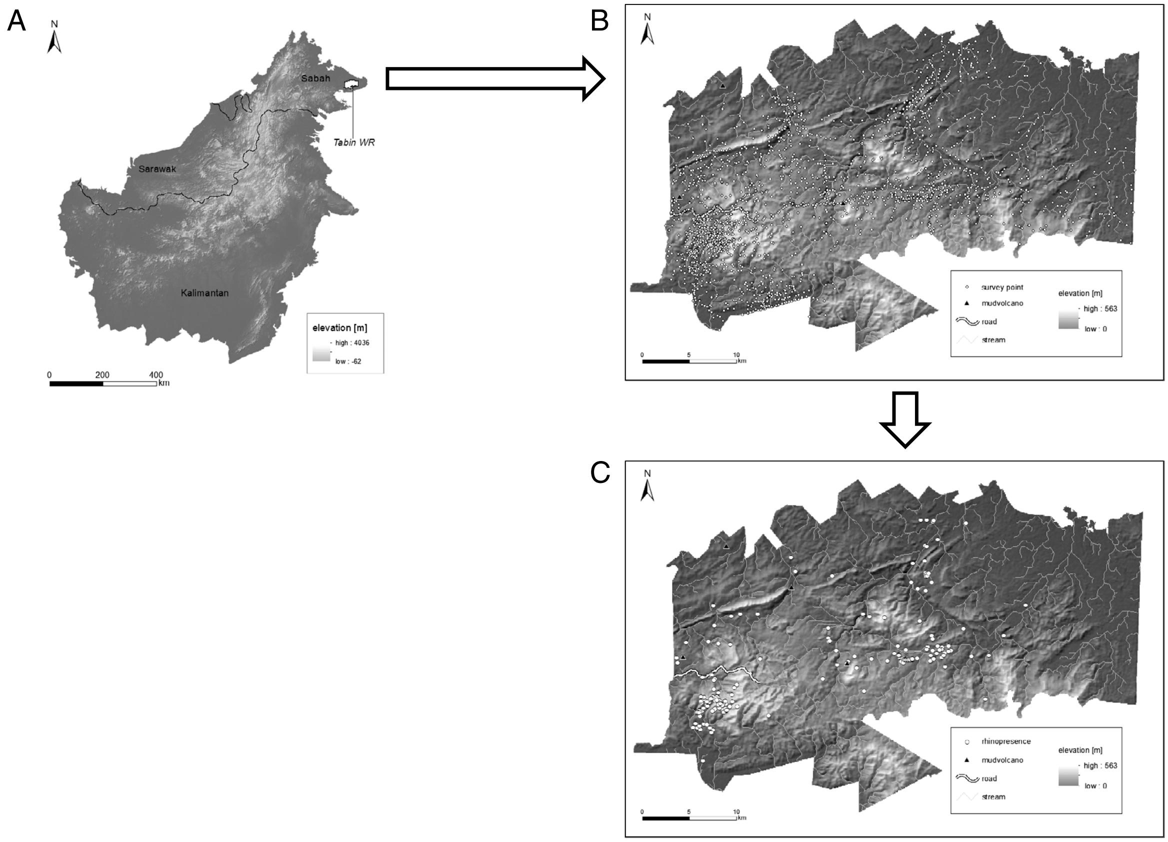

Fig. 1. Study site in the north east of Sabah on the island of Borneo (A), distribution of survey routes in the study site between 2000 and 2013 (B) and locations of rhinos indicated by footprints in combination with scratch-marks, feeding-marks, faeces and wallows (C).

was fragmentary. In the latter cases the duration of a survey was estimated using either the kilometres walked within a day or the duration of the following days as a reference. The distance walked per day was calculated as the shortest distance between the last coordinate of the day, the starting point and the consecutive coordinates. Additionally, the search intensity was estimated using the walking speed and the direction of a survey as a reference. The year of the survey, its duration, searching intensity and distance walked were used to estimate search effort within the statistical analysis.

Between June 2012 and November 2013, we conducted a camera trap survey in areas with known rhino presence in previous years (Figure A1). The survey was carried out in the central and northern part of the TWR and ranged over an area of 301 km^2. A total of 57 camera trap stations were placed along a square grid of 6 km^2. The grid size was chosen according to the minimum home range size of Sumatran rhinos of 10 km^2 (Strien, 1986). Cameras were spaced at an average of 2.4 km at locations preferred by rhinos, such as game trails, mud wallows or hill crest. This set up enabled us to sample all rhinos possibly ranging in the survey area. Two remotely triggered infrared cameras (Reconyx PC 800 Hyperfire Professional IR, Reconyx. Inc, Wisconsin, USA) were placed at each camera trap station. The cameras set to operate for 24 h each day. Stations were checked every two to three months and the number of days each camera trap station was functional over the total survey period was recorded.

2.3. Environmental predictors

We used seven high resolution satellite maps (RapidEye, BlackBridge, Berlin, Germany) covering the whole TWR to derive fine-scale land cover maps. The satellite maps were provided in L3A-format with a spatial resolution of 5 m. We applied radiometric corrections established for multi-temporal and multi-sensor data applications (Chavez, 1996; Chander et al., 2009) to reduce scene-to-scene variability. The image-based atmospheric corrections included 'dark object subtractions' and exo-atmospheric reflectance conversions (TOA).

We defined six land cover categories of biological relevance to the rhinos: dense forest, open forest, grassland, plantations, bare land and streams and performed a remote-sensing multispectral classification using ERDAS Imagine (Intergraph Corporation, Madison, USA) and ArcMap 10 (ESRI Inc., Redlands, USA). Clouds and cloud shadows were eliminated (Langner et al., 2012). The classifications were ground truthed with data for grassland, plantations and dense forest.

Table 1
Predictors used for assessing habitat use of the rhino population in the TWR.

Variable	Abbreviation	Type
Rhino presence (yes/no)	rhpr	Categorical
Year (year)	year	Continuous
Sampling effort		
Time spend walking (min)	dur	Continuous
Distance walked (km)	dist	Continuous
Search intensity (high/low)	surv	Categorical
Human disturbance variables		
Trespasser (yes/no)	hum	Categorical
Distance to logging road (m)	d_road	Continuous
Human population density in a square of 30″ (arc seconds)	hpd	Continuous
Topographic variables		
Elevation (m)	dgm	Continuous
Slope (%)	sl	Continuous
Land cover variables		
Dense forest[a]	f_dfo_x	Continuous
Open forest[a]	f_ofo_x	Continuous
Grassland[a]	f_gr_x	Continuous
Oil palm plantations[a]	f_pl_x	Continuous
Barren land[a]	f_bl_x	Continuous
Classify (1–5)	clas	Categorical
Food, shelter		
Distance to streams (m)	d_st	Continuous
Soil type (12, 13, 23, 32)	sp	Categorical
Distance to mudvolcano (m)	d_mvo	Continuous
Mud wallow (yes/no)	wal	Categorical

[a] = 100 m^2; 250 m^2; 500 m^2; 1000 m^2.

We deployed a focal or so-called neighbourhood analysis to include land cover connectivity in the surroundings of a rhino location (ArcGis 10, ESRI Inc., Redlands, USA). This analysis was employed for five land cover categories excluding streams and encompassed the area sizes of 100 m^2, 250 m^2, 500 m^2 and 1000 m^2 of potential relevance for daily movement distances of rhinos whilst foraging. Additional environmental variables of potential biological relevance for habitat use of the rhinos such as climatic, topographical variables or predictors indicating human impact were included in the analysis (Table 1, A2 and Table A4). Distances were calculated from each rhino location as well as for survey and systematic locations (see below) to the nearest border of these features.

2.4. Statistical analysis

We employed a use-versus-availability approach based on resource selection functions (RSF) (Boyce et al., 2002; Johnson et al., 2006) in a binomial generalised linear modelling (GLM) framework. Environmental covariates at the location where the rhino was present (use) were contrasted with covariates at locations taken from an area deemed to be available for selection (available). The size and spatial extent of the available sample was defined by the border of the TWR. In order to avoid multi-collinearity, only environmental variables were included in the analysis which were not highly correlated (Spearman rank $p < 0.75$; Table A2) and only one size scale of neighbourhood variables were included in each model. Two sets of availability locations were included in the analysis: (1) evenly distributed data points across the study site with a distance of 1 km to each other ("systematic"); (2) GPS locations collected during surveys ("survey") where rhinos were assumed to be present but no presence sign was detected. The inclusion of survey locations enabled us to incorporate variables indicating survey effort in the statistical analysis, such as year of the survey, its duration, searching intensity and distance walked. Spatial autocorrelation was addressed by using spatial filtering to reduce the number of occurrence and survey records in oversampled regions (Dormann et al., 2007; Veloz, 2009). We filtered all locations within a year by selecting only data points with more than 1 km distance to each other. This resulted in a data set of 109 rhino locations (use), 814 "systematic" (availability) and 1068 "survey" (availability) locations. We designed two sets of candidate models (defined by the two availability data sets) for Borneo rhino occurrence guided by three general hypotheses: (1) Human disturbance is the only driver for Borneo rhino presence or absence. (2) Habitat use is linked to food availability, access to safe areas and access to other ecological resources. (3) Human disturbance, food availability, access to safe areas and access to other ecological resources are all important in terms of habitat use of rhinos. A null model containing only the intercept was also included in the candidate set for comparison as well as models only containing the variables indicating survey effort. A set of 23 candidate models was designed for the systematic data and a set of 37 candidate models for the survey data (Table 2). In order to avoid linearity assumptions, we preliminarily explored the shape of the response for each predictor variable before fitting them to the final equations (Austin, 2002). To this end, we built binomial Generalised Additive Models (GAMs, R package 'mgcv', Wood, 2011) using rhino locations (use) versus systematic or survey points (availability), respectively, and

Table 2
Summary of models used to establish habitat use of Borneo rhinos employing two different sampling sets: rhino presence versus random/survey points. The models are organised in groups corresponding to different hypothesis of landscape factors potentially affecting habitat use of the species.

No	Rhino locations versus random points	No	rhino locations versus survey points
0	Null model	0	Null model
Human disturbance		**Controlling variables**	
1a	d_road+hpd+f_pl_x+f_dfo_x+f_gr_x	1a	year
1b	d_road+hpd+f_pl_x+f_gr_x	1b	year+dur+dist+surv
1c	hpd+f_pl_x+f_dfo_x +f_gr_x	1c	year+dist
1d	d_road+hpd+f_pl_x +f_gr_x+f_bl_x	1d	surv
1e	f_pl_x +f_gr_x+f_bl_x	1e	dist+surv
Food, terrain and other ecological resources		1f	dur
2a	d_st+d_mvo+f_dfo_x+f_gr_x+dgm+sl+sp	1g	dur+surv
2b	d_st+d_mvo+f_dfo_x+f_gr_x+dgm +sp	**Human disturbance**	
2c	f_gr_x+f_ofo_x+d_st+f_dfo_x+dgm+sl+sp	2a	year+dur+surv+d_road+hpd+f_pl_x+hum+f_gr_x+f_bl_x
2d	f_gr_x+f_ofo_x+d_st+f_dfo_x+dgm+sl	2b	year+dur+surv+d_road+hpd+f_pl_x+hum+f_gr_x
2e	f_gr_x+f_ofo_x+d_st+f_dfo_x+dgm	2c	year+dur+surv+hpd+f_pl_x+hum+f_gr_x
2f	f_dfo_x+dgm	2d	year+dur+dist+surv+hpd+hum
2g	f_dfo_x+dgm+sl	2e	year+dur+dist+surv+hum+f_gr_x
2h	f_dfo_x+dgm+sl+d_mvo	2f	dur+dist+surv+d_road+hpd+f_pl_x+hum+f_gr_x
2i	f_dfo_x+dgm+d_mvo	2g	dur+surv+d_road+hpd+f_pl_x+hum+f_gr_x
2j	f_dfo_x+dgm+d_mvo +f_gr_x	2h	dur+dist+surv+hpd+f_pl_x+hum+f_gr_x
2k	f_ofo_x+d_st+clas	2i	dur+surv+hpd+f_pl_x+hum+f_gr_x
2l	f_dfo_x+d_mvo	2j	dur+dist+surv+hpd+hum
2m	f_dfo_x+d_mvo+sp	2k	dur+surv+hpd+hum
2n	clas	**Food availability, access to safe areas and other ecological resources**	
Human disturbance, food availability, access to safe areas and other ecological resources		3a	year+dur+surv+d_st+wal+d_mvo+f_dfo_x+f_gr_x+dgm+sl+so
3a	d_road+hpd+f_pl_x+f_gr_x+f_dfo_x+d_st+d_mvo+dgm +sl+sp	3b	year+dur+surv+d_st+wal+d_mvo+f_dfo_x+f_gr_x+dgm+sl+sp
3b	hpd+f_pl_x+f_gr_x+f_dfo_x+d_st+d_mvo+dgm+sl	3c	year+dur+surv+d_st+wal+d_mvo+f_dfo_x+f_gr_x+dgm+sp
3c	hpd+f_gr_x+f_dfo_x+d_st+d_mvo+dgm+sl	3d	year+dur+surv+d_st+wal+d_mvo+f_dfo_x+f_gr_x+dgm
		3e	year+dur+surv+wal+d_mvo+dgm
		3f	year+dur+dist+surv+d_st+f_gr_x+f_ofo_x+f_dfo_x+dgm+sl+sp
		3g	year+dur+dist+surv+f_dfo_x+dgm+sl
		3h	year+dur+dist+surv+f_ofo_x+d_st+clas
		3i	year+dur+dist+surv+f_dfo_x+d_mvo
		3j	year+dur+dist+surv+f_dfo_x+d_mvo+sp
		3k	dur+surv+d_st+wal+d_mvo+f_dfo_x+f_gr_x+dgm+sl+sp
		3l	dist+dur+surv+d_st+wal+d_mvo+f_dfo_x+f_gr_x+dgm+sl+sp
		3m	dur+surv+wal+d_mvo+dgm
		3n	dist+dur+surv+wal+d_mvo+dgm
		Human disturbance, food availability, access to safe areas and other ecological resources	
		4a	year+dur+surv+hpd+hum+f_pl_x+f_gr_x+d_st+wal+d_mvo +f_dfo_x +dgm+sl
		4b	year+dur+surv+hpd+hum+f_gr_x+d_st+wal+d_mvo+f_dfo_x +dgm+sl+sp
		4c	year+dur+surv+hpd+hum+d_road+f_gr_x+d_st+wal+d_mvo +f_dfo_x+dgm+sp
		4d	year+dur+surv+hpd+hum+f_gr_x+d_st+wal+d_mvo+f_dfo_x +dgm

fitted smoothing splines with 3 degrees of freedom on the full model. Then, linearity was assessed by visual inspection of the partial residual plots and where appropriate, logarithmic or quadratic transformations of predictor variables were applied (Crawley, 2007). GLMs were then fitted and models were compared and hierarchically ordered using Akaike's Information Criterion (AICc) corrected for small sample size. We repeated model fitting using a randomisation method by selecting 100 rhino locations and an equal amount as well as a fourfold amount of systematic or survey points with replacement from the rhino locations and systematic or survey points, respectively. The size of the availability sample was carefully chosen to avoid a bias in our estimates (Northrup et al., 2013). This routine was iterated 1000 times. Each time, we fitted the set of candidate models, calculated the AICc and recorded the model with the lowest AICc value. The probability of model selection was estimated counting the number of randomisations in which each candidate model was scored as best. To then test the contribution of each variable within the selected model, we fitted the best model with the highest score probability to the respective data set and selected final models within $<2\Delta$AICc (package 'MuMIn'), i.e. the difference to the AICc of the best ranked model, as all of them should be considered competitive for interpretation (Burnham and Anderson, 2002). We then used model averaging to derive final coefficient values. All statistical analyses were performed using the R statistical software R 3.1.1 (R Development Core Team, 2014).

2.5. Literature search

We reviewed the literature on Sumatran rhinos (Rookmaaker, 2014) from 1874 onwards focusing on information about the number and distribution of rhinos on Borneo. Particular interest was paid to the year of the census, the quality of the data and the information provided about hunting of wildlife by local people or Europeans in the area. Additionally, the literature on surveys conducted in the TWR was reviewed and the estimated rhino numbers as well as the number of survey days, kilometres walked and methods analysed.

2.6. Population viability analysis

We used the stochastic population model VORTEX (Version 10, Lacy and Pollak, 2014) to identify possible factors responsible for the decline of the Borneo rhino in Sabah, Malaysia. We analysed two different scenarios, firstly a hypothetical rhino population in the 20th century with a yearly hunting quota of 120 animals between 1930 and 1950 (scenario (a)) and secondly, a population known to exist in the TWR (scenario (b)). Since population data on free-ranging Borneo rhinos do not exist, the model is based on information available from the Sumatran subspecies combined with data on other rhino species (Appendix B). Based on this information, we defined a standard set of parameters for both scenarios (Table 3) and modified individual parameters thereon. Population size (ps) and carrying capacity (cc) of scenario (a) were estimated based on a natural distribution of 10 rhinos per 100 km^2 (Strien, 1986) assuming a theoretical utilisation of 25% (ps) and 50% (cc) of the total land area of Sabah of 74,398 km^2 (Encyclopaedia of the Nations, 2015). This resulted in an initial population size of 3720 rhinos and a carrying capacity of 5580 rhinos. Yearly hunting was set to 60 adult males and 60 adult females between 1930 and 1950, using information from historical reports (see 3.2). For scenario (b) an initial population size of 15 individuals was chosen based on surveys conducted in TWR between 1980 and 1989 (Table A3). The carrying capacity was calculated on the basis of the size of TWR (1205 km^2) as described above. Three different models were calculated with different levels of harvesting to investigate the impact of hunting on the population: for scenario (b1) no harvesting was included in the model; for scenario (b2) a single harvesting event was included, which reflects the real situation where an adult male and an adult female were captured for breeding purposes; for scenario (b3) an adult male and an adult female were harvested every ten years. Results were predicted over 115 years (scenario (a)) and 35 years (scenario (b)) respectively. Output of the PVA included mean stochastic growth rate ($\pm$ SD), probability of population extinction (% $\pm$ SD), mean time to extinction ($\pm$ SD), mean population size ($\pm$ SD) and decline in genetic variability expressed as the expected genetic diversity (Gatti et al., 2011).

2.7. Sensitivity analysis

To evaluate the sensitivity of the simulation results to variation in specific parameters, we calculated a sensitivity index (S_y) as following:

$$S_y = (\Delta y/y)/(\Delta x/x)$$

where $\Delta y/y$ is the observed relative change in the predicted variable y resulting from the relative change $\Delta x/x$ in the predictor parameter x (Pulliam et al., 1992). We examined model sensitivity to variations in population size, lifetime reproductive period, length of harvesting period, number of males/females harvested, percentage of female breeding, carrying capacity, juvenile mortality (female/male), adult mortality (female/male) and percentage of mate monopolisation. Variation of predictor variables were limited to a moderate $\pm$ 10%.

3. Results

3.1. Resource selection

Comparing rhino locations ($n = 100$) with survey data ($n = 400$, 1000 repetitions) revealed that rhino presence in the TWR was best described by the four candidate models 4c, 4a, 4b and 3n -, in decreasing order of importance (Table 2). The best model with a selection probability of 34% (4c) and the two adjacent models (4a, 4b) are consistent with the hypothesis that human disturbance, food availability, access to safe areas and access to other ecological resources predict habitat use. Fitting the candidate models to the data set resulted in 3 best models with a ΔAICc < 2, each consisting of ten and eleven predictor variables respectively (Table 4). Model averaging revealed that the search effort variables 'year', 'duration of survey' and 'low search intensity' were all negatively correlated with rhino presence (Table 5). Rhino presence was thus highest in the first years of the study period (from 2000 onwards), during short surveys and when search intensity was high. The environmental predictors indicated that rhinos preferred elevated areas in the TWR with a low presence of human trespassers and a wallow on site, away from roads and in close distance to mud-volcanoes. Within a neighbourhood of 1000 m^2, rhinos prefer a high proportion of dense forest and grassland and favour fine textured thionic Fluvisols category 13, and orthic Acrisols category 23 and 32 (Table 5, Table A4). The environmental predictor 'distance to streams' was not included in the model anymore while the predictor variable 'distance to mudvolcanoes' was only present in two of the three models.

Table 3
Life history parameters used for population viability analysis of the historic rhino population scenario (a) and the rhino population living in the TWR scenario (b).

Parameter	Baseline values
Number of populations	1
Number of iterations	1000
Number of years **scenario a/scenario b**	115/35
Duration of each year (days)	365
Extinction definition	1 sex remains
Inbreeding depression[a]	6.29
Percent due to recessive lethal alleles (%)	50
Polygynous	yes
Age of first offspring female/male (years)	6/7
Maximum lifespan (years)	30
Maximum lifetime reproductive period of females/males (years)	20/25
Maximum number of broods/progeny per year	1/1
Sex ratio of males at birth (%)	50
Density dependent reproduction	none
Breeding females (%)	25
SD of breeding females due to environment variation (%)	0
Distribution of broods per year: 0/1 broods (%)	0/100
Mortality of females/males from	
age 0–1 years (%) **scenario a/scenario b**	20/20
age 1–2 years (%) **scenario a/scenario b**	5/5
age 2–3 years (%) **scenario a/scenario b**	5/10
age 3–4 years (%) **scenario a/scenario b**	5/10
age 4–5 years (%) **scenario a/scenario b**	5/5
age 5–6 years (%) **scenario a/scenario b**	4/10
age 6–7 years (%) **scenario a/scenario b**	4/10
>7 years (%) **scenario a/scenario b**	–/5
Catastrophes	none
Males in breeding pool (%)	80
Initial population size **scenario a/scenario b**	3720/15
Age distribution	stable age dist.
Carrying capacity (K) **scenario a/scenario b**	5580/120
SD (K)	0
Population harvested?	yes
First year of harvest **scenario a/scenario b1/b2** (year)	30/32/0
Last year of harvest **scenario a/scenario b1/b2** (year)	50/33/35
Interval between harvests **scenario a/scenario b** (year)	1/30
Optional criteria for harvest **scenario a/scenario b**	1/1
Optional criteria for individuals	1/1
Number of adult females (6 + years) harvested **scenario a/scenario b**	60/1
Number of adult males (6 + years) harvested **scenario a/scenario b**	60/1
Supplementation	none

[a] Mean effect of inbreeding on fecundity and first year survival (O'Grady et al., 2006).

Table 4
Summary of the best models for predicting habitat use of the Borneo rhino using the survey data to describe availability: 100 presence points were compared with 400 survey points, running 1000 repetitions.

	Int	sp	hum	surv	wal	d_mvo	d_st	d_road	f_dfo_1000	f_gr_1000	dur	dgm	year	df	logLik	AICc	delta	weight
Model 1	1342	+	+	+	+			+	+	+	+	+	+	13	−70.279	167.8	0	0.419
Model 2	1266	+	+	+	+	+		+	+	+	+	+	+	14	−69.224	167.8	0.08	0.403
Model 3	1326	+	+	+	+		+	+	+	+	+	+	+	14	−70.046	169.5	1.72	0.177

A comparison of rhino locations ($n = 100$) with systematic data ($n = 400$, 1000 repetitions) indicate that rhino presence in the TWR was best described by model 2c (Table 2) predicting that habitat use of Sabah rhinos was linked to food availability, access to safe areas and access to other ecological resources (model selection probability 48%). The second best model, with a selection probability of 35%, presumed that human disturbance, food availability, terrain and access to other ecological resources are equally important (3a, Table 2). Fitting the best candidate model (2c) to the data set resulted in 11 best models with a ΔAICc < 2 (Table 6). Model averaging resulted in three predictor variables which were consistently present in all models (soiltypes, focal grassland 100 m^2 and elevation) while the remaining variables were only represented in four models (Table 7). Habitat suitability for rhinos increased with increasing elevation and declined with increasing distance to streams and increasing gradient. Within an area of 100 m^2, rhinos preferred more densely forested areas and avoided areas with a high proportion of grassland and open forest. Locations with fine textured Thionic Fluvisols were more frequently used then areas of a soil category 23 and 32, in decreasing order of importance (Table 7).

Table 5
Results of the model averaging analysis using the survey data to describe absence of rhinos: 100 rhino presence points were compared with 400 survey (rhino absence) points running 1000 repetitions.

Abbreviation	Variable description	Averaged model coefficients	2.50%	97.50%	Present in model
Intercept		1305	802	1807	1, 2, 3
year	Year	−0.66	−0.91	−0.41	1, 2, 3
dur	Duration (min)	−0.0008	−0.0012	−0.0004	1, 2, 3
surv (low)	Search intensity low	−1.67	−3.38	0.05	1, 2, 3
sp (13)	Soil category 13	5.84	2.41	9.26	1, 2, 3
sp (23)	Soil category 23	7.26	4.09	10.44	1, 2, 3
sp (32)	Soil category 32	3.18	0.42	5.95	1, 2, 3
f_gr_1000	Focal grassland 1000 m^2	12.60	1.96	23.20	1, 2, 3
f_dfo_1000	Focal dense forest 1000 m^2	10.22	4.45	15.99	1, 2, 3
hum (yes)	Human trespassers	−18.84	−1952	1915	1, 2, 3
wal (yes)	Presence of wallow	3.85	1.74	5.96	1, 2, 3
d_road	Distance road (m)	0.0001	0.00004	0.0002	1, 2, 3
dgm	Elevation (m)	0.02	0.01	0.02	1, 2, 3
d_mvo	Distance mudvolcano (m)	−0.0001	−0.0003	0.00005	2

Table 6
Summary of the best models for predicting habitat use of the Borneo rhino using the systematic data to describe availability: 100 presence points were compared with 400 random points, running 1000 repetitions.

	Int	sp	d_st	f_dfo_100	f_gr_100	f_ofo_100	sl	dgm	df	logLik	AICc	delta AICc	weight
Model 1	−2.898	+			+			+	6	−169.992	352.2	0.00	0.141
Model 2	−2.654	+			+	+		+	7	−168.997	352.3	0.08	0.136
Model 3	−3.569	+		+	+			+	7	−169.088	352.5	0.26	0.124
Model 4	−2.858	+	+		+			+	7	−169.187	352.7	0.46	0.112
Model 5	−2.642	+	+		+	+		+	8	−168.401	353.2	0.97	0.087
Model 6	−3.459	+	+	+	+			+	8	−168.508	353.4	1.19	0.078
Model 7	−2.512	+			+	+	+	+	8	−168.603	353.6	1.38	0.071
Model 8	−2.763	+			+		+	+	7	−169.671	353.6	1.43	0.069
Model 9	−3.481	+		+	+		+	+	8	−168.646	353.7	1.46	0.068
Model 10	−2.711	+	+		+		+	+	8	−168.810	354.0	1.79	0.058
Model 11	−3.099	+		+	+	+		+	8	−168.822	354.0	1.82	0.057

Table 7
Results of the model averaging analysis using the systematic data to describe absence of rhinos: 100 rhino presence points were compared with 400 random (rhino absence) points running 1000 repetitions.

Abbreviation	Variable description	Averaged model coefficients	2.50%	97.50%	Present in model
Intercept		−2.96	−4.76	−1.16	
sp (13)	Thionic Fluvisols fine textured[a]	2.77	0.69	4.85	1–10
sp (23)	Orthic Acrisols medium to fine textured with Ferric Acrisols[a]	1.83	0.20	3.45	1–10
sp (32)	Orthic Acrisols medium to fine textured with Humic Acrisols[a]	0.78	−0.75	2.30	1–10
f_gr_100	Focal grassland 100 m^2	−5995	−570 700	558 709	1–10
f_ofo_100	Open forest 100 m^2	−1.15	−2.82	0.52	2, 5, 7, 10
f_dfo_100	Dense forest 100 m^2	0.91	−0.47	2.29	3, 6, 9, 11
d_st	Distance stream (m)	−0.001	−0.00169	0.0004	4, 5, 6, 10
dgm	Elevation (m)	0.01	0.003	0.01	1–10
sl	Slope (%)	−0.03	−0.08	0.03	7–10

[a] For more details see Table A4.

3.2. Historical distribution of Sumatran rhinos on Borneo

There is a wide range of historical information on Borneo rhinos from early explorers visiting the island as well as from residents and local inhabitants. However estimates about the abundance and distribution of rhinos on Borneo are vague. They reported that rhinos were common in Sabah and in Kalimantan (Indonesia) and less abundant in Sarawak (Malaysia) (Bartlett, 1891, Table 8). The reports are either based on hearsay or on estimates resulting from field trips in a restricted area. The rapid decrease of rhino numbers was most likely induced by the pacification of indigenous people in the interior of the island of Borneo by the respective governments at the beginning of the 20th century. Trade started between the interior and the coast and Chinese traders at the coast sourced rhino horn and rhino nails as aphrodisiacs and for medicinal purposes (Harrisson, 1946, Appendix C). From 1930 onwards firearms became numerous and cheap. With such arms, the indigenous people in the interior of Borneo began a wholesale slaughter of rhinos (Banks, 1937; Harrisson, 1946). On the basis of the reports by Harrisson (1956) it can be estimated that a minimum of 100 animals were killed per year between 1925 and 1931 in Sarawak alone (Appendix C). There are no data on the number of rhinos hunted in Sabah before 1961, but reports suggest

Table 8
Historic and recent estimates of the number and distribution of the Sumatran rhino in Borneo.

Source	Census year	Sabah	Sarawak	Kalimantan	Quality of data	Hunting evidence
Wallace (1874)	/	not abundant	not abundant	not abundant	guesstimate	rhino horn sold frequently in Kalimantan
Pryer (1881)	1881	frequent	/	/	estimate	/
Bock (1881)	/	/	/	exists	guesstimate	natives ask high price for rhino horn
Anonymous (1890)	1883–1888	frequent	/	/	guesstimate	frequently shot by natives
Bartlett (1891)	/	numerous	rare	common	guesstimate	/
Jentink (1897)	/	/	/	common	estimate	/
Shelford (1916)	/	common	/	/	estimate	high price for rhino horn
Ridley (1916)	/	common	/	/	estimate	/
Mjoeberg (1929)	1925	less common	common	/	estimate	numerous rhinos are killed every year
Banks (1931)	/	/	becoming scarce	/	estimate	36 trophies in Beluga, Sarawak in 2 years
Banks (1935)	1934/35	/	decreased	/	estimate	/
Heynsius Viruly and Heurn (1935)	/	/	/	scarce and decreasing	guesstimate	/
Banks (1937)	/	/	a few individuals	/	estimate	price for rhino between \$300–\$400
Comyn-Platt (1937)	/	/	/	few	guesstimate	Chinese will pay any price for the horn
Schneeberger (1945)	/	/	/	fairly large numbers	estimate	rhinos frequently hunted by Iban Dayaks
Harrisson (1946)	1945/1946	5	none	2	Sarawak: loc. Surv; Kalimantan, Sabah: estimate	16 rhinos killed by a native
Harrisson (1948)	1945/46	considerable number	none—few	some	estimate	/
Banks (1949)	/	/	scattered individuals	/	guesstimate	native hunters have driven rhinos into remote areas
Harrisson (1949)	1946/46	many	none	some	estimate	many hundred rhinos killed in Sarawak during this century
Harrisson (1955)	/	some	2–3	handful	guesstimate	/
Harrisson (1956)	1956	very few	2	a few	localised surveys	/
Harrisson (1961)	/	∼10	/	/	guesstimate	/
Burgess (1961)	1985	20–30	/	/	guesstimate	evidence of rhino poaching in Sabah
Bruton (1963)	/	20–30	/	/	status report	/
Harrisson (1965)	1961–1965	11–13	/	10 (5)	guesstimate	sea smuggling to Singapore stopped
Anderson (1968)	/	/	virtually extinct	/	status report	/
Silva (1968)	/	nearly extinct	/	/	guestimate	/
Carson (1968)	/	extinct soon	/	/	status report	/
MacKinnon (1970)	1969/1970	<100	/	/	estimate	hunters get 2000 M\$ out of a rhino.

(continued on next page)

Table 8 (*continued*)

Source	Census year	Sabah	Sarawak	Kalimantan	Quality of data	Hunting evidence
Strien (1974)	/	few	extinct?	few	estimate	/
Harrisson (1975)	/	10–20	none	1–2	guestimate	/
Rookmaaker (1977)		10–20	0–3	5	estimate	/
Zon (1977)	1976	/	2	/	estimate	/
Strien (1979)	1979	/	/	on verge of extinction	localised survey	/
Davies and Payne (1982)	1979–1981	15–30	/	/	survey	5+ rhinos have been killed during last 5 years
Flynn (1981)	1980	S: 8–10+	/	/	localised survey	2 rhinos poached in Silabukan since 1975.
Strien (1981)	1980 / 81	/	/	probably extinct	survey	/
Andau and Payne (1982)	1982	S: 5–10	/	/	localised survey	1 young rhino trapped 1981 in Silabukan
Payne (1986)	/	rhinos in central Sabah	/	/	status report	/
Andau (1987)	1982	T: 7	/	/	localised survey	2 rhinos poached between 1981 and 1984.
Andau (1987)	1986	T: 6, M./B: 3, few isolated rhinos			survey	
Nor et al. (1989)	1988	T: 3	/	/	localised survey	/
Khan (1989)	/	>38 (T: 20+, K: 8, DV: 10)	5–15	perhaps near border to Sabah	status report	/
Payne (1990)	1989	T: 15–20+, non-viable populations in other regions	/	/	survey	illegal hunting still occurs
Boonratana (1997)		11–33	/	/	survey	/
Martin (1989)	1988	30–100	very few	/	survey in horn trade	Sabah: A minimum of 10 pairs of horn are annually exported. Sarawak: no hunting since 1960
Rabinowitz (1992)	1992	DV: 13–23	/	/	localised survey	hunting evidence in the area
Khan (1993)		40–60	/	/	status report	/
Tajuddin Abdullah et al. (1995)	1995	DV: no fresh tracks found	/	/	localised survey	hunting activity in the area
Meijaard (1996)	1994	/	/	20 sightings since 1985	survey	/
Khan et al. (1999)	/	50–70	/	/	status report	/
Strien (2002)	/	~50	/	/	status report	/
Our camera trap study	2012/2013	T: 0	/	/	localised survey	/

Guesstimate = based on little evidence, estimate = based on a field trip without systematic survey, localised survey = systematic survey in a certain area, survey = systematic survey in several parts of the state, status report = information gathered from unknown origin.
T = Tabin; DV = Danum Valley, S = Silabukan, M = Malua, B = Bilong, K = Kretam.

Table 9
Stochastic growth rate and extinction risk of 23 population viability analysis scenarios for the historic rhino population in Sabah (means ± SD), using the computer program VORTEX. Growth rates are specified prior to carrying capacity truncation.

Number	Description	Growth rate	Probability of extinction (%)	Years until first extinction	Population size for extant populations	Genetic diversity (%)
1	Basic	−0.021 ± 0.047	0	50 ± 0	391 ± 186	98
2	Basic + 10% higher no. of males harvested	−0.022 ± 0.055	3 ± 2	64 ± 25	369 ± 191	98
3	Basic + 10% lower no. of males harvested	−0.018 ± 0.036	0	/±	508 ± 179	83
4	Basic + 10% higher no. of females harvested	−0.024 ± 0.06	0	/±	270 ± 139	98
5	Basic + 10% lower no. of females harvested	−0.018 ± 0.038	0	/±	511 ± 193	99
6	Basic + 10% higher reproductive age of females	−0.009 ± 0.026	0	/±	1415 ± 368	99
7	Basic + 10% lower reproductive age of females	−0.080 ± 0.16	89 ± 3	52 ± 12	41 ± 27	88
8	Basic + 10% higher duration of harvesting	−0.027 ± 0.068	7	54 ± 6	242 ± 135	97
9	Basic + 10% lower duration of harvesting	−0.017 ± 0.036	0	/±	541 ± 178	99
10	Basic + 10% higher percentage of breeding females	−0.005 ± 0.022	0	/±	2039 ± 415	100
11	Basic + 10% lower percentage of breeding females	−0.093 ± 0.179	98 ± 1	49 ± 6	12 ± 9	82
12	Basic + 10% higher mortality of juvenile females	−0.030 ± 0.072	8	65 ± 29	212 ± 141	97
13	Basic + 10% lower mortality of juvenile females	−0.016 ± 0.037	0	/±	618 ± 198	99
14	Basic + 10% higher mortality of juvenile males	−0.021 ± 0.047	0	/±	382 ± 186	98
15	Basic + 10% lower mortality of juvenile males	−0.021 ± 0.047	0.01	50 ± 0	395 ± 182	98
16	Basic + 10% higher mortality of adult females	−0.056 ± 0.125	49 ± 5	63 ± 24	60 ± 62	88
17	Basic + 10% lower mortality of adult females	−0.010 ± 0.026	0	/±	1251 ± 306	99
18	Basic + 10% higher mortality of adult males	−0.021 ± 0.048	1 ± 1	50 ± 0	375 ± 176	98
19	Basic + 10% lower mortality of adult males	−0.021 ± 0.047	1 ± 1	50 ± 0	384 ± 166	99
20	Basic + 10% higher perc. of males in breeding pool	−0.021 ± 0.05	1 ± 1	86 ± 0	411 ± 200	98
21	Basic + 10% lower perc. of males in breeding pool	−0.022 ± 0.05	1 ± 1	50 ± 0	369 ± 169	98
22	Basic + 10% higher initial population size	−0.018 ± 0.035	0	/±	580 ± 192	99
23	Basic + 10% lower initial population size	−0.031 ± 0.083	12 ± 3.2	62 ± 23	216 ± 160	96

that hunting pressure in Sabah was high (Comyn-Platt, 1937; Loch, 1937) and that after virtually exterminating rhinos in Sarawak, the indigenous people of Sarawak crossed the state borders to hunt rhinos in other states or countries of Borneo (Harrisson, 1946). In 1946, rhinos were still thought to exist at a considerable numbers in Sabah, mainly in the north east (Harrisson, 1949). Their numbers appeared to have dropped to very few in 1956 (Harrisson, 1956).

Following the first state wide faunal survey by Davies and Payne (1982), two isolated populations of 13–23 animals at a maximum each were rediscovered in the TWR and Danum Valley together with a few scattered individuals (Davies and Payne, 1982; Andau and Payne, 1982; Boonratana, 1997). Numerous surveys were carried out, especially in the Tabin Wildlife Reserve (Table A3). Resulting population estimates range from three to 20 individuals without an obvious trend in population development. Hunting of rhinos in Sabah continued until recent times, but at a much lower rate. Payne (1980) described four incidences of hunting between 1976 and 1980. The last evidence of rhino poaching was in the year 2001 (New Straits Times, Malaysia April 19, 2001) near the border to Sarawak. Since then no dead rhino has been reported but it cannot be assumed that this equated to zero hunting.

Our resource selection study reveals a clear trend in population development with high number of rhino sightings at the beginning of the study period in the year 2000 and low numbers at the end in 2013. Our camera trap study in the TWR between June 2012 and November 2013 confirms this result. A total of 781.9 km of surveys and a total of 10,316 trapping days (counting only functional camera traps) provided no evidence of Borneo rhino presence in TWR anymore.

Currently, the known population of Sumatran rhinos in Sabah consists of 3 animals in captivity. There is evidence of a few individuals in Kalimantan (WWF, 2013) and no evidence of Sumatran rhinos in Sarawak and Brunei.

3.3. PVA model results

Under scenario (a), the model predicted on average a negative population growth of $r = -0.021 \pm 0.047$ of the historical population of Sabah since the late 19th century with a mean population size of 391 ± 186 individuals after 115 years (Table 9, number 1). The probability of extinction of this population was zero and the mean time to first extinction 50 years. The sensitivity analysis revealed that the percentage of breeding females and the lifetime reproductive period of females – in decreasing order of importance – were the key factors in the population dynamics of Borneo rhinos (Table 10). A decrease in the percentage of breeding females and the lifetime reproductive period of females almost always led to an extinction of the population whereas an increase of both parameters had only little effect on population growth. This suggests a high sensitivity of the population to a reduction in female fertility or reproduction. In comparison to these biological parameters, anthropogenic parameters such as the duration of harvesting or the number of harvested males and females had a less pronounced influence on growth rate. When considering all analysed scenarios (Table 9), the chance of extinction of the

Table 10
Sensitivity indices for changes in parameters of ±10% in the model of the historical rhino population in Sabah.

Parameter	Relative influence on growth rate	
	Parameter +10%	Parameter −10%
Percentage of breeding females	6.35	29.00
Reproductive period of females	5.71	28.10
Total mortality of adult females	6.67	2.10
Total mortality of juvenile females	4.29	2.38
No. of males harvested	0.48	1.43
Duration of harvesting	2.86	1.90
No. of females harvested	1.43	1.43
Percentage of males in breeding pool	0.00	0.48
Total mortality of juvenile males	0.00	0.00
Total mortality of adult males	0.00	0.00
Initial population size	1.07	3.57

historical population was very low, but a decrease in the percentage of breeding females and in the lifetime reproductive period of females severely increased the risk of population extinction.

The model of the population in the TWR without hunting (scenario (b1)) predicted a mean population size of 10 ± 6 individuals after 35 years (Table 11, number 1). The probability of extinction was 20% and the mean time to first extinction 28 ± 6 years. The capture of a male and female for breeding purposes increased the probability of extinction of the population to 31% (Table 11, number 2). Hunting of additional adult males and females (scenario b3) further increased the probability of extinction to 47% and reduced the growth rate of the population to −0.033 ± 0.123. Similar to the historical population, the sensitivity analysis indicated that percentage of females breeding and lifetime reproductive period of females are the key factors in population dynamics (Table 12), independent of the level of hunting. Additional parameters influencing the population growth rate, but to a much lesser extent, were mortality of adult and juvenile females. The growth rate for such a population with a lower percentage of breeding females and a lower lifetime reproductive period of females combined with moderate hunting activity (scenario b3, Table 11, number 63), resulted in a very high probability of extinction of 75% ± 1% after 25 ±6 years. Management measures preventing poaching and aiming to increase the percentage of breeding females and lifetime reproductive period of females would result in a very low probability of extinction of 9% ± 1% and a population size slightly above the size of the initial population of 16 ± 9 (Table 11, number 58).

4. Discussion

We charted the historical development of the Sumatran rhino population in Borneo, and identified the main drivers responsible for its extinction in Sabah and the key demographic parameters which have the strongest influence on Borneo rhino population dynamics. Additionally we documented the resource selection functions of the population in the Tabin Wildlife Reserve and its preferred habitat features.

4.1. Resource selection and preferred habitat features

Our study on habitat use of the rhinos in the Tabin Wildlife Reserve revealed that human disturbance, food availability, access to safe areas and access to other ecological resources are the main factors influencing habitat selection of this population. Our hypotheses that habitat use is only linked to human disturbance or exclusively linked to food availability, terrain and access to other ecological resources were rejected.

A recent study on all remaining Sumatran rhino populations in Sumatra confirms our results, showing that habitat factors and human disturbance are important predictors for Sumatran rhinos, while preferences differed between the different sites (Pusparini et al., 2015).

Six environmental predictors influenced Borneo rhino habitat use in our study area: the soil type, the availability of grassland and dense forest patches within a vicinity of 1 km surrounding a rhino location, elevation, presence of wallows and distance to mud-volcanoes. The importance of the last four factors was already described by Strien (1974, 1986) from his studies in the early 1980s on the basis of opportunistic observations. Our study provides the first statistical quantification of this knowledge within a small scale or second order selection study (Johnson, 1980) on habitat use.

The strongest predictor of rhino presence in our analysis was the year of surveys. Rhino sightings were highest at the beginning of the study period in the year 2000 and lowest at the end of the study period in 2013. This result is being supported by the camera trap study conducted in the year 2012/2013 in the TWR which showed no evidence of rhinos. These results reveal that the rhino population has decreased continuously from 2000 onwards until it became locally extinct. The development of the TWR population therefore followed exactly the predictions of our PVA model for small isolated populations. A small population size combined with a low reproductive performance and an increased mortality rate lead to the extinction of the population in the TWR (see 4.2).

Table 11
Stochastic growth rate and extinction risk of 63 population viability analysis scenarios for the rhino population in the TWR (mean ± SD). Growth rates are specified prior to carrying capacity truncation.

Number	Description	Growth rate	Probability of extinction (%)	Years until first extinction	Population size for extant populations	Genetic diversity (%)
1	Basic b1 = no harvest	−0.021 ± 0.101	20 ± 1	28 ± 6	10 ± 6	80
2	Basic b2 = one time harvest of ♂ and ♀	−0.025 ± 0.109	31 ± 1	29 ± 5	10 ± 6	80
3	Basic b3 = harvesting of ♂ and ♀ every 10 years	−0.033 ± 0.123	47 ± 1	27 ± 5	9 ± 5	78
Impact of reproductive age of females						
4	Basic b1 + 10% higher rep. age of females	−0.013 ± 0.097	12 ± 1	28 ± 6	13 ± 7	82
5	Basic b2 + 10% higher rep. age of females	−0.020 ± 0.107	23 ± 1	30 ± 5	9 ± 7	81
6	Basic b3 + 10% higher rep. age of females	−0.027 ± 0.120	37 ± 2	27 ± 6	10 ± 6	79
7	Basic b1 + 10% lower rep. age of females	−0.028 ± 0.105	28 ± 1	29 ± 5	8 ± 5	78
8	Basic b2 + 10% lower rep. age of females	−0.033 ± 0.113	43 ± 2	29 ± 4	8 ± 5	78
9	Basic b3 + 10% lower rep. age of females	−0.039 ± 0.129	58 ± 2	26 ± 6	8 ± 5	78
Impact of percentage of breeding females						
10	Basic b1 + 10% higher perc. of breeding females	−0.011 ± 0.097	10 ± 1	28 ± 5	13 ± 8	82
11	Basic b2 + 10% higher perc. of breeding females	−0.017 ± 0.103	21 ± 1	30 ± 4	12 ± 7	82
12	Basic b3 + 10% higher perc. of breeding females	−0.026 ± 0.118	36 ± 2	27 ± 6	10 ± 7	80
13	Basic b1 + 10% lower perc. of breeding females	−0.030 ± 0.108	30 ± 1	28 ± 5	8 ± 5	78
14	Basic b2 + 10% lower perc. of breeding females	−0.033 ± 0.114	41 ± 5	30 ± 4	7 ± 5	77
15	Basic b3 + 10% lower perc. of breeding females	−0.041 ± 0.128	58 ± 2	26 ± 6	7 ± 4	76
Impact of mortality of juvenile females						
16	Basic b1 + 10% higher mort. of juv. females	−0.022 ± 0.102	19 ± 1	28 ± 6	10 ± 5	80
17	Basic b2 + 10% higher mort. of juv. females	−0.026 ± 0.110	23 ± 1	30 ± 5	11 ± 7	79
18	Basic b3 + 10% higher mort. of juv. females	−0.038 ± 0.135	61 ± 2	25 ± 6	7 ± 4	75
19	Basic b1 + 10% lower mort. of juv. females	−0.020 ± 0.10	18 ± 1	29 ± 5	11 ± 6	80
20	Basic b2 + 10% lower mort. of juv. females	−0.025 ± 0.109	29 ± 5	29 ± 5	7 ± 6	82
21	Basic b3 + 10% lower mort. of juv. females	−0.032 ± 0.132	45 ± 2	26 ± 6	9 ± 5	78
Impact of mortality of juvenile males						
22	Basic b1 + 10% higher mort. of juvenile males	−0.020 ± 0.101	20 ± 1	29 ± 5	10 ± 6	80
23	Basic b2 + 10% higher mort. of juvenile males	−0.026 ± 0.106	41 ± 5	30 ± 5	6 ± 5	78
24	Basic b3 + 10% higher mort. of juvenile males	−0.033 ± 0.125	48 ± 2	26 ± 6	9 ± 5	79
25	Basic b1 + 10% lower mort. of juvenile males	−0.021 ± 0.102	18 ± 1	29 ± 6	10 ± 6	80
26	Basic b2 + 10% lower mort. of juvenile males	−0.024 ± 0.108	32 ± 5	29 ± 5	10 ± 5	80
27	Basic b3 + 10% lower mort. of juvenile males	−0.033 ± 0.125	46 ± 2	26 ± 5	8 ± 5	78
Impact of mortality of adult females						
28	Basic b1 + 10% higher mort. of adult females	−0.025 ± 0.106	26 ± 1	28 ± 6	9 ± 6	80
29	Basic b2 + 10% higher mort. of adult females	−0.033 ± 0.114	47 ± 5	28 ± 6	5 ± 5	79
30	Basic b3 + 10% higher mort. of adult females	−0.039 ± 0.130	55 ± 2	26 ± 6	8 ± 5	77
31	Basic b1 + 10% lower mort. of adult females	−0.015 ± 0.096	14 ± 1	29 ± 5	12 ± 7	81
32	Basic b2 + 10% lower mort. of adult females	−0.020 ± 0.100	31 ± 5	30 ± 3	9 ± 8	82
33	Basic b3 + 10% lower mort. of adult females	−0.028 ± 0.119	39 ± 2	27 ± 6	10 ± 6	79
Impact of mortality of adult males						
34	Basic b1 + 10% higher mort. of adult males	−0.022 ± 0.105	22 ± 1	28 ± 5	10 ± 6	79
35	Basic b2 + 10% higher mort. of adult males	−0.024 ± 0.110	34 ± 5	29 ± 6	7 ± 6	79
36	Basic b3 + 10% higher mort. of adult males	−0.034 ± 0.124	51 ± 2	26 ± 6	8 ± 5	77
37	Basic b1 + 10% lower mort. of adult males	−0.019 ± 0.098	15 ± 1	28 ± 5	11 ± 6	81
38	Basic b2 + 10% lower mort. of adult males	−0.022 ± 0.106	27 ± 4	30 ± 5	10 ± 5	81
39	Basic b3 + 10% lower mort. of adult males	−0.032 ± 0.123	43 ± 2	27 ± 5	8 ± 5	78
Impact of percentage of males in breeding pool						
40	Basic b1 + 10% higher perc. of males in br. pool	−0.021 ± 0.102	20 ± 1	29 ± 5	10 ± 6	80
41	Basic b2 + 10% higher perc. of males in br. pool	−0.024 ± 0.107	37 ± 5	30 ± 4	11 ± 6	82
42	Basic b3 + 10% higher perc. of males in br. pool	−0.033 ± 0.124	49 ± 2	27 ± 6	9 ± 5	79
43	Basic b1 + 10% lower perc. of males in br. pool	−0.021 ± 0.102	20 ± 1	28 ± 5	10 ± 6	79
44	Basic b2 + 10% lower perc. of males in br. pool	−0.027 ± 0.114	34 ± 5	30 ± 4	10 ± 6	80
45	Basic b3 + 10% lower perc. of males in br. pool	−0.034 ± 0.124	47 ± 2	26 ± 5	8 ± 5	78
Impact of initial population size						
46	Basic b1 + 10% higher initial pop. size	−0.018 ± 0.095	13 ± 1	29 ± 5	12 ± 7	82
47	Basic b2 + 10% higher initial pop. size	−0.023 ± 0.102	20 ± 4	30 ± 3	9 ± 8	82
48	Basic b3 + 10% higher initial pop. size	−0.031 ± 0.118	37 ± 2	27 ± 5	10 ± 6	80
49	Basic b1 + 10% lower initial pop. size	−0.021 ± 0.108	25 ± 1	28 ± 5	9 ± 6	78
50	Basic b2 + 10% lower initial pop. size	−0.030 ± 0.116	54 ± 5	29 ± 5	5 ± 5	79
51	Basic b3 + 10% lower initial pop. size	−0.035 ± 0.132	61 ± 2	25 ± 6	7 ± 5	75

(continued on next page)

Table 11 (*continued*)

Number	Description	Growth rate	Probability of extinction (%)	Years until first extinction	Population size for extant populations	Genetic diversity (%)
Impact of harvest interval						
52	Basic b3 + 10% higher harvest int.	−0.033 ± 0.122	49 ± 2	27 ± 6	8 ± 5	79
53	Basic b3 + 10% lower harvest int.	−0.034 ± 0.123	47 ± 2	25 ± 5	8 ± 5	78
Impact of number of harvested females						
54	Basic b3 + 10% higher har. females	−0.040 ± 0.141	63 ± 2	25 ± 6	7 ± 4	77
55	Basic b3 + 10% lower har females	−0.026 ± 0.109	35 ± 2	26 ± 6	10 ± 6	80
Impact of number of harvested males						
56	Basic b3 + 10% higher har. Males	−0.037 ± 0.138	61 ± 2	25 ± 6	8 ± 5	77
57	Basic b3 + 10% lower har. males	−0.031 ± 0.111	41 ± 2	27 ± 5	9 ± 5	79
Impact of reproductive age and perc of breeding females						
58	4 + 10% higher percentage of breeding females	−0.006 ± 0.094	9 ± 1	28 ± 6	16 ± 9	83
59	5 + 10% higher percentage of breeding females	−0.011 ± 0.100	13 ± 1	30 ± 5	14 ± 8	82
60	6 + 10% higher percentage of breeding females	−0.019 ± 0.113	26 ± 1	27 ± 6	12 ± 8	80
61	7 + 10% lower percentage of breeding females	−0.035 ± 0.109	39 ± 2	28 ± 6	7 ± 4	77
62	8 + 10% lower percentage of breeding females	−0.039 ± 0.117	58 ± 2	29 ± 5	7 ± 4	77
63	9 + 10% lower percentage of breeding females	−0.05 ± 0.131	75 ± 1	25 ± 6	6 ± 3	75

Table 12
Relative influence on growth rate for changes in parameters of ± 10% for the rhino population in the TWR with different hunting scenarios.

Parameter	Scenario b1 Sensitivity indices		Scenario b2 Sensitivity indices		Scenario b3 Sensitivity indices	
	+10%	−10%	+10%	−10%	+10%	−10%
Reproductive age of females	3.81	3.33	2.00	3.20	1.82	1.82
Percentage of females breeding	3.97	3.57	2.67	2.67	1.77	2.02
Total mortality of juvenile females	0.48	0.48	0.40	0.00	1.52	0.3
Total mortality of juvenile males	0.48	0.00	0.40	0.40	0.00	0.00
Total mortality of adult females	0.76	1.14	1.28	0.80	0.73	0.61
Total mortality of adult males	0.24	0.48	0.20	0.60	0.15	0.15
Percentage of males in breeding pool	0.00	0.30	0.40	0.80	0.00	0.00
Initial population size	1.07	0.00	0.60	1.50	0.45	0.45
Females harvested	/	/	/	/	0.21	0.21
Males harvested	/	/	/	/	0.12	0.06
Harvest interval	/	/	/	/	0.00	0.30

To our surprise this decline has not been detected by the regular surveys conducted on a yearly and even monthly basis within the reserve. The lack of a rigid scientific sampling scheme as well as the shortage of information about the effort expended by the field teams in terms of search routes, distance covered and time spent searching are part of the problem. Repeated information about presence/absence data and individual identification, as required by an occupancy modelling framework (MacKenzie and Royle, 2005), is not available. The absence of such data is a regular problem in conservation studies, pointing towards serious shortcomings in the design or execution of management-oriented or conservation-oriented surveys (Karanth et al., 2003; Pusparini and Wibisono, 2013). Large amounts of money were spent with very few results, often leading to poor conservation practices (Karanth et al., 2003). We therefore highly recommend for all future studies on Sumatran rhinos as well as other endangered animals to conduct regular surveys in an appropriate season and in a habitat which is representative for the whole population. The survey team need to carefully record sampling effort and georeference the area. Decisions based on little evidence can be harmful to wildlife, habitat and the survival of both (Huettmann, 2005).

We studied resource selection and habitat use within the Tabin wildlife reserve. The study represents the only existing data on habitat use of the Borneo rhino. Our study utilised data collected during 277 surveys conducted over a study period of 13 years. It thus covers a long time period and includes data collected during both wet and dry seasons, providing a comprehensive summary of the range of conditions over which rhinos preferentially occur in time and space (Wisz et al., 2008). Our study area is comparably small and it has been modified by human activity. The assessments therefore need to be treated cautiously and we cannot assume that it reflects the preferences of rhinos in undisturbed situations. But such situations hardly exist for Sumatran rhinos anymore. In Sabah, less than 51% of the land area is covered with forest, 32% of these forests have been logged several times leaving extensive areas in a highly damaged condition and only 1% of undisturbed lowland forest remained (Reynolds et al., 2011). A similar situation exists in Kalimantan (Gaveau et al., 2014). Our resource selection study thus describes habitat preferences of a species that lived for more than 30 years in a human altered landscape in one of the few remaining lowland forests of Sabah. We applied a use-vs-availability design to identify relevant habitat covariates within this set of given choices. The exact number of rhinos included in this study is not known. The data on surveys conducted in the TWR (Boonratana, 1997: estimated 3–9 rhinos in 1997 and Thayaparan, 2008: 5 rhinos in 2005) in combination with the results of our PVA analysis for the TWR population suggest that there was a population of at least 5–9 individuals at the beginning of our study period. This assessment is consistent with a rough estimate of the number of rhinos which emerged when we grouped GPS locations of rhinos within a certain year. Here we assume that the maximum size of a male home range was 60 km^2 (Strien, 1986) and that home ranges did not overlap.

We studied resource selection and habitat use within a relatively homogenous forest reserve with comparably little variation in habitat factors. The high resolution satellite maps (5 m) used for the vegetation interpretation provided us with the best possible data currently available to detect small scale differences in vegetation (Niedballa et al., 2015). However, satellite data will not provide information on variation in the undergrowth of a forest where the main food of Sumatran rhinos is located. Vegetation assessments on the ground are therefore essential to complement vegetation assessments based on remote-sensing data. The data used in our study were not evenly spread across the whole study area and some areas were more frequently surveyed than others. Such a spatial bias can lead to an 'environmental bias' in the assessment of resource selection functions because of the overrepresentation of frequently represented environmental features (Kramer-Schadt et al., 2013). We addressed this problem by reducing the number of occurrence records in oversampled regions using spatial filtering (Dormann et al., 2007; Veloz, 2009; Northrup et al., 2013). This method has the apparent disadvantage that highly preferred habitats, which may be of great importance for the Sabah rhinos, will be downgraded in their apparent importance (Boyce et al., 2002). Such downgrading is less likely to happen if spatial filtering is applied for only a limited time frame. The covariates identified with such a filtering approach have thus been identified with a conservative method.

4.2. Population viability analysis

The historical population model predicted a low chance of extinction of the rhino population in Sabah after 115 years, despite a yearly harvesting quota of 120 animals between 1930 and 1950. The model indicates that population growth was mainly influenced by the percentage of breeding females and the lifetime reproductive period of females. A small decrease of 10% in these parameters resulted already in the near extinction of the entire rhino population.

Recent findings suggest that reproduction of the remnant Sumatran rhinos is being constrained by reproductive pathologies in females. In Sabah, two adult females caught in the past four years had large tumours in their reproductive tract which made it impossible for them to successfully conceive and deliver a young (TB Hildebrandt et al., unpublished data), and in peninsular Malaysia, 6 out of 9 rhinos captured in the 1980s had reproductive tract pathologies (Schaffer et al., 1994; Ahmad et al., 2013). In most cases, the tumours were present at time of capture and did not develop in captivity. Reproductive tract tumours in rhinos develop after long non-reproductive periods and prolonged exposure to sex steroids (Hermes et al., 2004, 2006, 2014), which eventually results in a shortening of the lifetime reproductive period of the females. Such non-reproductive periods can occur in small remnant populations of low population size and in areas of low population densities where mating partners have difficulties to find each other.

The hunting of rhinos most probably contributed towards such a low population density, and logging as well as agricultural and other human activities have likely fostered this trend. The first large-scale deforestation activities in Borneo started with the colonialisation. At that time forests on flat terrain were logged manually to meet the local and global demand for rice, rubber, palm oil and coconuts (Davies and Payne, 1982; Langner, 2009). An increasing demand for timber in the mid 1950s set off the beginning of commercial logging (Davies and Payne, 1982). From then on logging increased at an accelerating rate. From 1973 until 2010 around 30% of the primary forest area in Borneo was converted into oil palm plantations and agricultural land, with the highest losses of rainforest recorded in Sabah (40%) and Kalimantan (31%) (Gaveau et al., 2014).

The disturbance caused by logging and its associated human activities had a strong impact on the Sumatran rhinos. Individuals were scattered (Flynn, 1981) and rhino populations were isolated in patches of rainforest surrounded by agricultural land (Davies and Payne, 1982). One of these populations occurred in the TWR, the other in Danum Valley, Sabah. The PVA model of the TWR population showed that such small and isolated populations have a negative growth rate, even in cases of zero hunting and a moderate (zero hunting) to high (moderate level of hunting) probability of extinction within 30 years. The model indicated that the combined efforts of total protection and an increase in the reproductive performance of females could have saved the Tabin population. Capturing of individuals in areas of low population densities and assembling them into suitable areas with high levels of protection could have been such a possible measure.

The PVA model of the TWR population also indicates that a species with such a low reproductive output and with proven reproductive health problems needs further measures to guarantee its long term persistence. These measures should aim to increase the chance of successful mating and conception and shortening the intercalving interval. Assisted reproduction techniques could be such possible measures.

The predictions made by the PVA model need to be interpreted cautiously because of the limited data available (Ellner et al., 2002; Brook et al., 2002). As some of the crucial biological information was unavailable, we chose conservative estimates for the parameters in order to ensure that any factor likely to emerge as important would do so despite these conservative assumptions.

4.3. Conclusions

Small isolated populations of Sumatran rhinos are deemed to go extinct unless measures designed to prevent hunting, increase fertility, enhance the chance of encounters of potential mating partners in the wild or shorten the intercalving interval are undertaken. The predominant conservation practice of governments and NGOs to avoid interfering with free-ranging populations and to rely on natural breeding will not solve the problem. A scientifically rigorous surveying regime ought to be applied in order to identify small populations, monitor their development and forecast any potentially negative population developments. The experiences with the rhinos in Sabah show that a remnant population with less than 15 individuals and with its inherent reproductive specifics have a high chance of extinction if left to their own devices. Our PVA analysis suggests that a combination of zero hunting and improvements in reproductive performance of females will make a crucial difference to the viability of such a remnant population. Improving reproductive performance usually requires comprehensive checks on the reproductive health of all members of the population and intensive efforts to maximise fertility and successful encounters with potential mating partners. This will require an intensive conservation management, which may require rhinos which occur in areas with high human encroachment as well as in areas with low nutrient and mineral concentration to be translocated to more suitable areas to provide optimal conditions for them to breed. It may also include the capture and reproductive management of key individuals within a confined space where the animals are easily accessible and where the monitoring of their health, fertility and pregnancies can be ensured. Such efforts will be too late for the Borneo rhinos in Sabah, but the Sumatran subspecies can still be saved. The success of the coordinated captive breeding program of the Iberian lynx (*Lynx pardinus*) (Vargas et al., 2009), the most endangered felid worldwide, is an example which demonstrates how this could be done.

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Appendix A. Supplementary data

Supplementary material related to this article can be found online at http://dx.doi.org/10.1016/j.gecco.2016.02.006.

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<u>Supplementary material</u>

The catastrophic decline of the Sumatran rhino (*Dicerorhinus sumatrensis harrissoni*) in Sabah: Historic exploitation, reduced female reproductive performance and population viability

Kretzschmar, P., Kramer-Schadt, S., Ambu, L., Bender, J., Bohm, T., Ernsing, M., Göritz, F., Hermes, R., Payne, J., Schaffer, N., Thayaparan, S.T. , Zainal, Z.Z., Hildebrandt, T.B., Hofer, H.

Appendix A

Literature review on Sumatran rhinos:

A literature review of English articles published at an online platform for rhino literature (Rookmaaker 2014) revealed that out of 101 publications published within the last 20 years on Sumatran rhinos most of them focused on reproduction (24), followed by articles on conservation status (16), surveys (14) and health (10). Studies describing basic habitat preferences of free ranging Sumatran rhinos can only be found in literature dating back in the 1980ies: Borner 1979, van Strien 1985. They observed that the Sumatran subspecies (*D. s. sumatrensis*) occurs in primary forest of different altitudes, it avoids open space and finds its food in the undergrowth and understory in the primary rainforest, on landslides, tree falls and along river banks (Borner 1979, van Strien 1985). The only study reporting on habitat preferences of rhinos on Borneo describes a preference for primary over secondary forests (Boonratana 1997).

Appendix B

Derivation of population parameters:

Information about the mating system of the Sumatran rhino is very limited. A long term field study in the Gunung Leuser National Park in Indonesia (Van Strien, 1985) reports, that groups of two animals, other than a cow and her calf, have rarely been observed, this point to a short-term polygamous mating system.

Territoriality can exclude non-dominant males from breeding such as in white rhinos (Owen-Smith 1973). Van Strien (1985) observed different frequencies in marking activity depending on the age of individual males and clearly separated core areas. This indicates that male Sumatran rhinos are territorial, however they seem to be less exclusive compared to other rhinos as male ranges tend to overlap in the periphery (van Strien 1985). We set the percentage of breeding males to 80 % expecting that most males contribute to the breeding pool in a given year.

Information on sexual maturation was derived from a study on captive born Sumatran rhinos, showing that males reach sexual maturity with 7 years of age and females with 6 years (Roth et al. 2013).

The maximum lifespan of captive Sumatran rhinos (♀ = 21 – 25 years and ♂ = 32 – 33 years of age, pers. observations), appears quite short in comparison to age estimates given for free ranging black and captive Indian rhinos with a maximum lifespan of 40 years (Owen-Smith 1988, Hermes et al. 2014). All Sumatran rhinos in captivity were caught in the wild and their age may have been underestimated. We therefore assume a slightly higher maximum lifespan of 30 years for both males and females.

The reproductive lifespan is difficult to assess due to the small number of reproducing males and females. A captive female Sumatran rhino in Cincinnati, America died with 21 years of age. Her last child was born at 19 years of age. Her male partner did at an age of 33 years and sired his last child with 25 years. In Sabah, Malaysia a female rhino was still reproductively active with an estimated age of 15 years and ceased cycling with an age of 20 years (Hildebrandt pers. comment). We used a reproductive lifespan of 20 years in females and 25 years in males in our PVA analysis. A recent study on captive Indian rhinos revealed that female Indian rhinos cease reproducing at the age of 18 years due to tumours developed in their reproductive tract (Hermes et al. 2014). Reproductive tumours are also common in wild caught Sumatran rhinos (Schaffer et al. 1994, Ahmad et al. 2013). We therefore tested the influence of different reproductive lifespan on population growth.

There is no indication of a skewed sex ratio for Sumatran rhinos (two ♂: one ♀ born in Cincinnati Zoo); we therefore set this parameter at parity.

The captive female in Cincinnati gave birth to one young with an interval of approx. three years between consecutive births. Free ranging Sumatran rhinos are likely to have a longer calving interval especially in areas of low rhino density where males and females have problems finding each other. For free ranging Javan rhinos an estimated calving interval of 4 – 5 years has been reported (Seal & Foose 1993). In our PVA analysis, a base line interval of 4 years was used and the length was varied in different modelling steps.

There is no study on mortality of free ranging and captive Sumatran rhinos and data on other free ranging rhino species is very limited. We therefore used estimates on Javan rhinos (Seal & Foose 1993) and adapted them according to our experience on free ranging white rhinos. In white rhinos, juvenile males are more frequently killed by adult males than females. They tend to defend their mothers against adult males in the process of mating and often get killed or heavily injured. At the age of 5 - 6 they face a high risk of mortality when they start challenging adult males. This risk continues throughout their life, but it is less pronounced (P.Kretzschmar, unpublished data). We therefore increased the mortality rate of males in comparison to females (see Table A5).

Appendix C

Hunting of rhinos in Borneo:

Rhinos have always been hunted in Borneo mainly as a source of food (Rookmaaker 1976). At the beginning of the 20th century trade was opened up with the coast for the first time and

Chinese traders sourced the rhino horn and nails for aphrodisiac and medicinal purposes (Harrisson 1946).
The reasons for the hunting are clear, “the rhinos in Borneo were equivalent of a great diamond in Africa or gold nugget in Australia. It was the way to get rich quick. In historic times a good male rhino might earn the skilful hunter thousands of dollars. There was no other way for a Dayak or Kelabit to get anything like such a large sum of money “ (Harrisson 1956). The hunting of rhino was not confined to Borneo, a similar development has been recently described for the Javan rhinos in South East Asia (Brook et al. 2014). Rhino numbers rapidly decreased, especially in Sarawak, and the number of rhinos hunted each year drastically increased. In less than 10 years the rhino was exterminated in Sarawak (Banks 1978). Banks (1931) noted that “36 rhino trophies were brought into Beluga (Sarawak) and I have met men who have claimed to have shot over 30 in the course of their life time”. Harrisson (1956) wrote: “The records of the district office, Marudi (Barum) in the Fourth Division of Sarawak listed rhinos known to be killed as: 1925: 18, 1926: 14, 1927: 8, 1928: 12, 1929:11, 1930: 12, 1931: 4 and Marudi was only one slaughter station; others were Lawas, Limbang, Beluga, Sibu, Kapit, Kanowit and Bintulu in Sarawak alone”. In less than 10 years the rhino was exterminated in Sarawak (Banks 1978). Hunting of rhinos still continued until recent times. In Sabah, five rhinos have been poached from 1976 to 1981 (Davies & Payne 1982, Andau 1982) and one in the year 2000 (personal observation authors).

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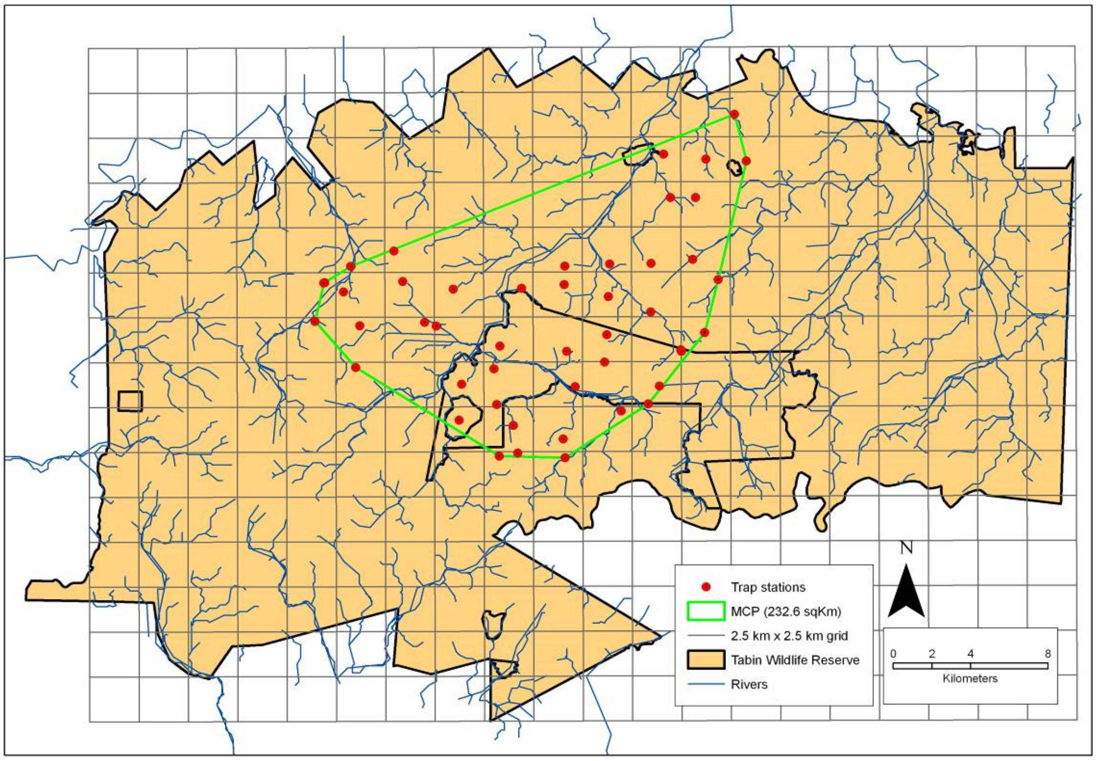

Figure A1: Position of camera trap stations within the TWR.

Table A1: Frequency, duration and length of surveys in the TWR between 2000 and 2013

	mean				total		
	surveys/ month [n]	**survey days/month [n]**	**transect route/month [km]**		**surveys/ year [n]**	**survey days/year [n]**	**transect route/year [km]**
2000	/	/	/		1	/	/
2001	1	/	/		13	/	/
2002	0	/	/		5	/	/
2003	3	8	137		36	285	1639
2004	2	7	83		23	158	830
2005	2	7	76		31	213	833
2006	4	8	136		45	337	1335
2007	4	8	158		45	357	1262
2008	3	11	161		33	347	1452
2009	2	13	94		21	282	943
2010	1	9	72		12	106	360
2012	1	6	59		8	57	532
2013	2	5	63		4	18	250
mean	**2**	**8**	**89**	**total**	**277**	**2160**	**9436**

Table A2: Potential predictor variables considered in the models of habitat use. Only uncorrelated variables were used in the resource selection study.

Variable	Abbre-viation	**Definition**	**Reference**	**uncorrelated variables**
Annual mean Temperature [°C *10]	t	Bioclim 1, derived from monthly temparature values	Hijmans et al., 2005, http://worldclim.org/bioclim	/
Annual precipitation [mm]	pr	Bioclim 12, derived from monthly rainfall values	Hijmans et al., 2005, http://worldclim.org/bioclim	/
classify (1-5)	clas	Vegetation categories resulting from a supervised clasification: 1- dense forest, 2-open forest, 3-grassland, 4-plantation, 5-water	/	x
Distance to water courses:	Calculated from a stream net which was delineated from a digital elevation model (DEM) using a single-flow direction approach (Spatial Analyst ArcView 9.3.1). The resulting cut-off was combined with a layer of major water bodies of Borneo (the Digital Chart of the World, www.diva-gis.org) and set to:			
1) Distance to small rivers with a catchement size of 42 km^2 [km]	d_50	5,000 flow accumulation cells with an approximate catchement size of 42 km^2	Kramer-Schadt et al. 2013	/
2) Distance to medium rivers with a catchement size 850 km^2 [km]	d_100	100,000 flow accumulation cells with an approximate catchment size 850 km^2	Kramer-Schadt et al. 2013	/
3) Distance to main water courses with a catchement size 4250 km^2 [km]	d_5000	500,000 flow accumulation cells (catchment size 850 km^2	Kramer-Schadt et al. 2013	/
4) Distance streams 100 [m]	d_st	100 flow accumulation cells with an approximate catchement size of 0.85 km^2	Kramer-Schadt et al. 2013	x
distance road [m]	d_road	The distance to the core area road was calculated using ArcGIS "spatial join"	/	x
Distance mudvolcano [m]	d_mvo	The distance was calculated using ArcGIS "spatial join"	/	x
distance reserve border [m]	d_res	The distance to the reserve border was calculated using ArcGIS "spatial join"	http://en.wikipedia.org/wiki/World_Database on Protected Areas	/
Distance to wetland [km]	d_wet	Based on maps from SarVision 2007 on peatswamp, mangroves and lakes	http://sarvision.nl	/
Distance walked [km]	dist	Controlling variable: Summed up per day and survey	/	x
DGM Tabin [m]	ta_dgm	Elevation, calculated from SRTM 90m Digital Elevation Model void filled	http://srtm.csi.cgiar.org	x
Elevation [m]	dgm	Calculated from SRTM 90m Digital Elevation Model (DEM) void filled	http://srtm.csi.cgiar.org	x
focal dense forest	f_dfo_x	Frequency of occurence of the focal feature within the neighborhood scale.	/	x

focal open forest	f_ofo_x	Frequency of occurence of the focal feature within the neighborhood scale.	/	x
focal grassland	f_gr_x	Frequency of occurence of the focal feature within the neighborhood scale.	/	x
focal oil palm plantations	f_pl_x	Frequency of occurence of the focal feature within the neighborhood scale.	/	x
focal barren land	f_bl_x	Frequency of occurence of the focal feature within the neighborhood scale.	/	x
Human population density in a square of 30"[arc seconds]	hpd	Average number of human inhabitants present at any given time in a 24-hour period.	LandScan 2007^{TM} high resolution global population data set, UT-Battelle, LLC, Oak Ridge National Laboratory	x
land cover categories [1-17]	lc	Reclassification of 50-m resolution PALSAR land-cover map (2007) validated for Borneo (Hoekman et al. 2009) updated with DEM data in 500m elevation steps resulting in 17 land cover classes	Kramer-Schadt et al. 2013	/
Mud wallow (y/n)	wal	Binary variable (1-presence, 0-absence)	/	x
Primary forest (0-2)	pf	The zone insight the core area defined by the boundaries (binary variable, 1,2 prim forest, 0-sec. forest)	/	/
Rhino presence (y/n)	rhpr	Binary variable (1-presence, 0-absence)	/	x
Ruggedness (1-7)	rug	Expresses the elevation differences between adjacent cells of a 90m resolution digital elevation model on a scale ranging from 1 to 7 (extremly rugged).	Kramer-Schadt et al. 2013	/
Search intensity (h/l)	surv	Binary controlling variable: (1-high, 2-low)	/	x
Slope tabin [%]	sl	calculated from SRTM 90m Digital Elevation Model void filled	http://srtm.csi.cgiar.org	x
Soil type	sp	Digital soil map of the world, version 3.6, 28/02/2007 at 1:5.000.000 scale	FAO-UNESCO Terrastat 2007	x
Trespasser (y/n)	hum	Binary variable (1-presence, 0-absence)	/	x
Controlling variables:				
Time spend walking [min]	dur	Time spend walked summed up per day and survey	/	x
Year [year]	year	Year when survey took place	/	x

Table A3: Surveys conducted in the TWR and estimated rhino numbers.

Source	**date of survey**	**search intensity:** **no. days walked**	**distance walked [km]**	**area**	**rhino density**	**No. of juv. tracks**	**estimated rhino numbers**
Flynn 1981	1980	5	/	Silabukan Forest Reserve, between Tabin and Tagas river	/	/	> 4 - 6
Davies & Payne (1982)	1980/81	5	1.5	Ulu Tabin & Tabin Salt Spring	1/30-60 km^2	> 2	7 - 12+
Andau (1987)	1982	8	/	undisturbed forest Tabin	/	/	7
Andau (1987)	1986	7	157	core area	1/20 km^2	/	6
Khan (1989)	status report	/	/	/	/	/	> 20
Nor et al. (1989)	1988	8	229	core area, western border and area north east of core area of Tabin	1/30 km^2	/	3
Khan et al. (1993)	status report	/	/	/	/	/	7 - 17
Foose et al. (1995)	status report	/	/	/	/	/	20+
Boonratana (1997)	/	?	210 qkm	TWR and adjoining areas	/	/	3 - 9
Thayaparan (2008)	2007	12	/	Tabin	/	2	5
Our study	2012/2013	88	782	Tabin	0	/	0

Table A4 : Soil categories derived from the soil map of the world, by the FAO/UNESCO

Soil category	Definition of the soil unit
12	Dystric Gleysols fine textured, Humic Gleysol and Gleyic Cambisols with Dystric Fluvisols and Dystric Histosols; level to undulating
13	Thionic Fluvisols, fine textured, Dystric Histosols and Dystric Gleysols, with Regosols and Podzols; level to undulating
23	Orthic Acrisols medium to fine textured, Ferric Acrisols and Luvisols with Dystric Gleysols; rolling to hilly
32	Orthic Acrisols, medium to fine textured, Humic Acrisols Dystric Cambisols with Chromic Cambisols and Gleyic Acrisols steep dissected to mountainous