Effects of environmental change on population growth: monitoring time-varying carrying capacity in free-ranging spotted hyenas

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April 11, 2024

Abstract

Trends in population sizes influence conservation decisions, but such trends can be misleading since a population can grow even as carrying capacity falls. Population growth requires population size to be below carrying capacity but is agnostic to trends in carrying capacity. We developed an approach to estimate time-varying carrying capacity (K_{t}), an integrative metric to monitor all environmental variables impacting vital rates in a population. We used individual-based modelling to quantify K_{t} for a recovering population of spotted hyenas and investigated whether population growth could be explained by recent environmental change. Population growth occurred despite no linear trend in K_{t}, suggesting that the observed growth is the lingering effect of past, rather than recent, environmental improvements. This study illustrates that recovery can occur at different time scales for the environment and for a population. Considering this demographic lag matters for the effective conservation of long-lived species.

1 Introduction

The world is confronting an acute biodiversity crisis, with population declines and extinctions occurring across major taxonomic groups (Barnosky et al., 2011; Ceballos et al., 2017; Pimm et al., 2014; WWF, 2022). Changes in the biotic and abiotic environment, such as the expansion of invasive species, habitat loss, and climate change, are key factors driving modern biodiversity loss (Mazor et al., 2018). Consequently, many conservation programs strive to improve environmental conditions to achieve species conservation. For example, conservation programs may protect habitats from human disturbance (Maxwell et al., 2020), reduce competition from invasive species (Prior et al., 2018), or increase the availability of limited resources such as food and shelter (Lindenmayer et al., 2009; Murray et al., 2016). In contrast, the evaluation of conservation outcomes often relies on measuring trends in population size rather than changes in environmental conditions (Badalotti et al., 2022; Crees et al., 2016; IUCN, 2012; Mace et al., 2008; WWF, 2022). Unfortunately, population size is an unreliable indicator of recent changes in environmental conditions, potentially undermining effective conservation decision making.

Both population growth and decline can occur independently of recent trends in environmental conditions (Fig. 1). In some cases, such as in short-lived and highly fecund species, population growth can occur rapidly in response to improving environmental conditions (Fig. 1A; e.g. Monaghan et al., 2020). However, the maximum attainable population growth rate is restricted by population demography (e.g. sex ratio) and species-specific life-history constraints (e.g. maximum litter size; Ackleh et al., 2018; Coulson and Hudson, 2002; Koons et al., 2007), meaning that population growth often cannot occur as rapidly as changes in the environment. In this case, trends in population size do not accurately reflect recent environmental change, but rather the combined effect of environmental change that has occurred at various times in the past.

Limits on population growth are particularly important in species with longer generation times, such as long-lived mammals (Coulson and Hudson, 2002). In such circumstances, population growth may persist even after environmental conditions have stabilised (Fig. 1B). In fact, such lingering effects of past environmental improvement can mask recent declines in environmental conditions (Fig. 1C). To complicate matters further, changes in population size can also occur due to non-environmental processes such as demographic stochasticity (Lande, 1993) or positive density dependence (i.e. Allee effects; Courchamp et al., 1999; Stephens et al., 1999). Therefore, trends in population size are an inaccurate proxy for recent trends in environmental conditions. Alternative metrics directly derived from population size (e.g., instantaneous growth rate; Sibly and Hone, 2002) have similar limitations.

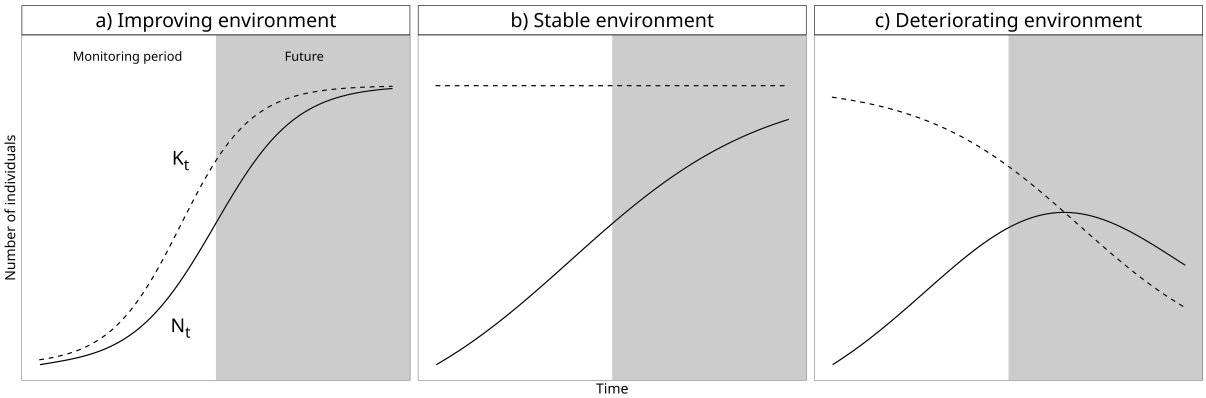

Figure 1: **Population growth can occur under drastically different scenarios of environmental change.** Plots show changes in population size (N_t; solid line) and time-varying carrying capacity (K_t; dashed line) under three hypothetical scenarios. Population monitoring is ongoing in the white region (left). The grey shaded region (right) shows future changes. Population size at the beginning or end of the monitoring period is identical across all three panels. a) Improving environment: The population is near carrying capacity at the start of the monitoring period. Carrying capacity increase (e.g. due to successful conservation) and population size increases rapidly in response. b) Stable environment: Carrying capacity increases before the monitoring period but has been constant since monitoring began. Population growth rate is less rapid than changes in carrying capacity and the population is still below carrying capacity at the start of the monitoring period (i.e. $N_t < K_t$). During the monitoring period the population grows while carrying capacity remains stable. c) Deteriorating environment: Similar to scenario b), population size is below carrying capacity at the start of the monitoring period (i.e. $N_t < K_t$); however, during the monitoring period carrying capacity declines. Deterioration in environmental conditions will eventually lead to population decline once $N_t > K_t$. The three scenarios were generated assuming a simple discrete time logistic growth model. In scenario a) and c), carrying capacity is also itself a logistic function of time (*sensu* Meyer and Ausubel, 1999).

To avoid the problems caused by a reliance on population size, conservation assessments should also attempt to measure changes in the biotic and abiotic environment over time. *Carrying capacity* (often referred to as K) is one metric that can be adapted for this purpose. This metric is indeed commonly used in conservation to capture the effects of all environmental variables that influence a target population, even those that may be hard, or impossible, to measure directly. K is often treated as a fixed number of individuals that could be supported by the environment (Chapman and Byron, 2018; Dhondt, 1988). However, the environment, and therefore carrying capacity, both vary over time. Variation in the environment necessarily influences the size of a population through the vital rates (functions describing variation in survival and fertility) of its individuals. Therefore, carrying capacity should be understood as an emergent property of the vital rates of all the individuals of a population (Mallet, 2012). Rather than treating carrying capacity as static as it is usually done, it is therefore useful to consider carrying capacity as variable (e.g. Britten et al., 2017; Fukasawa et al., 2013; Hinrichsen and Paulsen, 2020; Kaeriyama et al., 2009; Meyer and Ausubel, 1999; Zehnder and Hunter, 2008). For clarity, we refer to carrying capacity that is allowed to vary over time as *time-varying carrying capacity* or K_t.

In this paper, we introduce a method to quantify K_t using a combination of vital rate estimation and population projection performed using individual-based modelling (DeAngelis and Grimm, 2014; Judson, 1994). To demonstrate our method, we apply it to a free-ranging population of large carnivores: the spotted hyenas (*Crocuta crocuta*) of Ngorongoro Crater, Tanzania. This population has been monitored continually for almost three decades (April 1996-present), making it one of the most closely monitored large carnivore populations in the world (Bonnet et al., 2022). For much of the first two decades of study, spotted hyenas in Ngorongoro Crater experienced population growth (Höner et al., 2005, 2012). This population growth could be attributed to conservation interventions and natural phenomena that have occurred during the study period, such as increased restrictions on road use (Table S2) or changes in spotted hyena prey abundance (Höner et al., 2005). However, as we have discussed above, such population growth could also be the consequence of the lingering effects of past environmental change. Quantifying K_t helps to disentangle these possible explanations.

In our analysis, we quantify time trends in population size, vital rates, and K_t in spotted hyenas between 1997 and 2021. We use K_t to estimate environmental conditions in each year and assess whether population growth in spotted hyenas indicates a recent improvement in environmental conditions or lingering effects of past environmental change. We expected physiological constraints on reproduction in spotted hyenas to place limits on maximum possible population growth, making observed population growth more likely to be affected by past environmental change. By estimating K_t, we also determine whether the population has reached demographic equilibrium and estimate how different variables (e.g. disease, competition) have driven carrying capacity over the past 25 years. Finally, we discuss how our method could be used for similar assessments in other populations or species.

2 Results

2.1 Population size and demographic composition

In the late 1960s, Kruuk (1972) assessed the number of adult spotted hyenas in Ngorongoro Crater at 385 individuals. Between the 1960s and 1990s, the population experienced a large decline, with population size falling to 31% of previous estimates (119 adults, 65 juveniles; April 1996). Long-term monitoring since April 1996 has documented population growth (Fig. 2a). Between April, 1996 and April, 2012, population size grew at a rate of 23 individuals of all ages per year until reaching numbers comparable to Kruuk's estimates from the 1960s (375 adults, 180 juveniles). At this point, we consider the population to have recovered from the population decline that occurred prior to 1996. Since recovery in 2012, the population has varied around a median of 463 individuals (range: 350 – 608), with periods of decline in 2012-2013 and in two consecutive periods 2018-2019 and 2019-2020. The most recent decline occurred during an outbreak of *Streptococcus* infection, with the population reaching its lowest level since 2012 (350 individuals) in May, 2020.

The age ratio of the population was strongly biased against juveniles ($\leq$ 24 months) for the full study period (median ratio juveniles/all individuals = 0.335; range = 0.209-0.407; red line in Fig. 2b). Bias against juveniles increased slightly during the study period (β_{ageratio} = -0.003, 95% Confidence Interval or $\text{CI}_{95\%}$ = -0.005/-0.001; Likelihood Ratio Test p = 0.004). Adult sex ratio (number of adult males/total number of adults) showed a slight female bias for the majority of the study period, ranging from 0.417 to 0.527 (median = 0.464, black line; Fig. 2b). Adult sex ratio showed no significant change over time (β_{sexratio} = -0.002, $\text{CI}_{95\%}$ = -0.004/0.001; LRT p = 0.108).

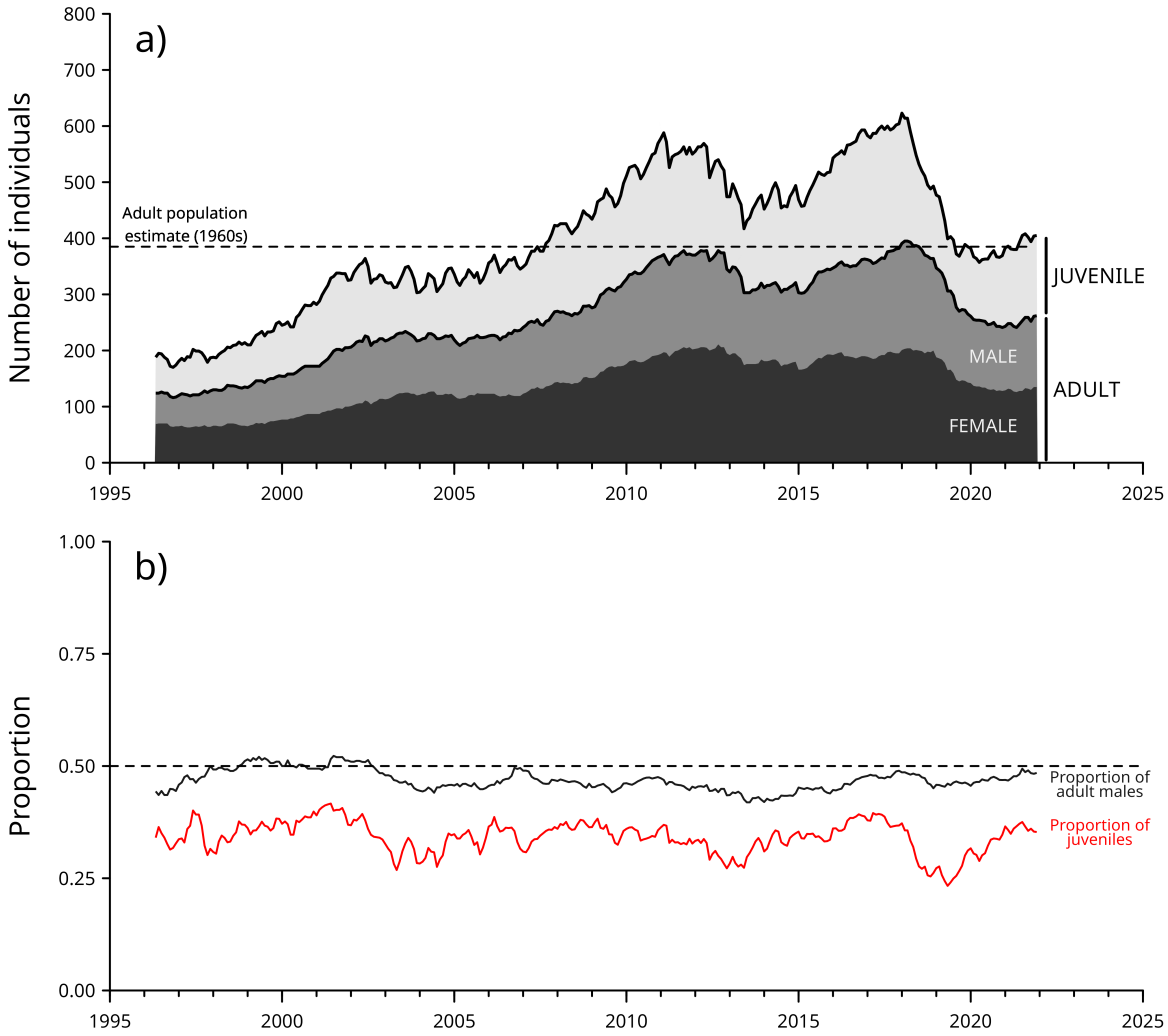

Figure 2: **Yearly population size, proportion of adult males, and proportion of juvenile spotted hyenas in Ngorongoro Crater, Tanzania since 1996**. a) Population size. Colours distinguish adults ($\geq$ 24 months) of known sex (female: darkest grey; male: dark grey) and juveniles (light grey). Seven adults with unknown sex were excluded. Horizontal dashed line represents estimated number of adult individuals during the 1960s (Kruuk, 1972). b) Proportion of juveniles (juveniles/all individuals; red line) and proportion of adult males (adult males/all adults; black line). Dashed line represents a value of 0.5 at which there would be no bias towards a particular age group or sex. Data rely on re-sightings and parentage analysis to estimate dates of death and birth and are thus slightly less reliable in the last year (2022), where such information was not fully available at the time of analysis.

2.2 Carrying capacity

To assess environmental conditions over the study periods we estimated time-varying carrying capacity (K_t) for each year from 1997 to 2021, using an individual-based modelling approach. Carrying capacity was not estimated in 1996 as demographic information was incomplete in this first year of monitoring. Carrying capacity in each year (t) was estimated as the asymptotic population size around which our individual-based model stabilised when conditions observed in year t were assumed to persist indefinitely. Our individual-based

model relies on a set of statistical models fitted on vital rates using the R package spaMM (Rousset and Ferdy, 2014), which we parameterised with the long-term data collected on spotted hyenas in Ngorongoro Crater (see Supplementary material 1). These models were used to simulate the reproduction and survival of individuals at each time step of the simulation (months) conditional on random effects describing yearly environmental variation. We assumed that density dependence operates at the level of spotted hyena social groups (clans), meaning that the size of each of the eight clans in a simulation run also stabilises around an asymptotic clan size. Our approach estimates a value of carrying capacity for each clan individually (denoted K_{tc}) as well as the population as a whole (K_{t}). Density dependence acting on individual vital rates within each clan translates into density regulation that impacts population growth (Supplementary material 2).

Although we use the letter K to denote carrying capacity, this should not be confused with the term K in the logistic growth model. The statistical models fitted on vital rates used within the individual-based model are mechanistic and so we do not directly impose an upper limit on population size as is the case in the traditional logistic growth model. As mentioned in introduction, K_{t} is instead an emergent property of the individual-based model (Grimm and Railsback, 2005; Radchuk et al., 2019).

In contrast to population growth, there was no linear trend in time-varying carrying capacity (K_{t}) during the study period (Fig. 3; $\beta_{K_{\mathrm{t}}}$ = -2.36; $\mathrm{CI}_{95\%}$ = -9.22/4.58; LRT p = 0.531). During the study period, there were three periods of sharp environmental decline where K_{t} declined to $\leq$ 80% of the previous year (2001-2002, 2010-2011, 2017-2019). At the clan level, only one of the eight clans experienced a significant linear decrease in K_{tc} with time (β_{year} = -1.96; $\mathrm{CI}_{95\%}$ = -3.10/-0.68; see Supplementary material 3 section S3.2). There was also no significant trend in either K_{t} or K_{tc} when focusing only on the period of population growth between 1996 and 2012 (see Supplementary material 3 section S3.2).

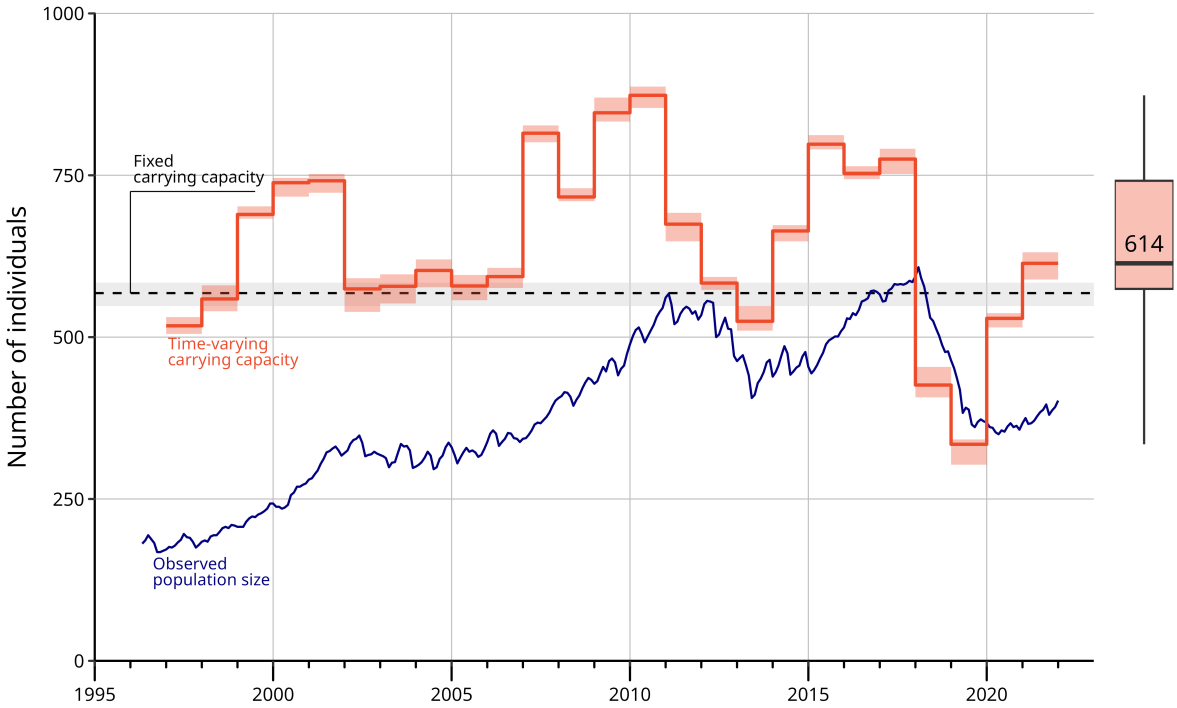

Figure 3: **Carrying capacity of spotted hyenas shows large inter-annual variation but no linear trend over the years.** The solid red line shows annual median carrying capacity estimated using the spotted hyena individual-based model (SHIM). The marginal boxplot shows the distribution of median carrying capacity values across all years (1997 - 2021). The median value of all annual estimates was 614. The dashed line shows fixed carrying capacity estimated from SHIM without considering inter-annual variation, which closely matches estimates using traditional demographic models (Supplementary material 3 section S3.3). The shaded areas around carrying capacity values show the range of carrying capacity estimates across ten simulation runs. The blue solid line shows annual population size of all spotted hyenas in Ngorongoro Crater (juveniles and adults of both sexes) since April 1996.

Since there was no significant linear trend in carrying capacity, average global K_t during the monitoring period (median = 610 individuals; harmonic mean = 612 individuals) was close to carrying capacity estimates produced using traditional demographic equations that assume a static carrying capacity. For example, Ricker and Beverton-Holt models (Johst et al., 2008) yielded carrying capacity estimates that were ca. 85% of average K_t from our individual-based model (range = 521 - 533). Treating predictions of vital rates as independent from time yielded a similar (fixed) estimate of carrying capacity (median = 566 individuals; range = 549 - 586; see Supplementary material 3 section S3.3).

2.3 Population size and carrying capacity

Population size was over 300 individuals below carrying capacity when K_t was first estimated in 1997, and continued to be more than 100 individuals below carrying capacity until 2012. By comparing trends in population size and carrying capacity we can observe empirical examples of all the scenarios described in Fig. 1. There were seven years with concurrent increases in

both carrying capacity and population size (Fig. 1a; top right quadrant in Fig. 4). In three other cases, we observed population growth even though carrying capacity was decreasing (Fig. 1c; top left quadrant in Fig. 4), while in four cases population size grew although carrying capacity was mostly unchanged (i.e. did not grow or decline by more than 5%). In all 14 of these years, population growth occurred when $N_{\mathrm{t}} \leq K_{\mathrm{t}}$. In two additional cases, $N_{\mathrm{t}} > K_{\mathrm{t}}$ which caused population size to decline. From 2018 to 2019, both population size and carrying capacity declined concurrently (bottom left quadrant; Fig. 4a). In 2019 to 2020, we observed a case where population size declined although carrying capacity increased (bottom right quadrant; Fig. 4a). The other eight years included cases where both N_{t} and K_{t} declined (three cases), N_{t} declined despite K_{t} being stable (one case), and cases where N_{t} remained mostly unchanged regardless of changes in K_{t} (less than 5% change; four cases). We never observed N_{t} to decline when $N_{\mathrm{t}} < K_{\mathrm{t}}$, which supports the validity of our demographic model.

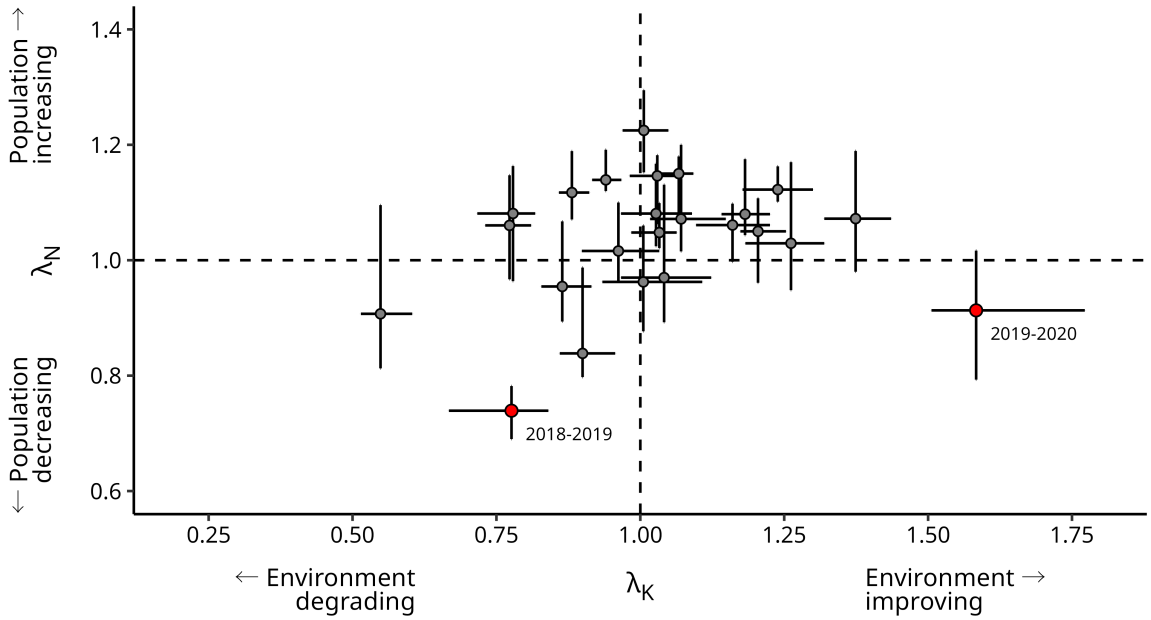

Figure 4: **Change in population size (λ_N) is uncorrelated with change in time-varying carrying capacity (λ_K) in spotted hyenas.** The points represent median values of λ. Red points highlight the two cases where $N_{\mathrm{t}} > K_{\mathrm{t}}$ (2018-2019, 2019-2020) as discussed in the text. The horizontal error bars represent uncertainty in λ_K and show the range of possible λ_K values calculated from all possible combinations of simulation runs between years. See Supplementary material 3 section S3.4 for plot with year labels for all points.

Inter-annual change in carrying capacity ($\lambda_K = K_{\mathrm{t+1}}/K_{\mathrm{t}}$) and population size ($\lambda_N = N_{\mathrm{t+1}}/N_{\mathrm{t}}$) were not significantly correlated (Pearson's correlation = 0.218; p = 0.306; Spearman correlation = 0.228; p = 0.283), illustrating that population growth is not a reliable indicator of recent changes in environmental conditions.

2.4 What drives variation in carrying capacity?

While we observed no significant linear trend in time-varying carrying capacity, we did observe large inter-annual variation in time-varying carrying capacity between 1997 and 2021 (range = 327 - 865; σ = 131). The presence of such variation in K_{t} provides us with the opportunity to study the intrinsic drivers of population change (i.e. vital rates). It also provides us with the opportunity to explore the effect of external drivers (i.e. abiotic and biotic environmental variables) that may impact carrying capacity.

2.4.1 Carrying capacity and vital rates

Time-varying carrying capacity (K_{t}) is an emergent property from our individual-based model and it stems directly from internal statistical models fitted for six vital rates: female survival, juvenile male survival, adult male survival, female primiparous reproduction, female non-primiparous reproduction, and twinning. All six model fits accounted for density dependence (at the clan level) and effects of confounding variables, such as age and social rank (see Supplementary material 1 for a full description of models). All models assumed that vital rates fluctuated over time due to changing environmental conditions within each clan and this variation was captured by a nested random intercept term (year within clan). See Supplementary material 1 for more detail on model structure.

To test for linear trends in vital rates we tested the significance of a quantitative year term in our existing statistical models of vital rates. Monthly probability of female survival, male survival, and twinning showed no significant linear trend (Fig. 5; Supplementary material 3 Fig. S11). The probability of both primiparous and non-primiparous reproduction significantly *decreased* over time after accounting for confounding variables (Fig. 5; Supplementary material 3 Fig. S11).

To measure the extent to which variation in individual vital rates would affect K_{t}, we ran an elasticity analysis of our individual-based model and measured the response of K_{t} to proportional changes in each vital rate. Time-varying carrying capacity (K_{t}) was much more sensitive to changes in female survival than to any of the other vital rates (Supplementary material 3 Fig. S7).

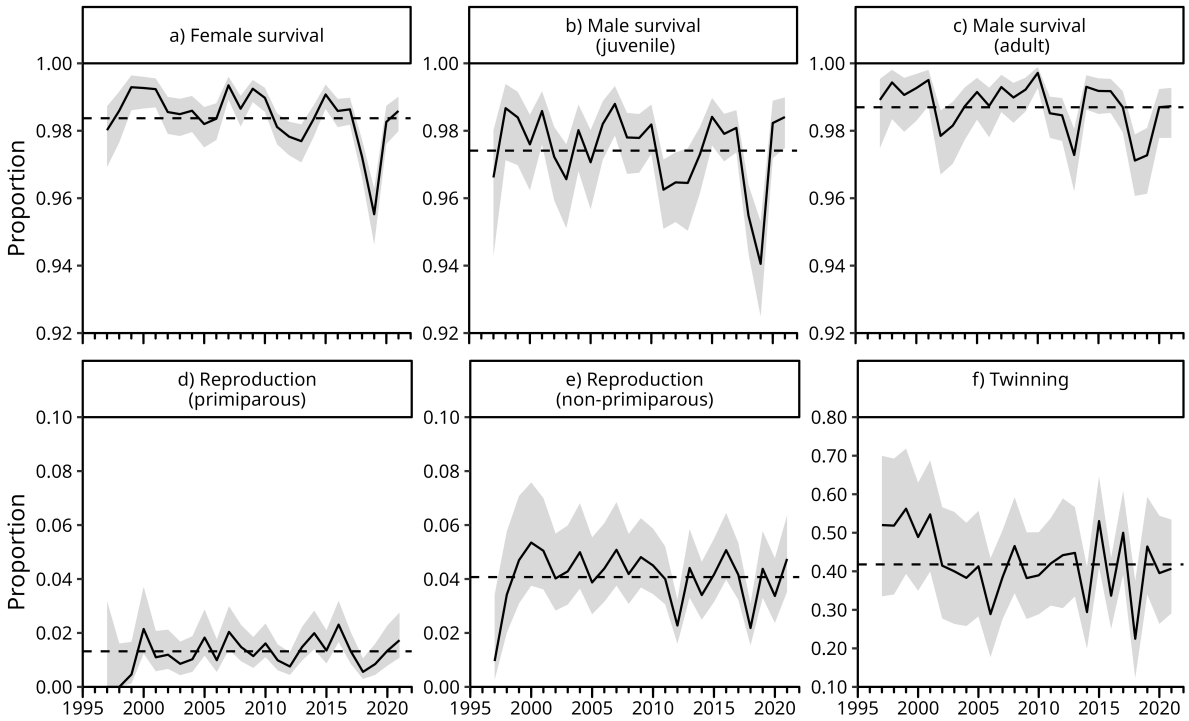

Figure 5: **Vital rates of spotted hyenas show no positive linear trends over the years.** The solid lines represent the monthly proportion of 'successful' outcomes for each vital rate, with shaded regions showing 95% confidence intervals calculated using the Wilson method (Wilson, 1927) Dashed horizontal line represents the mean of each vital rate over the full study period. We observed no significant linear change in survival or twinning over time. Rates of reproduction significantly declined when accounting for additional co-variates (e.g. age, clan) as shown in partial dependence plots in Supplementary material 3 Fig. S11. Note that the range of the y-axis is not the same for all panels.

2.4.2 Carrying capacity and environmental drivers

To assess how changes in the environment could explain variation in K_{t} we fitted a statistical model with carrying capacity at the clan level (K_{tc}) as the response variable and five potential candidate predictors. Predictors were selected *a priori* so as to capture major potential drivers of population change (inter-specific interactions, infectious disease and anthropogenic impacts/conservation measures). We conducted analysis at the clan level to account for variation in predictors expected between clans (e.g. heterogeneity in abundance of prey and competitors). We included a semi-quantitative estimation of prey abundance and a quantitative estimation of the abundance of lions (*Panthera leo*) – the main competitor of spotted hyenas – as two variables capturing the impact of inter-specific interactions. We included a quantitative variable to estimate the proportion of spotted hyenas observed with signs of infectious disease to account for effects of pathogens. *Streptococcus* infection is associated with clinical signs that can be identified in the field (Höner et al., 2006). We also included two binary variables characterising known conservation measures (whether road use was restricted and whether Maasai pastoralists were allowed to visit Ngorongoro Crater with cattle; Table S2). All quantitative variables were Z-scored for comparison.

Carrying capacity was significantly impacted by prey abundance, infectious disease, and lion competitors (Table S6, Fig. 6, Fig. S12). Clan territories were able to support more individuals when there was higher prey abundance (β_{prey} = 4.77; $\text{CI}_{95\%}$ = 1.46/9.01; LRT p = 0.015). In contrast, carrying capacity was significantly negatively effected by infectious disease (β_{disease} = -4.20; $\text{CI}_{95\%}$ = -7.47/-0.50; LRT p = 0.03) and lion density (β_{lion} = -5.30; $\text{CI}_{95\%}$ = -9.69/-0.03; LRT p = 0.04). Management interventions to restrict road use and cattle grazing in Ngorongoro Crater had no significant effect on carrying capacity estimates. See full models results in Supplementary material 3 section S3.6.

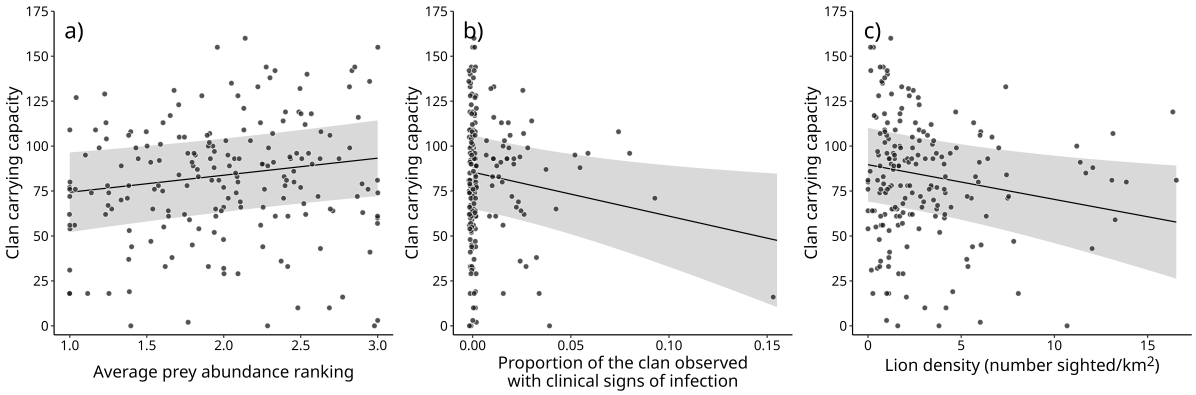

Figure 6: **Carrying capacity is affected by prey, infectious disease, and competitor density.** Plot shows marginal predictions and 95% confidence intervals from fitted models for a) prey abundance, b) proportion of infectious disease sightings, and c) lion density. Other results are shown in Fig. S12. Carrying capacity of clans increases with local prey abundance. Conversely, carrying capacity is lower in clans with more sightings of infectious disease and higher lion density. Note that points on all plots are slightly jittered by 0.002 units on the x-axis to make them easier to distinguish.

2.5 Discussion

Modern conservation places a strong focus on monitoring trends in population size (IUCN, 2012; WWF, 2022), but this approach has its limitations because population size is an unreliable indicator of recent environmental conditions. In this paper, we show how time-varying carrying capacity (K_t) can be used to more directly estimate environmental conditions and provide additional information to that gained from population size alone. We apply our approach to study a free-ranging population of spotted hyenas in Ngorongoro Crater, Tanzania using an individual-based model parameterised on 25 years of long-term data (1997 - 2021) — the Spotted Hyena Individual-based Model (SHIM). Time-varying carrying capacity of the population showed large inter-annual variability, likely as a consequence of changes in prey abundance, infectious disease outbreaks, and competition with lions. However, in contrast to population size, carrying capacity showed no significant linear trend over the study period. We now discuss what these findings can tell use about the current demographic status of the population and the efficacy of past and future conservation interventions. We then discuss how our approach could be applied to other wildlife populations.

When monitoring began in 1996 the population size of spotted hyenas in Ngorongoro Crater was substantially smaller than in the late 1960s (Höner et al., 2005; Kruuk, 1972). Our estimates of time-varying carrying capacity suggest that environmental conditions in 1997 (the first full year of monitoring) were already sufficient to support a much larger population. Despite this, it took the population at least 16 years to return to its previously observed population size. Similar extended recovery rates have also been observed in spotted hyenas in the Serengeti (Benhaiem et al., 2018). Population growth during this period therefore appears to be a delayed response to environmental improvement that occurred prior to the monitoring period, rather than an immediate response to concurrent environmental change. Our results suggest that conservation actions over the past decades (Table S2) did not lead to a net improvement in conditions for spotted hyenas in Ngorongoro Crater despite observed population growth. Such conclusions would be impossible to draw using measurements of population size alone.

Our results illustrate that population size may take years or even decades to reflect changes in environmental conditions (Ackleh et al., 2018; Capdevila et al., 2022; Raimondo and Donaldson, 2003). The speed at which a population responds to environmental change varies greatly between species and populations (Ackleh et al., 2018; Coulson and Hudson, 2002; Koons et al., 2007). Slower responses are typical of species with longer generation times that often experience physiological constraints on reproduction (Coulson and Hudson, 2002; Koons et al., 2006, 2007), such as the maximum litter size and the minimum inter-birth interval. The spotted hyena exhibits a late age at first reproduction (3-5 years; Davidian et al., 2016; Gicquel et al., 2022; Holekamp et al., 1996; Höner et al., 2010, see

Supplementary material 2), long inter-birth interval (20 months average; Supplementary material 2), and small litter size (commonly 1-2 cubs Frank, 1986; Holekamp et al., 1996). These features constrain maximum population growth in spotted hyenas and likely explain the long period of recovery from declines seen in spotted hyenas (Benhaiem et al., 2018, this study). In a similar example, long-lived red deer on the Isle of Rum took 10 years to reach carrying capacity despite an immediate removal of mortality from hunting in 1972 (Albon et al., 2000; Coulson and Hudson, 2002).

In the most favourable years, we estimate that Ngorongoro Crater could have supported as many as 865 spotted hyenas. However, the population never reached this maximum theoretical size due to periods of poor environmental conditions that caused population declines and led to extended periods of recovery. Infectious disease and inter-specific interactions (prey abundance and competitor density) were key factors affecting carrying capacity in spotted hyenas, in agreement with our existing knowledge of the species. Infectious disease outbreaks are known to be major sources of mortality in spotted hyenas (Höner et al., 2012; Marescot et al., 2018) and other large carnivores (Kissui and Packer, 2004; Young, 1994). Outbreaks of *Streptococcus* infection in both 2002 and 2019 were major sources of mortality for spotted hyenas in Ngorongoro Crater specifically (Dheer et al., 2022; Höner et al., 2012; Höner et al., 2006). Similarly, variation in prey abundance is a key environmental factor in spotted hyenas (Hofer and East, 1993) and has been proposed as one of the potential causes of spotted hyena decline in Ngorongoro Crater prior to 1996 (Höner et al., 2005). Importantly, conservation efforts since 1996 to limit road use and Maasai pastoralism activity inside Ngorongoro Crater had no discernable effect on carrying capacity, supporting previous findings that pastoralism had no negative effect on spotted hyena recruitment (Dheer et al., 2022) and helping explain the lack of a significant linear trend in time-varying carrying capacity over time.

If prey and competitor population dynamics and the frequency of infectious disease outbreaks remain similar in the future to those of the past 25 years we would expect population size to show similar patterns to those observed since recovery was reached in 2012. However, patterns of prey abundance and infectious disease are likely to shift in the context of climate change. Temporal shifts in climatic conditions have already become evident in East Africa over the past century, with increasingly frequent heavy rain events contrasted with more frequent and severe droughts (Nicholson, 2017). Heavy rainfall can elevate disease risk by increasing the abundance of disease vectors, such as biting insects (Chowell et al., 2019; Gallana et al., 2013). Conversely, drought events can increase disease transmission by increasing aggregation of potential hosts around limited water resources (Franz et al., 2018; Gallana et al., 2013) and acting as an additional stressor on wildlife, making them more vulnerable to infection (Acevedo-Whitehouse and Duffus, 2009).

Changes in the prey community are also expected as a consequence of climate change (Moehlman et al., 2020). Long-term trends towards hotter and drier conditions will likely

favour smaller-bodied herbivores, such as gazelle, over those larger-bodied herbivores that depend on bulk-forage, such as buffalo (Moehlman et al., 2020). At the same time, increased rainfall variability is expected to lead to increased variation in the abundance of many key prey species for spotted hyenas (Moehlman et al., 2020). Climate change is also expected to affect the availability of suitable forage for herbivores by facilitating the spread of unpalatable invasive weeds during heavy rain events (Ngondya and Munishi, 2021; Nyarobi et al., 2022). Spotted hyenas are flexible in both their diet and hunting strategies (Hofer and East, 1993; Höner et al., 2002; Yirga et al., 2012) which should allow them to adjust to shifts in prey communities. However, any changes to hunting behaviour that require spotted hyenas to forage over larger distances will likely reduce vital rates, particularly for individuals lower in the social hierarchy (Hofer and East, 1993).

Our case-study of spotted hyenas illustrates the conceptual and practical insights that can be gained by combining time-varying carrying capacity as an integrative measure of environmental conditions with long-term data on population size. Time-varying carrying capacity should be thought of as an *enhancement* rather than *replacement* for measuring population size. Large carrying capacity does not guarantee population growth in cases where population reach such low population sizes that their dynamics can be governed by non-environmental factors, such as demographic stochasticity (Lande, 1993) or positive density dependence (i.e. Allee effects; Courchamp et al., 1999; Stephens et al., 1999). Small populations in favourable environmental conditions may still benefit from conservation interventions that directly promote population growth, such as population supplementation (Seddon et al., 2014) or reducing inbreeding depression (Hohenlohe et al., 2021; Kardos et al., 2021). Only by measuring *both* population size and time-varying carrying capacity can the most appropriate conservation actions be identified.

2.5.1 Application of the method to other populations and species

Individual-based modelling provides a powerful and flexible tool to estimate time-varying carrying capacity that can integrate complex species-specific behavioural and ecological characteristics (e.g., Neil et al., 2020; Ovenden et al., 2019; Piacenza et al., 2017; Radchuk et al., 2021). In theory, other modelling approaches that are capable of population projection – such as matrix-based demographic models and integral projection models (IPM; Easterling et al., 2000) – present possible alternative methods to estimate time-varying carrying capacity. The only structural requirement is that the model can predict population size and reach demographic equilibrium when environmental conditions are stable.

Regardless of the method chosen, estimating time-varying carrying capacity will require reliable estimates of vital rates. Ideally, vital rate information should be collected under a

range of demographic and environmental conditions that approximate as close as possible the conditions that are to be simulated (e.g. varying population size). For long-lived species, the collection of such data necessarily entails the long-term study of individuals in the wild. Such data are difficult and costly to collect (Sheldon et al., 2022) and thus are most likely to be available for large flagship conservation or research programs (e.g., Culina et al., 2021; Morrison et al., 2022). Where possible, missing information may be drawn from other populations of the same species or closely related species with similar life-history characteristics (Coulson and Hudson, 2002; Heppell et al., 2000; Hernández-Camacho et al., 2015).

When collecting individual-level data is infeasible, there is still a possibility to estimate trends in time-varying carrying capacity using ecological proxies such as food availability (e.g., Hayward et al., 2007; Karanth et al., 2004) or territory availability (e.g., Jones et al., 2022). Environmental proxies reduce the need for individual-level data but present their own limitations. Measuring environmental proxies can still impose non-trivial data collection and computational challenges (Jones et al., 2022; Karanth et al., 2004). Unlike time-varying carrying capacity, environmental proxies cannot provide information about how close a population is to its demographic equilibrium, which limits any possibility to predict future population growth and abundance. It is also usually unknown how well environmental proxies correlate with time-varying carrying capacity. If the correlation between an environmental proxy and time-varying carrying capacity is weaker than expected, relying on environmental proxies can lead to unreliable results. Nevertheless, ecological proxies provide a key alternative method to estimate environmental conditions and supplement information on population size in cases of data limitation.

2.6 Conclusions

In this paper, we have proposed time-varying carrying capacity as an additional source of conservation information that overcomes the limitations created by a reliance on measuring population size. Time-varying carrying capacity allows better assessment of environmental conditions important to a target species or population and provides a more direct metric to assess conservation effectiveness. Our results show how time-varying carrying capacity can disentangle effects of recent environmental change from lingering effects of past environmental change, something which would be impossible using population size alone. Lingering effects of past environmental change are particularly common in long-lived species, making such effects directly relevant for modern conservation, where many charismatic ‘flagship’ species that garner public attention and investment tend to be long-lived (Clucas et al., 2008; Davies et al., 2018). Quantifying time-varying carrying capacity greatly expands the toolkit available to conservation managers and facilitates evidence-based conservation outcomes, which is vital to most effectively address the global biodiversity crisis.

3 Methods

3.1 Study species and population

The spotted hyena (*Crocuta crocuta*) is a large social carnivore that plays an important role in the African savannah ecosystem as a regulator of herbivore disease (Packer et al., 2003), a competitor of other large carnivores (Höner et al., 2002), and as a species capable of digesting large bones and thus releasing calcium and phosphorus concentrated within bones back into the ecosystem (Abraham et al., 2022). Although the spotted hyena is categorised as a species of 'Least Concern', many populations are declining due to impacts of human activity such as culling, poisoning, snares, and roadkill (Benhaiem et al., 2023; Bohm and Höner, 2015; Naciri et al., 2023). Spotted hyenas form clans, consisting of multiple matrilines organized into a relatively stable linear dominance hierarchy (Kruuk, 1972), where cubs obtain a social rank within the dominance hierarchy directly below that of their mother and above older siblings (Frank, 1986; Vullioud et al., 2019). Dispersal is strongly male biased (East and Hofer, 2001; Höner et al., 2005). Most males disperse to new clans once reaching adulthood, where they join the bottom of the social hierarchy (Höner et al., 2007), although male philopatry is also observed (Davidian et al., 2016).

Reproductive success in spotted hyena females is predominantly determined by the position of an individual in the social hierarchy (e.g., Frank, 1986; Höner et al., 2010) – as evidenced by the large skew observed in reproductive success between high and low ranking females (Holekamp et al., 1996). Females reproduce year round, with a gestation time of around 110 days (Matthews, 1939). Litter size ranges from one to three cubs, although competition between siblings means that subordinate siblings in multi-cub litters have a reduced survival (Gicquel et al., 2022; Hofer and East, 2008). Cubs are typically not weaned until 12-20 months of age (Hofer and East, 1995; Holekamp et al., 1996; Watts et al., 2009), and are generally considered sexually mature around 24 months (Matthews, 1939) although age at first reproduction usually occurs between 3-5 years old (Davidian et al., 2016; Gicquel et al., 2022; Holekamp et al., 1996; Höner et al., 2010, Supplementary material 2).

The population of spotted hyenas in the Ngorongoro Crater, Tanzania (3°12'36"S, 35°27'36"E) includes eight clans that defend territories within the 250km^2 area of Ngorongoro crater floor. The population has been monitored since April 1996 as part of the Ngorongoro Hyena Project (`https://hyena-project.com`). Individuals are identified by their unique spotting patterns as well as distinct characteristics like ear notches and scars. Observations of dyadic interactions and genetic-based parentage analyses have allowed for an accurate estimation of the social hierarchy within each clan (Vullioud et al., 2019). Extensive behavioural observations have provided a strong understanding of both male dispersal and female mate choice behaviour (Davidian et al., 2016; Höner et al., 2007).

3.2 Spotted Hyena Individual-based Model (SHIM)

Individual-based models (IBMs) are suitable for modelling complex systems and are used across a range of fields (Farmer and Foley, 2009), including in conservation science (e.g., Boult et al., 2018, 2019; Neil et al., 2020; Ovenden et al., 2019; Piacenza et al., 2017). IBMs integrate effects of demographic and environmental stochasticity. They can also integrate a wide range of mechanisms that may influence population dynamics, including complex animal life-cycles (Piacenza et al., 2017) and extrinsic pressures such as climatic change (Boult et al., 2019).

To study time-varying carrying capacity (K_t) in our study population, we created an IBM that simulates the eight spotted hyena clans within the Ngorongoro Crater. We named this model the 'Spotted Hyena Individual-based Model' (SHIM). We present a brief overview of the simulation model here, but a full description of the model following the 'Overview, Design Concepts, and Details' (ODD) framework (Grimm and Railsback, 2012; Grimm et al., 2006) can be found in Supplementary material 1.

SHIM simulates the life cycle and behaviour of spotted hyenas using discrete time steps (months). In a given month, individuals may reproduce (give birth), die, and disperse - whichever are appropriate for their particular age and sex. These events are determined by stochastic predictions stemming from seven statistical models (Generalised Linear Mixed-effects Models or GLMMs) fitted on observed data from Ngorongoro Crater collected since 1996 using the package spaMM (Rousset and Ferdy, 2014). These statistical models estimate effects of individual characteristics such as age, sex, and rank within the hierarchy, on the survival, reproduction, twinning, and dispersal of spotted hyenas (described in detail in Supplementary material 1).

In each time step, sexually mature females ($\geq$ 24 months) attempt to select a mate following typical mate choice patterns documented in this population (Höner et al., 2007). If at least one suitable male is present in the clan, females have a chance to reproduce with a probability determined by one of the two statistical models for reproduction – one for primiparous females and one for non-primiparous females. Suitable males must be adults ($\geq$ 24 months) and have been born or immigrated into the clan after the female was born. Females that reproduce may have a litter with 1 or 2 cubs. Cases of 3 cub litters are rare in the wild and not considered within the simulation. Each new cub from a reproduction event is given a rank just below that of their mother and above their older siblings following the social inheritance behaviour documented in the system (Frank, 1986).

Field observation of cubs in their first few weeks of life are difficult as they spend most of their time within their birthing den. Young cubs may thus die before ever being observed. To circumvent limitations caused by the unreliable estimation of cub survival, we chose to

integrate early life survival into our measure of reproduction. In our reproduction models, we therefore define a reproduction event as a female that gives birth to a litter where at least one cub survives to 6 months of age. In the simulation, this means that all cubs from a successful reproduction event are assumed to survive for at least 6 months.

The probability that a female has a multi-cub litter was determined by our statistical model for twinning. This statistical model also integrates early life survival such that a multi-cub litter is a litter where more than one cub survives to at least 6 months of age. In our statistical model, we grouped observed litters of both 2 and 3 cubs together, which allowed us to work with a binomial response variable. As mentioned above, cases of 3 cub litters are rare in the wild and so all multi-cub litters in the simulation have a litter size of 2. For convenience, we refer to the probability of multi-cub litters as 'twinning' throughout the manuscript, although multi-cub litters with mixed paternity are possible.

All individuals 6 months or older may die during a time step with a probability determined by our statistical models for survival. Cubs younger than 6 months are excluded from this process as early life survival is already integrated into our statistical models for reproduction and twinning. We used separate survival models for females, juvenile males ($<$ 24 months), and adult males ($\geq$ 24 months). Due to the structure of our male dispersal model (described below) all adult males are necessarily males that have selected a clan (including philopatric males).

Males reaching 24 months are assumed to be adults. At this point, they prospect for a possible new clan in which to disperse. The clan a male chooses is determined by a multinomial model, where the probability of selecting a clan is a function of the relative number of females between one and five years old present in the clan (Höner et al., 2007). The male's birth clan is considered as a possible choice, allowing for the possibility of philopatry (Davidian et al., 2016). If a male enters a new clan (i.e. a non-philopatric male), he is placed at the bottom of the social hierarchy. In contrast, philopatric males keep their previous social rank upon reaching 24 months.

Once a male has selected his first clan (either philopatric or non-philopatric), he has a probability to disperse again at each subsequent time step determined by our statistical model for additional male dispersal. In the field, it is difficult to identify cases where adult males might prospect new clans but do not ultimately disperse. Therefore, this statistical model only considers cases where males move from their current clan to a new clan, and so males cannot reselect their current clan. The probability with which a male selects a new clan is again drawn from a multinomial model with the probability a function of the relative number of young females (between one and five years old) in all clans but their current clan. Males that disperse from their birth clan and return to their birth clan after having lived elsewhere

are not considered philopatric (i.e. they join the bottom of the social hierarchy after dispersal back into their birth clan).

We undertook a pattern oriented modelling approach (Grimm and Railsback, 2005, 2012), to demonstrate the reliability and biological realism of SHIM. We compared the emergent properties of our model to observed demographic patterns in the wild, including patterns of lifetime reproductive success and lifespan of both sexes. SHIM was able to recreate a range of complex demographic patterns observed in Ngorongoro Crater. These comparisons are detailed in Supplementary material 2.

3.3 Estimation of the time-varying carrying capacity

We used SHIM to estimate K_t in Ngorongoro Crater. All statistical models, except for that of male additional dispersal, included inter-annual variability in vital rates through the inclusion of a random effect when simulating life history events using the fitted statistical models. To estimate K_t for a given year (t), we ran SHIM with environmental conditions kept constant to those observed in year t by fixing the inferred realisation of the random effect for that year. In each simulation run, SHIM continued for 1,200 time steps (100 years). Stochasticity in demographic outcomes due to individual characteristics (e.g. age, rank) was included. The value of K_t for a single simulation run was computed as the median population size once the population was considered to have reached equilibrium. We used this method to estimate carrying capacity for every year from 1997 to 2021. The year 1996 was excluded as the population was not monitored for the full year. We excluded recent years (2022-2023) as we considered estimates of survival and reproduction to be less reliable in this period due to fewer opportunities for resightings and time required to process genetic samples used for parentage assignment.

For each year, we carried out 10 independent simulation runs. Each simulation was initialized using the same snapshot of the population observed in April, 1996 (178 individuals), including correct age, sex, rank, and parental relationships. Our final estimate of K_t in each year was then the median value of K_t across all 10 replicates. In this way we could estimate K_t across the study period.

To remove initialization bias (i.e. impact of starting conditions) the first half of each simulation run (50 years) was considered a warm-up period and discarded before estimating K_t. Following the removal of the warm-up period, visual inspection of population size over time was carried out for all replicates to check for trends in population size that would suggest carrying capacity had not been reached. We considered carrying capacity to have been reached in all simulation runs following visual inspection and no further action was taken.

3.4 Comparison to estimates assuming a fixed carrying capacity

We compared our estimate of K_{t} from SHIM with methods that assumed a fixed carrying capacity over time. We reran SHIM using the same statistical models as described above but where stochastic outcomes were produced by marginal rather than by conditional simulations. To produce marginal simulations, we first computed marginal predictions of the vital rates, which are function of coefficients of the fixed effects, and of the variance of the random effects. Specifically, we averaged, over the fitted distribution of random effects, the predictions of our vital rates expressed on the scale of the response (i.e. back-transformed from the scale of the linear predictor) and conditional on the fixed and random effects. Unlike the conditional predictions computed for a specific value of the random effects (typically 0), such computation provides unbiased predictions. It should thus be favoured in the context of GLMMs where random effects act non-additively on the expected response (Bland and Cook, 2019). To turn these marginal predictions into marginal simulations of the vital rates, we then drew random binary events using the function rbinom from the stats package in R using the marginal predictions as inputs for the probabilities. We used the same starting population, number of simulation runs, and number of time steps for our simulation as described above.

We also estimated fixed carrying capacity using the traditional Ricker (Ricker, 1954) and Beverton-Holt (Beverton and Holt, 1957) demographic models. We considered both the exponential and hyperbolic version of these models (Johst et al., 2008), and estimated carrying capacity using a range of different non-linear optimisers (see Supplementary material 3 section S3.3 for details).

3.5 Temporal trends in carrying capacity

To quantify temporal trends in carrying capacity we modelled change in K_{t} over time with a linear model including a fixed quantitative year term. We also modelled temporal trends in carrying capacity at the clan level (K_{tc}) using a linear model that included a quantitative term for year interacting with a categorical variable clanID. Due to the presence of temporal auto-correlation of residuals when modelling K_{tc} we also included an AR1 term to account for auto-correlation between successive time steps. We also tested for trends in both K_{t} and K_{tc} specifically during the period of initial population growth (1997-2012). These models assumed a Gaussian distribution of residuals with mean 0 and variance σ^2. We tested effects of year using log-likelihood ratio tests and calculated the 95% confidence interval ($\mathrm{CI}_{95\%}$) of the year term using likelihood profiling.

3.6 Temporal trends in vital rates

To test for temporal trends in vital rates we extended models used inside SHIM (described in Supplementary material 1) to include a fixed effect of year modelled as a quantitative variable. These models allowed us to test for temporal trends while accounting for the effect of known covariates, such as age and clan, also impacting vital rates. In all models, we tested effects of year using log-likelihood ratio tests and calculated the 95% confidence interval of the year term using likelihood profiling.

3.7 Elasticity of time-varying carrying capacity

For each vital rate i, we calculated the elasticity of the time-varying carrying capacity ($E_{K_{\mathrm{ti}}}$) as the change in absolute time-varying carrying capacity (ΔK_{t}) given a consistent shift in vital rates. We modified individual statistical models used inside SHIM to change (increase or decrease) vital rates and then recalculated K_{t} in each year using the same methods as described above. Vital rate models were adjusted by shifting the intercept term, leaving all other estimates, and thus the effect of all co-variates in the vital rate models (e.g. age, social rank), the same. The intercept of each model was shifted to achieve a 25% change in odds (i.e. odds ratio of 1.25) considering the mean vital rate value conditional on the observed characteristics of all observed individuals used to fit the model.

3.8 Time-varying carrying capacity and environmental drivers

To assess how changes in the environment could explain variation in K_{t} we fitted a statistical model with carrying capacity at the clan level (K_{tc}) as the response variable and five potential candidate predictors. Predictors were selected *a priori* so as to capture major potential drivers of population change (inter-specific interactions, disease and anthropogenic impacts/conservation measures). We conducted analysis at the clan level so that we could account for variation in predictors expected between clans (e.g. heterogeneity in abundance of prey and competitors).

We included a semi-quantitative estimation of prey abundance based on the ordinal ranking of prey abundance around spotted hyena den sites, recorded during every den visit (1 = low density; 2 = medium density; 3 = high density). To estimate prey density for a clan we treated these categories as numeric variables and took the average across all den visits in a year.

To test for potential effects of competitors, we included a quantitative estimation of the abundance of lions in each clan and year. We first estimated territory boundaries of each spotted hyena clan using 95% minimum convex polygons applied to sightings of adult females. Adult females were used because sightings of males may include males prospecting or dispersing to new clans, which is not indicative of clan space use. Clan territories were calculated separately for two periods, 1996-2011 and 2012-present. These different periods

were used to account for known shifts in prey space use within Ngorongoro Crater, which we expected would also affect spotted hyena territories. More details about shifts in prey and justification for using different periods are provided in Dheer et al. (2022). Once territories were calculated, we counted the total number of lions sighted within each clan territory in each year and determined the lion density (lions/km^2) within each territory.

Prevalence of infectious disease was quantified in each clan each year using sightings of spotted hyenas with clinical signs of infectious disease. In each year, we calculated the proportion of individuals in each clan observed with clinical signs of disease.

To account for effects of conservation management, we also included two binary variables that account for whether certain conservation measures were in effect during a year (whether or not tourist road use was restricted and whether or not Maasai pastoralists were allowed to visit the Crater with cattle; Table S2).

To test the potential drivers of carrying capacity we fitted a linear mixed effects model. We included all five variables described above (lion density, prey abundance, disease prevalence, road use restrictions, pastoralism ban) plus a categorical term for clan to account for differences in quality between clan territories. We included an AR1 term to account for temporal auto-correlation between successive time steps. We tested effects of each variable using log-likelihood ratio tests and calculated the 95% confidence interval of each term using likelihood profiling.

4 Code availability

All code used for analyses is available through the GitHub repository Bailey2024K (`https://github.com/hyenaproject/Bailey2024K`).

5 Data availability

All data required to reproduce analyses has been deposited on Zenodo (`https://zenodo.org/records/10955615`).

6 Author contributions

CRediT (Contributor Roles Taxonomy) author statement. Note the "Project" is here considered to refer to the current study. ED also contributed to the project administration and funding acquisition of the larger Ngorongoro Hyena Project.

CRediT	LDB	OPH	ED	AD	VR	LFW	EWW	AC
Conceptualization	✓				✓			✓
Methodology	✓							✓
Software	✓					✓		✓
Validation		✓				✓		
Formal analysis	✓							✓
Investigation	✓	✓	✓	✓				✓
Data Curation	✓	✓						✓
Writing - Original Draft	✓							✓
Writing - Review & Editing		✓	✓	✓	✓	✓	✓	
Visualization	✓							
Supervision		✓						✓
Project administration	✓	✓						✓
Funding acquisition	✓	✓						✓

7 Acknowledgements

Many thanks to Dr. Sarah Benhaiem for feedback on the manuscript and to François Rousset for advice on statistics as well as the development of the R package spaMM. Thanks also to thank Philemon Naman and Bettina Wachter for their invaluable contributions to data collection and project management. We thank the Tanzania Commission for Science and Technology, the Tanzania Wildlife Research Institute and the Ngorongoro Conservation Area Authority for permission to conduct the study. This study was funded by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation) - BA 6703/2, and the Leibniz Institute for Zoo and Wildlife Research.

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