
Population responses to natural and human-mediated disturbances: assessing the vulnerability of the common hippopotamus (*Hippopotamus amphibius*)

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Abstract

Vulnerable wildlife populations can face a suite of anthropogenic activities that may threaten their persistence. However, human-mediated disturbances are likely to be coincident with natural disturbances that also influence a population. This synergism is often neglected in population projection models. Here I evaluate the effects of natural (rainfall fluctuation) and human disturbances (habitat loss and unregulated hunting) using a multi-matrix environmental state population model for the common hippopotamus (*Hippopotamus amphibius*). By evaluating each disturbance type (natural and human) alone and then together, I explicitly consider the importance of incorporating realistic environmental variability into population projection models. The model population was most strongly affected by moderate habitat loss, which yielded the highest probability of crossing the risk thresholds over the 60 year time period, although these probabilities were relatively low (≤ 0.31). However, the likelihood of crossing the risk thresholds were two to five times as high when human-mediated and natural disturbances were considered together. When these probabilities were calculated per year of the simulation, the results suggested that even relatively mild human disturbances, when considered in conjunction with realistic natural disturbance, resulted in a high probability (>0.50) of substantial declines within decades. The model highlights the importance of integrating realistic natural disturbances into population models, and suggests that, despite locally abundant populations, protected hippopotamus populations may

decline over the next 60 years in response to a combination of environmental fluctuations and human-mediated threats.

Key words: catastrophe, environmental stochasticity, habitat loss, hippopotamus, multi-matrix population model, population persistence, sensitivity to disturbance

Résumé

Les populations sauvages vulnérables peuvent être confrontées à une suite d'activités humaines qui risquent de menacer leur persistance. Cependant, les perturbations causées par l'homme sont susceptibles de coïncider avec des perturbations naturelles qui influencent aussi une population. Cette synergie est souvent négligée dans les modèles de projection des populations. Ici, j'évalue les effets des perturbations naturelles (fluctuations des chutes de pluie) et humaines (perte d'habitat et chasse non réglementée) en utilisant une chaîne de matrices aléatoires pour l'état environnemental d'une population d'hippopotames (*Hippopotamus amphibius*). En évaluant chaque type de perturbation (naturelle et humaine) seul et ensemble, je considère explicitement l'importance qu'il y a d'intégrer une variabilité environnementale réaliste dans les modèles de projection des populations. La population modèle était surtout affectée par une perte d'habitat modérée, qui réunissait la plus grande probabilité de dépasser les seuils de risque en une période de 60 ans, même si cette probabilité était relativement faible ($\leq 0,31$). Cependant, la probabilité de franchir les seuils de risque était 2 à 5 fois plus grande lorsque les perturbations d'origine humaine et naturelle étaient considérées ensemble. Lorsque ces probabilités étaient calculées par année, les résultats de la simulation suggéraient que même des perturbations humaines faibles, quand on les considérait en conjonction

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avec une perturbation naturelle réaliste, résultaient en une forte probabilité ($>0,50$) de déclin substantiel en quelques décennies. Le modèle souligne l'importance qu'il y a d'intégrer les perturbations naturelles réalistes dans les modèles de population et suggère que, malgré des populations localement abondantes, les populations protégées d'hippopotames peuvent décliner au cours des 60 prochaines années en réaction à une combinaison de fluctuations environnementales et de menaces d'origine humaine.

Introduction

Successful wildlife conservation requires timely management and conservation actions. Because of the need for proactive management, conservation of long-lived animals, in particular, relies heavily on our ability to project future population trends. As a result, population models are a *sine qua non* of species viability management, despite uncertainty associated with model components and structure (Beissinger & Westphal, 1998; Ludwig, 1999; Regan *et al.*, 2003). The primary focus of many such models is the impact of current human activities on future population trends (Crowder *et al.*, 1994; Doak, Kareiva & Klepetka, 1994; Heppell, Crouse & Crowder, 2000; Kareiva, Marvier & McClure, 2000). However, human-mediated disturbances are likely to be coincident with natural disturbances that also can influence population trends. Although the conceptual importance of including environmental variability, including catastrophes, has been identified as a necessary component of population models (Mangel & Tier, 1994; Ludwig, 1996; Ripa & Lundberg, 2000; Drake & Lodge, 2004; *et al.*, 2004), realistic natural disturbances are not typically a primary element within population projection models (but see Liu, Menges & Quintana-Ascencio, 2005). This omission may lead model results to be overly optimistic, i.e. when anthropogenic activities are considered in conjunction with natural disturbances, even relatively moderate or mild human-mediated disturbances may lead to significant population changes.

Populations of common hippopotamus (*Hippopotamus amphibius*) have declined in response to human disturbances. Common hippopotamus (hippos) were once found throughout sub-Saharan Africa, although only estimated historic distributions are available. The current distribution is primarily concentrated in Eastern and

Southeastern Africa where hippo populations tend to occur at high densities (Fig. 1). Information from The World Conservation Union (IUCN) surveys suggests that in many countries where common hippos are found, their populations are declining (Fig. 2). These declines have been attributed to two anthropogenic activities: habitat loss as wetlands are converted or impacted by agricultural development (Smuts & Whyte, 1981; Jacobsen & Kleynhaus, 1993) and unregulated hunting for meat and ivory from the common hippo's large canine and incisor teeth (Vega, 1995). Small-scale habitat loss is most commonly the result of weirs or dams redirecting water from rivers and lakes to crop areas (Cole, 1992; Jacobsen & Kleynhaus, 1993; Viljoen, 1995; Viljoen & Biggs, 1998). Adult hippos are hunted for meat and ivory across a gradient of hunting intensities in which the intensity of the hunting pressure reflects the nutritional needs and density of coincident human populations (Weiler, De-Meulenaer & Vanden-Block, 1994; Vega, 1995; Shambaugh, Oglethorpe & Ham, 2001).

Because hippos spend most daytime hours in or next to water (Field, 1970), they exhibit notable demographic sensitivity to annual rainfall variability. Field records and research conducted over the past 50 years have quantified marked changes in hippo demographic rates in response to rainfall fluctuations (Moffett, 1958; Atwell, 1963; Pienaar, Van Wyk & Fairall, 1966; Smuts & Whyte, 1981). In low rainfall or drought years, hippo populations can crash, because of a dramatic decline in conception and an abrupt increase in mortality, most likely due to lack of forage, heat stress and increased vulnerability to disease (Sayer & Rakha, 1974; Smuts & Whyte, 1981). The proportion of females likely to conceive in a drought year has been estimated to drop from 30% to $<5\%$ (Smuts & Whyte, 1981). Historical accounts from as early as 1929 from protected areas in many African countries (South Africa, Tanzania, Zambia, Zimbabwe) provide support for this pronounced response to low rainfall conditions (Sayers, 1930). Conversely, in response to higher than average rainfall, common hippo populations exhibit dramatic population surges. During these surges, the population can return to predrought levels, often in 1 or 2 years, because of high forage availability and increased reproductive activity from sexually mature adults. In high rainfall years, individuals younger than the average age of sexual maturity also may become sexually active in response to favourable conditions and contribute to

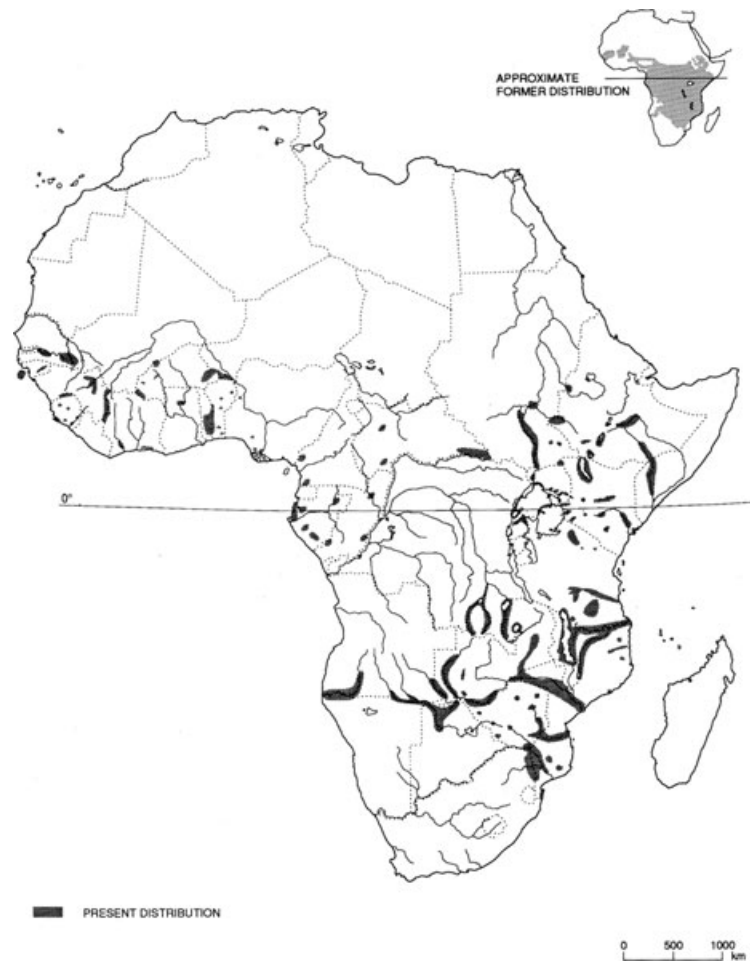


Fig 1 Estimated (a) former (c. 1959) and (b) current (c. 1993) distribution of common hippopotamus (from IUCN, 1993)

population growth (Sayer & Rakha, 1974; Smuts & Whyte, 1981).

Given their sensitivity to natural disturbance regimes, and the human-mediated threats that have been linked to population declines, hippos are a good case study to consider the synergistic effects of natural and human disturbances on population growth. Here, I present an assessment of the sensitivity of a model hippo population to both natural and mild or moderate human disturbances. I measured population sensitivity to these disturbances by identifying population thresholds that signify increased risk to the persistence of the population and calculated the likelihood of crossing these thresholds over the time horizon of the model. The goal of this exercise was to evaluate population sensitivity to realistic disturbances and project likely responses of a common hippo population within African protected areas.

Methods

Model structure and parameters

I constructed the model using a Leslie–Lefkovich matrix based on the known demographic demarcations of hippos (Sayer & Rakha, 1974). The age distribution was divided into six age classes (Table 1). The annual probability of an individual growing into the next age class was calculated as:

$$\gamma_i = \frac{\left(\frac{\sigma_i}{\lambda}\right)^{T_i} - \left(\frac{\sigma_i}{\lambda}\right)^{T_i-1}}{\left(\frac{\sigma_i}{\lambda}\right)^{T_i} - 1} \lambda = 1 \quad (1)$$

where T_i is time in stage i , σ_i is survivorship in stage i , and λ is rate of population change, assumed to be 1 (Caswell, 2001).

Model parameters were taken from multi-year studies across multiple populations. This included field data col-

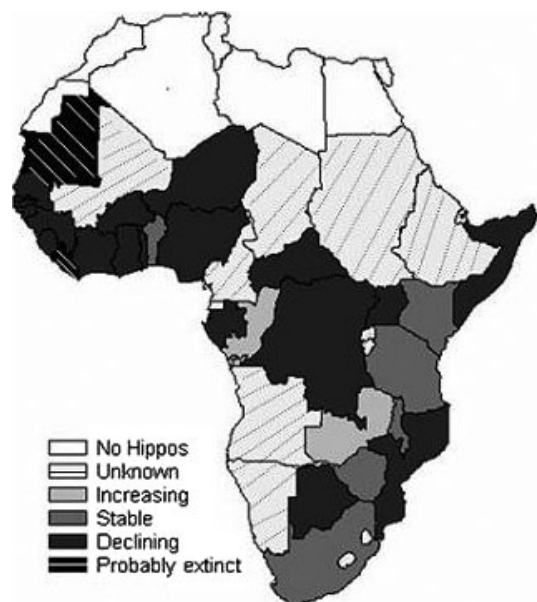


Fig 2 Estimated common hippo population trends (adapted from IUCN, 1993)

Table 1 Age classes for common hippos based on known demographic demarcations

Age class	Description	Duration (year)
1	Newborn	1
2	First year calf	1
3	Juvenile	5
4	Subadult	2
5	Adult	21
6	Senescent adult	5

lected between 1996 and 1998 in Katavi National Park (KNP), in southwestern Tanzania (R. Lewison, unpublished data) and from published studies from the 1950s to 1980s from unthreatened populations in Uganda, Zambia, Zimbabwe and South Africa (Bere, 1959; Pienaar *et al.*, 1966; Mackie, 1976; Marshall & Sayer, 1976; Smuts & Whyte, 1981; O'Connor & Campbell, 1986). These unthreatened populations were not, however, subject to the human-mediated disturbances considered here. Thus the demographic values derived are not subject to 'double dipping', i.e. the demographic rates do not already incorporate the effects of the human disturbances and thus will not tend to overestimate potential declining trends (Brook, 2000). Survivorship estimates were based on life tables derived from 350 carcasses found in protected areas across

multiple studies (Laws, 1968; R. Lewison, unpublished data). Annual survival incorporates the probability of surviving and remaining in the same age class (for classes that extend beyond one year), and the probability of surviving and growing into the next age class, P and G respectively. Fecundity was based on standardized female : offspring estimates averaged across years in KNP and on the percent of culled females whose reproductive organs showed evidence of conception from five cropping regimes (Bere, 1959; Laws & Clough, 1966; Sayer & Rakha, 1974; Marshall & Sayer, 1976; Smuts & Whyte, 1981). Thus, fecundity was the product of the proportion of females in the population and the proportion of females likely to have conceived during a given year.

Demographic stochasticity was also included. At each 1 year time step, matrix elements were sampled from a beta distribution (using a Monte Carlo method) to incorporate temporal variability and estimation error in the parameters. The model also implicitly accounted for density-dependent responses as the population exhibits higher fecundity and recruitment following a population crash (i.e. when the population is low), assuming habitat conditions improve. The model assumed a postbreeding census, i.e. the yearly sampling follows birthing events. Because hippos are polygynous and assumed to have an even sex ratio, the model only accounted for female individuals.

The initial age distribution was taken from standardized age-class ratios based on census counts conducted in four African protected areas (Masai Mara Game Reserve, Kenya; Katavi NP, Tanzania; Queen Elizabeth NP, Uganda; Luangwa NP, Zambia). An initial population size of 5000 females was based on median population sizes in 56 protected areas from the 1993 IUCN Action Plan (IUCN, 1993). The population was assumed to be closed to immigration, which realistically represents most protected hippo populations. The model was run in @Risk[®] software (Palisade Decision Tools, Palisade Corporation), which is an Excel add-in programme.

Environmental stochasticity: modelling rainfall variability

To incorporate environmental stochasticity, I used the described demographic data in a multi-matrix environmental state model. In this type of model, multiple matrices are used to represent a range of environmental conditions (*sensu* Beissinger, 1995). In this case, the model was composed of four matrices representing four rainfall states – drought, low, average and high (Table 2). The four

Table 2 Demographic values for each matrix representing one of the four rainfall states (a) drought, (b) low, (c) average, and (d) high. The average matrix (c) represented a stable population with $\lambda \approx 1$

Age class	Annual survival	Annual fecundity
(a)		
1	0.45	0
2	0.60	0
3	0.73	0
4	0.78	0
5	0.85	0.10
6	0.42	0.02
(b)		
1	0.55	0
2	0.70	0
3	0.75	0
4	0.85	0.23
5	0.92	0.31
6	0.47	0.14
(c)		
1	0.67	0
2	0.74	0
3	0.85	0
4	0.88	0.26
5	0.95	0.36
6	0.50	0.15
(d)		
1	0.76	0
2	0.78	0
3	0.88	0.04
4	0.95	0.35
5	0.97	0.43
6	0.52	0.25

matrices were calibrated with demographic data from field studies collected between 1959 and 1998 (Bere, 1959; Pienaar *et al.*, 1966; Mackie, 1976; Marshall & Sayer, 1976; Smuts & Whyte, 1981; O'Connor & Campbell, 1986; Lewison, unpublished data). Inter-matrix variability in adult survival is lower than variability of juvenile survival (Gaillard, Festa-Bianchet & Yoccoz, 1998).

At each time step in the model, a rainfall submodel selected one of the four matrices to reflect one of four rainfall states. The submodel used a discrete, first-order Markov chain with stationary transition probabilities to represent stochastic variation in rainfall (Stewart, 1994). This assumes that the rainfall state at time $t + 1$ depends only on the rainfall state at time t . The transition probabilities (Table 3) among the rainfall states were derived from a 50-year-rainfall record collected in and around KNP

Table 3 Transition probabilities used in the rainfall submodel

From	To			
	Drought	Low	Average	High
Drought	0.00	0.50	0.50	0.00
Low	0.00	0.13	0.75	0.12
Average	0.03	0.16	0.75	0.06
High	0.25	0.00	0.50	0.25

Probabilities were determined from the Katavi National Park (KNP) data shown in Fig. 3, after assigning each annual rainfall records to one of the four rainfall states based on its deviation from the overall mean rainfall value.

(Fig. 3), annual rainfall was assigned to one of the four rainfall states based on the mean rainfall value. *Drought* was defined as rainfall that was greater than or equal to two standard deviations below the mean. The *high* and *low* rainfall states were defined as rainfall that was greater or equal to one standard deviation above or below the mean, respectively. Although the rainfall data come from a specific field site, the pattern is likely to be representative of other African protected areas with bimodal rainfall.

Disturbance scenarios

I evaluated the model population's sensitivity to three relatively mild or moderate human disturbance scenarios – small-scale habitat loss, and two levels of hunting pressure (Table 4). A mild form of habitat loss occurs when water is diverted from rivers and lakes to agricultural areas via small dams and weirs. When water is diverted, although the rainfall pattern *per se* remains unchanged, the rainfall that the hippos experience is reduced, i.e. water diversion is in effect less rainfall. Because the most dramatic demographic response to low water availability is an abrupt decline in conception, I represented this habitat loss by decreasing fecundity by 5%. I considered unregulated hunting that occurred at two levels – low and moderate hunting pressure. I assume hippo populations adjacent to low human density areas experience a low level of unregulated hunting pressure, whereas hippo populations adjacent to more densely populated areas would experience higher hunting pressure. Unregulated hunting was modelled by decreasing adult survival (age classes 4 & 5) by 0.05% and 1%, to represent low and moderate hunting pressure respectively.

The model population's sensitivity to each of the disturbances was assessed by the proportion of simulation

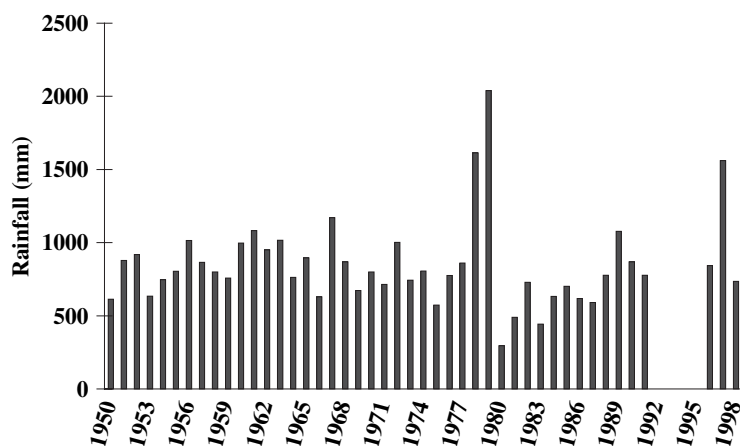


Fig 3 Rainfall data from Katavi National Park, Tanzania. Data were compiled from local (International Research Institute for Climate Prediction, Rukwa Region Land Planning Office) and Park records. Data for 1993–1995 were incomplete

Table 4 The human disturbances included in the model

Disturbance	Cause	Modelled as
Small-scale habitat loss	Water diverted from lakes and rivers for agriculture	5% reduction in fecundity
Low hunting pressure	Unregulated hunting targeting adults	0.05% reduction in annual adult survival
Moderate hunting pressure	Unregulated hunting targeting adults	1% reduction in annual adult survival

Table 5. The impact of disturbance scenarios on the model hippo population with and without consideration of typical rainfall variability

	Without rainfall variability			With rainfall variability		
	<i>P</i> (30)	<i>P</i> (40)	<i>P</i> (50)	<i>P</i> (30)	<i>P</i> (40)	<i>P</i> (50)
Habitat loss	0.31	0.08	0	0.61	0.49	0.37
Moderate hunting pressure	0.14	0	0	0.58	0.47	0.34
Low hunting pressure	0	0	0	0.41	0.28	0.17

P (30), *P* (40), *P* (50) are the probabilities of the model population declining to 30%, 40% and 50% of its original size of 5000 individuals. The probability values were calculated as the percentage of the simulation iterations that crossed each threshold over 60 years.

runs in which the population dropped below three population size thresholds – 3500, 3000 and 2500, individuals. Population thresholds are often used to represent quasi-extinction or minimum viable population levels (Brook & Kikkawa, 1998). Here the thresholds represent a boundary into a larger risk category – a population that has declined 30%, 40%, or 50% from its original size. These thresholds were based on IUCN Red List specifications that rely on similar population reductions in the criteria for endangered, threatened, or vulnerable status for an entire population (IUCN, 2001). Each simulation was run for 60 time steps, or years. This approximates three generations, where generation length is defined as the average age of parents of the current cohort. This time horizon has been

chosen by the IUCN as the standard length of time over which population declines should be assessed (IUCN, 2001). Each disturbance simulation was run for 1000 iterations.

Results

Impact of disturbances

I measured the impact of the disturbances on the model hippo population as the proportion of simulation runs in which the population dropped below one of three-risk thresholds (Table 5). Across the entire simulation time period, habitat loss alone yielded the largest likelihood of

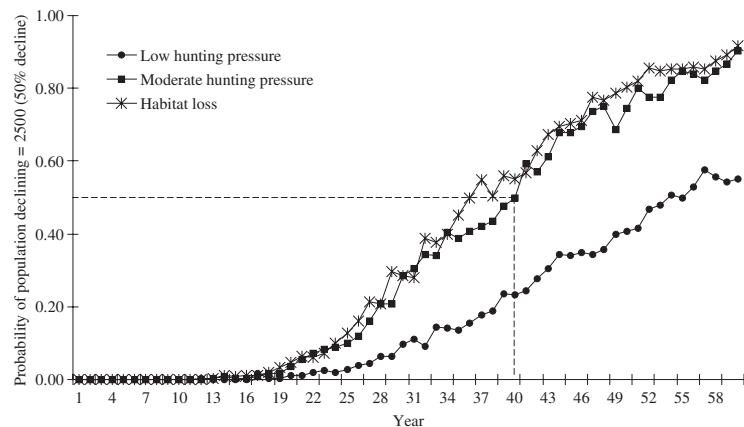


Fig 4 Projections of the likelihood of the model population dropping to 50% of its original size, calculated for each year of the model. The dashed line marks a probability of 0.50

crossing the population-risk thresholds, although even the largest probabilities of decline for this disturbance were low ($P \leq 0.31$). However, the same disturbances when considered in conjunction with rainfall variability resulted in risk likelihoods that were two to five times higher (Table 5). When rainfall variability is included, the cumulative probabilities of crossing even the smallest risk threshold across the entire time period, i.e. 30% population decline, were fairly high for all three disturbances ($P = 0.41$ – 0.61).

To estimate when declines were likely to occur during the simulations, I calculated the per-year probability of the model population crossing the 50% risk threshold, i.e. declining to <2500 individuals. The results suggest that by year 40, even a large hippo population may decline to <50% of its original size in response to some mild or moderate disturbances and environmental variability (Fig. 4).

Discussion

Although the projected trajectories are not powerful as absolute predictors of future trends in hippo populations, these findings point to the importance of integrating human disturbances with natural disturbance regimes. There is evidence that hippo populations in some areas face far more severe disturbances than those included here. For example, recent field surveys found that common hippo populations in Democratic Republic of Congo, once home to the largest hippo populations among African countries, have declined >95% during recent years from very intense hunting pressure (Shoumatoff, 2000; Hillman Smith *et al.*, 2003). In addition, some climate models predict that in many areas of East Africa, the frequency of

drought will increase as global temperatures rise (Bwango *et al.*, 2000). Although it is clear that including more intense or severe disturbances would lead to greater population declines, it is important to note that even relatively mild to moderate human disturbances, when coupled with realistic environmental variability, led to substantial population changes. Because population models must balance biological realism and model complexity, incorporating realistic environmental variability may be challenging. However, without considering natural disturbance regimes, population projections for environmentally sensitive species may be overly optimistic in assessing the effects of anthropogenic activities.

The use of population risk thresholds as indicators of vulnerability has been applied to population models before (Gerber, DeMaster & Kareiva, 1999; Gerber & DeMaster, 1999). Shifting the focus from population viability to vulnerability acknowledges the uncertainty inherent in population models and redefines population models as tools to determine relative, rather than absolute, threats (Beissinger & Westphal, 1998; Groom & Pascual, 1998; Regan, Colyvan & Burgman, 2002). Delineating risk thresholds can also facilitate classification of increased vulnerability and population recovery (Gerber & DeMaster, 1999). This approach also provides a means for land-managing agencies to identify risk thresholds relevant to management, i.e. population sizes thresholds below, which intervention or management is likely to be less effective or too costly.

The hippo population modelled here is designed to characterize wild hippo populations in African regions, particularly East, Southeast and South Africa where the largest numbers of common hippo are currently found.

Because the model is based on demographic data from several protected areas, and incorporates typical features of hippo populations from several countries, the model population is representative of large, wild hippo populations. The model's primary assumption is that hippo demographic rates are not constant over time. Previous research strongly supports the assertion that these rates fluctuate with rainfall (see Introduction). Despite their large size, longevity, and flexible demographic rates, wild hippo populations are likely to exhibit sensitivity in response to the combined effects of responses to annual rainfall fluctuations and anthropogenic factors. Given our current understanding of hippo ecology and available demographic data, substantial population declines for common hippos are likely if wetland habitat loss continues, particularly if hunting pressure also intensifies. For hippos, and for other environmentally sensitive species, considering the impacts of both natural and human-mediated disturbances is likely to be important to ensure population persistence.

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