

The relative role of intrinsic and extrinsic drivers in regulating population change and survival of African wild dogs (*Lycaon pictus*)

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Contributions

All authors contributed to the study's conception and design. Material preparation, data collection and analyses were performed by DGM, DJD and MJS. The first draft of the manuscript was written by DGM, DJD and MJS, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Abstract

Evaluating how intrinsic (intraspecific density), extrinsic (interspecific density and prey density) and anthropogenic (management intervention) factors affect African wild dog (*Lycaon pictus*) population performance is key to implementing effective conservation strategies. Lions (*Panthera leo*) can affect wild dog populations, and in small and highly managed protected areas, populations of wild dogs and lions often co-occur at high densities. It is unknown what mediates these co-occurring high densities and how trophic interactions facilitate the persistence of wild dogs in areas with high lion densities. In this study, we modelled how intrinsic and extrinsic factors affected population change and survival of 590 individually identifiable wild dogs in Hluhluwe–iMfolozi Park (HiP), South Africa, an area with

high lion density. The wild dog population in HiP grew significantly and comprised one of the highest population densities and the largest pack sizes in Africa. Pup survival rate was also the highest known in Africa, and the median individual survival was 29 months. During low lion density periods, the rate of wild dog population change increased despite low prey density, while at higher lion density, the rate of population change decreased only when prey density decreased. Survival for all age classes increased as population density increased, suggesting there is an important density-dependent effect on survival for all age classes that manifests at the population level. While increasing lion density had negative effects on adult and yearling survival, it did not affect pup survival. Our results suggest that both intrinsic and extrinsic drivers regulated the HiP wild dog population. Importantly, populations of wild dogs in small ($\sim 900 \text{ km}^2$), fenced protected areas are highly adaptable and can co-exist at high levels of interspecific competition over many generations as long as there is an intact and abundant prey base.

Keywords: Intraspecific competition; Population size; Prey availability; Rate of population change; Survival

Introduction

Carnivore populations are primarily regulated by extrinsic, bottom-up processes such as prey availability (Carbone and Gittleman 2002; Fuller and Sievert 2001). When prey availability is high, intrinsic, density-related drivers regulate populations of large carnivores (McRoberts and Mech 2014). The role of intrinsic drivers, especially intraspecific density, may be pronounced in group-living carnivores that are driven by dominance (Holekamp et al. 2012), group size (Gusset and Macdonald 2010) and infanticide (Packer 2000), which can result in early dispersal and increased mortality risk (Creel and Creel 2002). Consequently, density-dependent access to food resources can exert strong selective pressure on the regulation of carnivore populations, particularly those forming large social groups.

Carnivore populations are also regulated by extrinsic processes such as interference competition (Mills and Biggs 1993), kleptoparasitism (Hunter et al. 2007), predation (Groom et al. 2017), disease (Ginsberg et al. 1995; Peterson et al. 1998) and human beings (Dorresteijn et al. 2015; Kissui and Packer 2004). Moreover, interspecific competition with dominant carnivores limits access to food resources for mesocarnivores (Mills and Gorman 1997). For example, mesocarnivores respond to interspecific competition through dietary partitioning and spatio-temporal avoidance of dominant carnivores (Davies et al. 2021; Hayward and Slotow 2009). Reduced access to food can then affect vital rates through decreased adult survival (Durant et al. 2004) and increased starvation of juveniles (Packer and Pusey 1995). Therefore, evaluating how extrinsic top-down processes affect carnivore populations is key to conservation programmes designed to increase the population size of threatened carnivores.

Small populations are prone to extinction (Lande 1988) due to the high potential for inbreeding and increased vulnerability to stochastic events like disease outbreaks (Peterson et al. 1998). Small, isolated and highly managed populations of carnivores in South Africa have rapidly attained high densities (Davies-Mostert et al. 2015; Miller and Funston 2014) through the establishment of intensive management and human-mediated dispersal of African wild

dogs (*Lycaon pictus*), cheetahs (*Acinonyx jubatus*) and lions (*Panthera leo*). In these managed metapopulations, founders have been reintroduced into suitable but geographically isolated fenced protected areas. As natural dispersal and colonisation between areas are limited due to fragmentation of habitat and electric fences surrounding protected areas restricting movement, active translocations are required. These isolated and enclosed populations could be more prone to density-dependent population regulation (Kissui and Packer 2004), although the effects of this can be alleviated by human-mediated dispersal. The high variability in population density and prey density within each enclosed and monitored subpopulation provide an opportunity to test how intrinsic and extrinsic drivers affect individual and group-level survival and population growth. The management goal for threatened carnivore species is to increase population size and resilience to avoid extinction. Therefore, in small, isolated and highly managed systems, it is imperative to understand the factors affecting the growth and the probability of persistence of threatened populations of carnivores.

Wild dogs are endangered throughout their distribution (Woodroffe and Sillero-Zubiri 2012), while in South Africa, their populations are stable due to the growing managed metapopulation that has ameliorated the declining free-roaming and Kruger National Park populations over the last 20 years (Nicholson et al. 2020). The wild dog population has grown rapidly in the metapopulation reserves and attained high densities (Davies-Mostert et al. 2015). While wild dog population growth in free-roaming areas is density-dependent (Creel and Creel 1995, 2002; Frame et al. 1979), it remains unknown whether this is the same for the enclosed metapopulation in South Africa. At high population densities, high levels of intraspecific competition could occur, and wild dog packs might have reduced resource intake which could compromise pack persistence and population growth. Wild dogs must offset extrinsic top-down effects of lions (Creel and Creel 2002), which they achieve using areas of reduced prey availability to avoid interference competition (Marneweck et al. 2019a; Mills and Gorman 1997), selecting prey unfavoured by lions (Somers et al. 2017), and being active when (Dröge et al. 2017) or in habitats where (Davies et al. 2021) lions are less active. Spatial avoidance of lions during the denning season (Alting et al. 2021; Jackson et al. 2014; Marneweck et al. 2021), when pups are particularly vulnerable, is critical to ensure the survival and recruitment of pups (Davies et al. 2016). In the metapopulation reserves where lion populations have grown rapidly (Miller and Funston 2014), it is not clear how a population of wild dogs might further offset resource losses against high levels of interspecific competition to ensure their persistence. It is expected that lions should exert substantial pressure on wild dogs that negatively impact populations of the latter. This prediction is largely corroborated by studies of free-roaming populations showing that population density, prey availability and hunting success, intraspecific competition and human effects may all limit wild dog population dynamics (Creel and Creel 1998). Extrinsic bottom-up factors, such as prey availability, should exert positive effects on wild dog populations, yet this is often not considered or deemed less important than top-down forces (Mills and Gorman 1997). However, high prey availability has been found to initiate reproduction in wild dogs (Marneweck et al. 2019b) and drive high wild dog densities (Hayward et al. 2007). In small and enclosed reserves with high population densities of both wild dogs and lions, the relative role of intrinsic versus extrinsic drivers on wild dog population performance remains unknown.

In this study, we modelled how intrinsic (population density and pack size) and extrinsic (prey availability, lion abundance and human management actions) drivers regulated individual survival and rate of population change of a reintroduced wild dog population in a small and fenced protected area—Hluhluwe–iMfolozi Park (HiP), South Africa. This ecosystem comprises a high density of wild dogs (intraspecific competition) and lions (interspecific competition), and a highly variable prey population density. As individual wild dogs are uniquely identifiable based on their coat patterns (Maddock and Mills 1994), we were able to track the fate of 590 wild dogs over a 22-year period. We broadly predicted positive effects of prey availability as an extrinsic factor on survival and population growth when prey availability is high. We also predicted that high levels of inter- (lion density; extrinsic) and intraspecific competition (pack density and pack size; intrinsic) would negatively affect survival and population growth due to increased competition for food and mates, respectively. During periods of low prey availability, interspecific competition for limited resources could further negatively affect wild dog population growth, which could be exacerbated at high competitor densities.

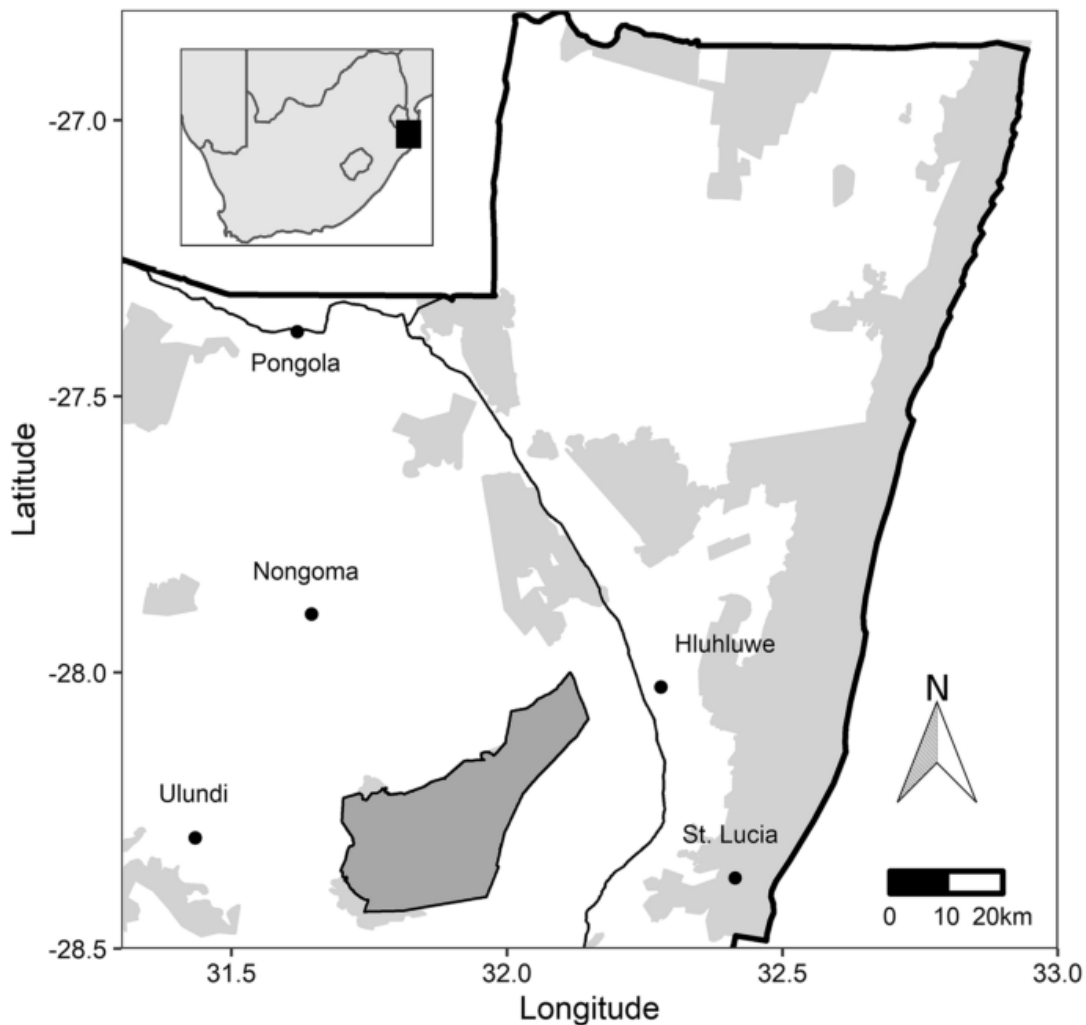


Fig. 1. Map showing the study site, Hluhluwe–iMfolozi Park (HiP) (dark grey), located in the north-eastern area of the KwaZulu–Natal province (thick black line) in South Africa (small inset in top left). Protected areas in the region are shown (light grey) as are the main local towns and the national highway (thin black line)

Methods

Study site

We conducted our study in the 896 km² HiP, located in the sub-tropical region of north-eastern KwaZulu–Natal province, South Africa (Fig. 1). HiP's perimeter is completely enclosed by predator-proof electrified fencing. The large carnivore guild has been re-established through reintroductions and population augmentations (Somers et al. 2017), following extensive persecution in the early-mid twentieth century. Wild dogs, lions and cheetahs were extirpated in HiP but have been actively reintroduced. Spotted hyenas (*Crocuta crocuta*) and leopards (*Panthera pardus*) suffered less persecution and remained extant (Somers et al. 2017). The park supports a wide variety of herbivores, including the preferred prey of wild dogs (impala [*Aepyceros melampus*], nyala [*Tragelaphus angasii*] and greater kudu [*Tragelaphus strepsiceros*]; Hayward et al. 2006), of which impala and nyala survive at high densities (le Roux et al. 2019).

Wild dog population

Wild dogs were first reintroduced into HiP in 1980, with subsequent augmentations between 1997 and 2003 (Somers et al. 2008) after the initiation of the managed metapopulation in South Africa (Mills et al. 1998). For a detailed account of reintroductions of wild dogs into HiP prior to 2004, see Maddock (1999), Somers et al. (2008) and Somers et al. (2017). We collated historical data for the period 1980–2013 and collected additional data from 2014 to 2018. Historical data sources included ad hoc sightings from the Natal Parks Board and Ezemvelo KZN Wildlife (EKZNW) archives based on staff reports (1980–1992), direct observations and photographs (1992–1996; Maddock 1999), and an intensive monitoring programme initiated in 1997 (Mills et al. 1998) that ran until 2018. We continued the intensive monitoring programme for all packs in HiP from 2014 to 2018 using VHF and GPS satellite tracking collars (a range of makes and models) usually fitted to at least one individual from each pack. The intensive monitoring enabled each pack to be located regularly where the following data were collected at each sighting: (1) identity, sex, age and number of individuals, (2) health condition of individuals, (3) dominance (known from overmarking, mate guarding and scent marking), (4) pregnancies, (5) hunting success and (6) location. In general, wild dogs were tracked twice daily but this frequency depended on various factors such as accessibility to the wild dogs, logistical constraints, weather and the availability of a monitor.

Individual wild dog identification

Each wild dog is uniquely identifiable based on the colour, size and shape of distinct coat patterns (Maddock and Mills 1994; Fig. 2). Photographic identity (ID) kits, including high-resolution profile images (Supplementary Material, Fig. S1), were compiled for each wild dog within the HiP population. Initial identification photographs were taken for each wild dog from ~ 3 to 6 months old and updated with better and more recent photos whenever possible. These ID kits were used during monitoring sessions to identify individuals present at each re-sighting. Utilising this individual-based approach for monitoring wild dogs, we were able to track individuals at a monthly resolution throughout their lifespan and determine individual-based survival. We also used this individual-based monitoring approach to

determine group composition (sex and age breakdown), and pack size, which further allowed us to estimate the total population size. Only population-level data were available from 1980 to 1995, while individual-level data were used from 1996 onwards. Thus, we compiled individual life history data from January 1996 until December 2018 for 590 wild dogs comprising of 16,276 total cumulative sample months.



Fig. 2. Example of identifying right-side photographs of a female wild dog from the Crossroads pack in Hluhluwe-iMfolozi Park (HiP). Month and years are shown within each photograph. The bottom right panel shows the same female with another natal pack member, illustrating the usefulness of photographic kits for identifying individual wild dogs during re-sightings

Definitions

We defined a wild dog ecological year from 1 June to 31 May as the period between two consecutive denning seasons (Marneweck et al. 2019b). Some analyses included age (years), but we also defined three broader age classes: pups (< 1 year old), yearlings (1–2 years old) and adults (> 2 years old), allowing for comparisons to other populations.

Estimating survival

We categorised each individual wild dog's status (i.e. alive/dead), their age (years) and age class at the start of every month-year (i.e. December 2006) based on field observations. We also considered individuals that disappeared to have died as undetected emigration does not have appreciable effects on patterns of survival in wild dogs (Creel and Creel 2015). For these

individuals that disappeared, we assigned their month of disappearance as the month after their last confirmed observation. Some individuals were of unknown age (due to reintroduction from an external area), and we removed these from the survival analyses. We defined survival probability as the proportion of individuals alive in a month compared to the previous month, which thus relates survival of individual wild dogs over their lifetimes. We also defined annual survival rates as a proportion of individuals in year N_{t+1} compared to individuals in year N_t . We calculated this annual survival rate for the three wild dog age classes.

Mortality causes

For confirmed mortalities (i.e. directly observed, carcass and/or collar found), we coded the cause as human (road accident, snaring, shooting), natural (predation, intraspecific, hunting) or disease (e.g. rabies, distemper) following Woodroffe et al. (2007). We also recorded months in which individuals were removed for management purposes, permanently emigrated, or temporarily held in captive enclosures.

Intrinsic factor: population dynamics

We defined a pack as a group of wild dogs with at least one adult male and one adult female, and dispersal groups as ones containing a cohort of a single sex. We calculated pack size and population size at the start of the ecological year as the sum of yearling and adult wild dogs. We did not include pups in these counts as they do not contribute to the functional population (i.e. they do not breed nor actively participate in hunts) (Creel and Creel 2002). We calculated population and pack density as the population size and number of packs per 100 km², mean annual pack size as the population size divided by the number of packs and the annual instantaneous population growth rate (r) as:

$$r = \log_e (N_{t+1}/N_t),$$

which is the natural log of the current year's population size (N_{t+1}) divided by the previous year's population size (N_t) (Caughley and Sinclair 1994).

Extrinsic factor: lions

We used historical data from Somers et al. (2017) and the consolidated EKZNW database of the estimated minimum annual lion population size in HiP for the period 1992–2018. Some annual estimates were missing from the dataset, so we used the mean of the previous year's estimate and the following year's estimate if a single year's estimate was missing ($n = 1$). When data for two or more consecutive years were missing, we used linear regression to incorporate the period before and after to determine population size (three data gaps missing 2, 2 and 5 annual estimates, respectively; Fig. S2A). Lions maintained a high population density over the study period (mean annual $9.44 \pm \text{SE } 0.31$ per 100 km², range = 6.36–12.72, estimated from the full range of values used in Fig. S2A) when compared to lion population density estimates elsewhere in Africa (Packer et al. 2013).

Extrinsic factor: prey availability

We used population size estimates from EKZNW's biennial herbivore distance-sampling surveys to estimate the abundance of wild dog preferred prey biomass in HiP. In this regard, we equate wild dog preferred prey biomass abundance as prey availability, since we did not have other surrogates for assessing true availability that is normally dependent on age-class distribution, sex, time of survey and habitat availability. This survey program estimates herbivore population sizes using distance-sampling along established transects every two years in the dry season (see le Roux et al. 2017 for further details). From this, we extracted the abundance estimates for wild dog preferred prey species, impala and nyala, which account for 96% of wild dog diet in HiP (Somers et al. 2017). Using average female body weight from Owen-Smith (1988) (impala = 44 kg, nyala = 63 kg), we calculated park-wide preferred prey biomass per annum per species using the function:

$$B = N (w * 0.75),$$

where B is the amount of available biomass, N is the abundance estimate from the distance-sampling, w is the mean female body weight and 0.75 is the correction factor to account for younger individuals in the population. We then summed the two herbivore species' biomass per annum as a total park-wide estimate of available preferred prey biomass (in tons). Finally, we expressed this as biomass density by dividing the park-wide preferred prey biomass by the area size to ensure equal scale to both wild dog and lion densities. Herbivore survey data were available for 1986–1988, 1991, 1994 and biennially after that, and we filled the data gaps utilising the same linear regression method as described for the lion data (Fig. S2A). The biomass (tons/100 km²) of preferred prey maintained a mean annual density over the study period of $25.56 \pm \text{SE } 1.20$ (range = 13.07–45.55; Fig. S2A).

Extrinsic factor: management

As part of the managed metapopulation of wild dogs in South Africa, individuals and packs were introduced and removed from HiP at ad hoc intervals (Table S1). We investigated how introduction or removal might affect population size after non-lethal anthropogenic interference. We determined the annual proportional influence of introductions and removals by dividing the number of individuals introduced or removed by the population size, giving the proportion of the population affected by anthropogenic interference. As pups have also been reintroduced into the population, this factor included all age categories (Table S1).

Statistical analyses

We used a variety of non-parametric tests and model evaluation procedures for these data. In all model evaluations, we assessed the correlation between independent variables prior to each analysis using Spearman rank tests. When we found high levels of correlation (Spearman's $\rho > 0.6$) between variables, we discarded one from the analysis in the final model set. Predictor variables were rescaled and centred prior to analysis in all models.

Population dynamics

We used univariate linear regression models to test the effect of year on population density (1), the number of packs (2), mean annual pack size (3) and population growth rate (4), the effect of population density on mean annual pack size (5) and the effect of population density on pack density (6).

Factors affecting rate of population change

We created seven a priori candidate models to test which factors affected the wild dog rate of population change (Table A1). We used generalised linear models (GLMs) with Poisson distribution and specified population size in the sample year as response and population size from the year prior as the offset. This changes the response from a count to a rate and allows us to create a rate of population change (Dalgaard 2008). We tested how covariates of intraspecific competition (pack density), interspecific competition (lion density), anthropogenic influence (proportion of population introduced or removed) and resource availability (preferred prey density) affected the rate of population change. We also tested relevant pair-wise interactions in the candidate models. We identified the best model(s) using model averaging and selection. Specifically, we selected models based on the Akaike information criterion corrected for small sample size (AICc). If several models were selected (i.e. $\Delta AICc \leq 2$), we then followed Burnham and Anderson (1998) to perform model averaging. We corrected for model weights to provide full model-averaged coefficients and confidence intervals.

Survival and mortality

We used Chi-squared tests to investigate sex-specific differences in annual survival rate for yearlings. We then used linear regression models testing the effect of age (years) on sex-specific annual survival rates. We also used Chi-squared tests to investigate if there were differences in the proportion of natural, human-induced, disease or unknown caused mortalities.

Factors affecting survival probability

We used semi-parametric cox-proportional hazard (*coxph*) models to determine drivers of individual wild dog survival probability. We omitted wild dogs reintroduced into the park ($n = 38$) in this analysis as the individuals' survival prior to reintroduction was influenced by factors external to the park. We included dispersers and residents in our models. We tested covariates of pack density (highly correlated with population density; Fig. A1), pack size, prey biomass density and lion population density. We coded the response as 1 = died/disappeared and 0 = alive. We performed right censoring for months in which individuals were held in a temporary captive enclosure or if they permanently emigrated from HiP. We initially constructed a model with one covariate (pack density) and sequentially added one additional covariate for each subsequent model until the final model contained the additive effects of all covariates. We then evaluated each of the final four candidate models' predictive ability based on likelihood ratio tests and model concordance to determine the top supported model. From the top model, we considered that covariate(s) of which 95% CIs around the

coefficient overlapped zero were not important in their effect on survival. We conducted this procedure for two model sets; one with only pup age class included and the other with only the adult and yearling age classes combined, to test if drivers of wild dog survival differed between age classes.

We performed all statistical analyses and constructed all figures in the RStudio GUI, desktop version 1.1.456 (RStudio Team 2015) that used R version 3.5.1 (R Core Team 2018) for Windows, using functions in the packages *stats v3.5.1* (RStudio Team 2015), *lme4 v1.1–18-1* (Bates et al. 2015), *car v3.0–2* (Fox and Weisberg 2011), *MuMIn 1.42.1* (Barton 2013), *ggplot2 v3.1.0* (RStudio Team 2015) and *survival* (Therneau 2021).

Results

Population dynamics

Despite the slight annual fluctuations throughout the study period (1980–2018), the wild dog population size increased steadily from 2003 onwards, reaching a peak of 120 individuals in 2011 (83 adults and yearlings, 37 pups in seven packs; Fig. 3). Thereafter, the population decreased to 70 individuals in 2018. Measured as a linear change, population density (Table 1) increased significantly between 1980 and 2018 ($F_{(1,37)} = 63.32$, $p < 0.01$, $R^2 = 0.62$; Fig. S2B).

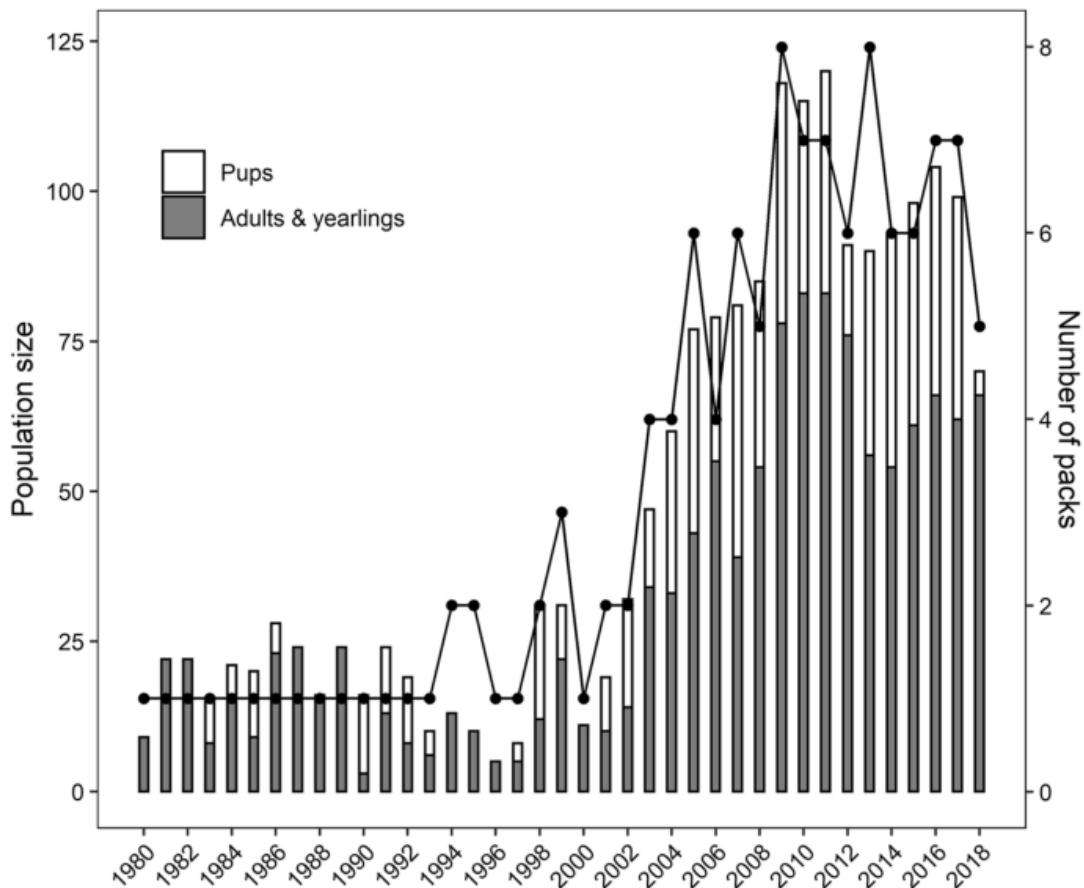


Fig. 3. Wild dog population size in Hluhluwe–iMfolozi Park (HiP) between 1980 and 2018. Bars represent the total number of individuals, and the solid line represents the number of packs on the secondary y-axis

Table 1. Descriptive patterns of annual population dynamics and survival of wild dogs in Hluhluwe–iMfolozi Park, illustrating the mean, standard error (SE) and 95% confidence intervals (CI)

Variable	Mean \pm SE	95% CI
Population density (adults + yearlings/100 km ²)	3.57 \pm 0.46	2.68–4.46
Number of packs	3.15 \pm 0.39	2.39–3.92
Pack size (adults + yearlings)	10.91 \pm 0.91	9.13–12.69
Proportion of pups	0.29 \pm 0.03	0.23–0.36
Instantaneous population growth rate	0.05 \pm 0.10	– 0.15–0.25
Adult survival rate	0.71 \pm 0.04	0.63–0.79
Yearling survival rate	0.74 \pm 0.04	0.65–0.82
Pup survival rate*	0.65 \pm 0.05	0.55–0.75

*This includes pups of unknown sex that died/disappeared before sex could be determined

There was a significant linear increase in the number of packs over time ($F_{(1,37)} = 100.90$, $p < 0.01$, $R^2 = 0.72$) starting from one pack in 1980 and increasing to five packs in 2018 (Fig. 3; Table 1). Mean annual pack size (Table 1) did not change over time ($F_{(1,37)} = 3.24$, $p = 0.08$, $R^2 = 0.06$). Population density had no effect on the mean annual pack size ($F_{(1,37)} = 0.92$, $p = 0.34$, $R^2 = 0.00$). Pack density and population density were highly positively correlated ($F_{(1,37)} = 168.80$, $p < 0.01$, $R^2 = 0.82$; Fig. A1). Although the annual instantaneous population growth rate fluctuated greatly (Table 1), across the entire study period, the linear trend did not support either an increasing nor a decreasing trend in growth rate ($F_{(1,36)} = 0.02$, $p = 0.88$, $R^2 = -0.03$).

Factors affecting rate of population change

Top model for factors affecting wild dog rate of population change included the interaction of lion density and prey density (Table A1). The coefficient and 95% CIs for the interaction of prey density and lion density did not overlap zero (Table 2); hence, we consider only this interaction to be important. When lion density was low, the wild dog population change rate increased despite low prey density (Fig. 4). As lion density increased, the rate of population change for wild dogs decreased if prey density remained low (Fig. 4). However, at high lion densities, there was a positive rate of population change for wild dogs if prey density increased (Fig. 4). At high prey densities and low lion densities, the rate of population change for wild dogs decreased (Fig. 4), however, there were very few data points in this range (Fig. S3).

Table 2. Effects of covariates on rate of population change, pup survival and combined adult and yearling survival in Hluhluwe–iMfolozi Park

Covariate	$\hat{\beta}$	SE ($\hat{\beta}$)	Lower 95% CI	Upper 95% CI
<i>Rate of population change model</i>				
Lion: prey density	0.008	0.003	0.001	0.014
Prey density	- 0.041	0.050	- 0.141	0.059
Pack density	- 0.628	0.905	- 2.471	1.214
Lion	- 0.204	0.113	- 0.435	0.027
Anthropogenic	- 0.011	0.715	- 1.498	1.476
Prey density: pack density	0.042	0.034	- 0.030	0.115
Lion: pack density	0.023	0.119	- 0.225	0.271
<i>Pup survival model</i>				
Pack density	- 1.92	0.63	-3.151	- 0.680
Pack size	0.09	0.02	0.052	0.119
Prey density	0.04	0.01	0.016	0.071
Lion population density	0.05	0.05	- 0.047	0.143
<i>Adult and yearling survival model</i>				
Pack density	- 1.96	0.43	- 2.800	- 1.129
Pack size	0.08	0.01	0.050	0.103
Prey density	0.06	0.01	0.035	0.085
Lion population density	0.22	0.04	0.137	0.296

Rate of population change effects were determined from generalised linear models (showing full model-averaged coefficients), while survival effects were determined from cox-proportional hazard models. Important covariates from each model are highlighted in bold

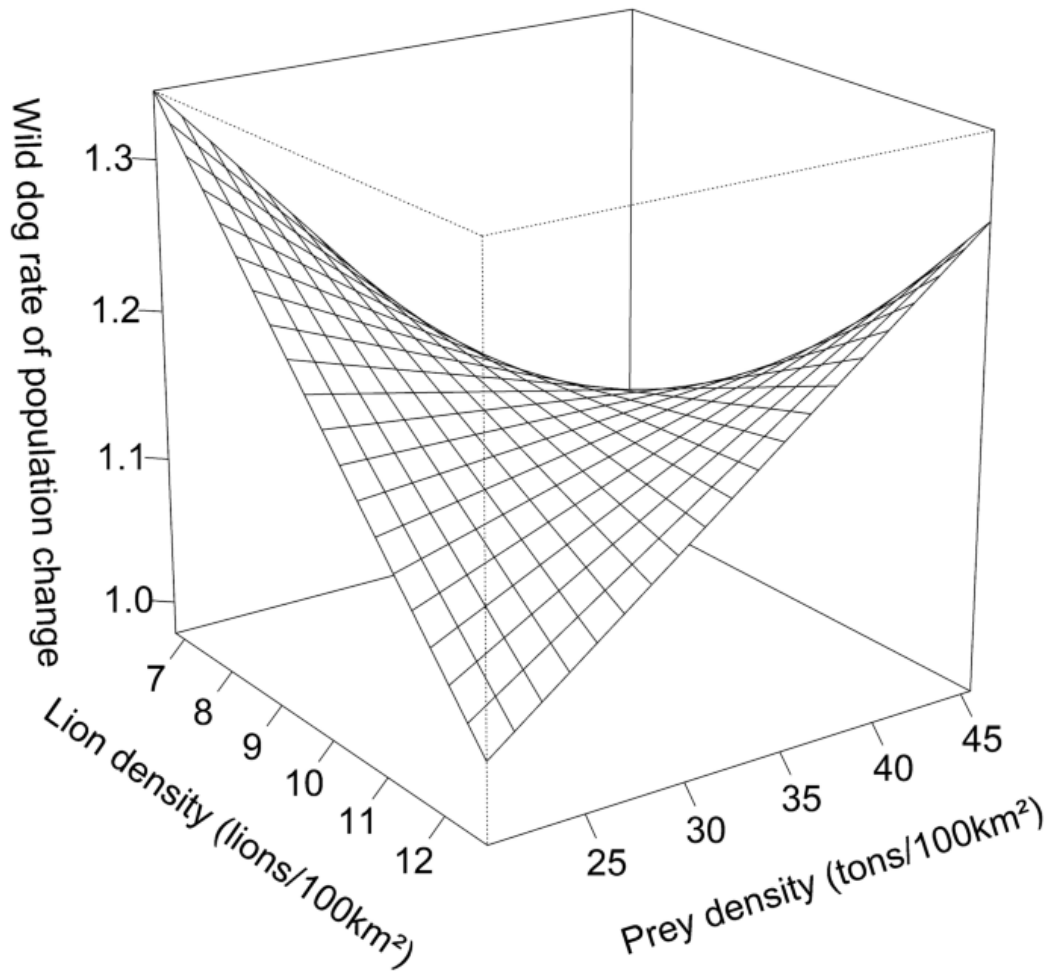


Fig. 4. The interaction of lion density (lions/100 km²) and prey density (tons/100 km²) on wild dog rate of population change in Hluhluwe–iMfolozi Park (HiP) between 1996 and 2018, fitted with generalised linear models

Survival patterns

The median survival duration for an individual wild dog born in HiP was 29 months (95% CIs: 26–32 months; $n = 590$; Fig. 5). For wild dogs born in HiP, 48% of the pups survived to adulthood. We found no sex-specific difference in yearling survival to adulthood ($\chi^2_{(1)} = 1.12$, $p = 0.29$; Table S2). For adults, male survival was highest for four- and five-year olds with a significant decrease in survival with age ($F_{(1,8)} = 27.68$, $p < 0.01$, $R^2 = 0.75$). For adult females, survival was highest for five-year olds but survival did not decrease with age ($F_{(1,10)} = 2.80$, $p = 0.13$, $R^2 = 0.14$). The mean annual adult, yearling and pup survival rates did not change over time (adult: $F_{(1,28)} = 0.33$, $p = 0.57$, $R^2 = -0.02$; yearling: $F_{(1,18)} = 0.01$, $p = 0.91$, $R^2 = -0.05$; pup: $F_{(1,26)} = 1.41$, $p = 0.25$, $R^2 = 0.02$; Table 1).

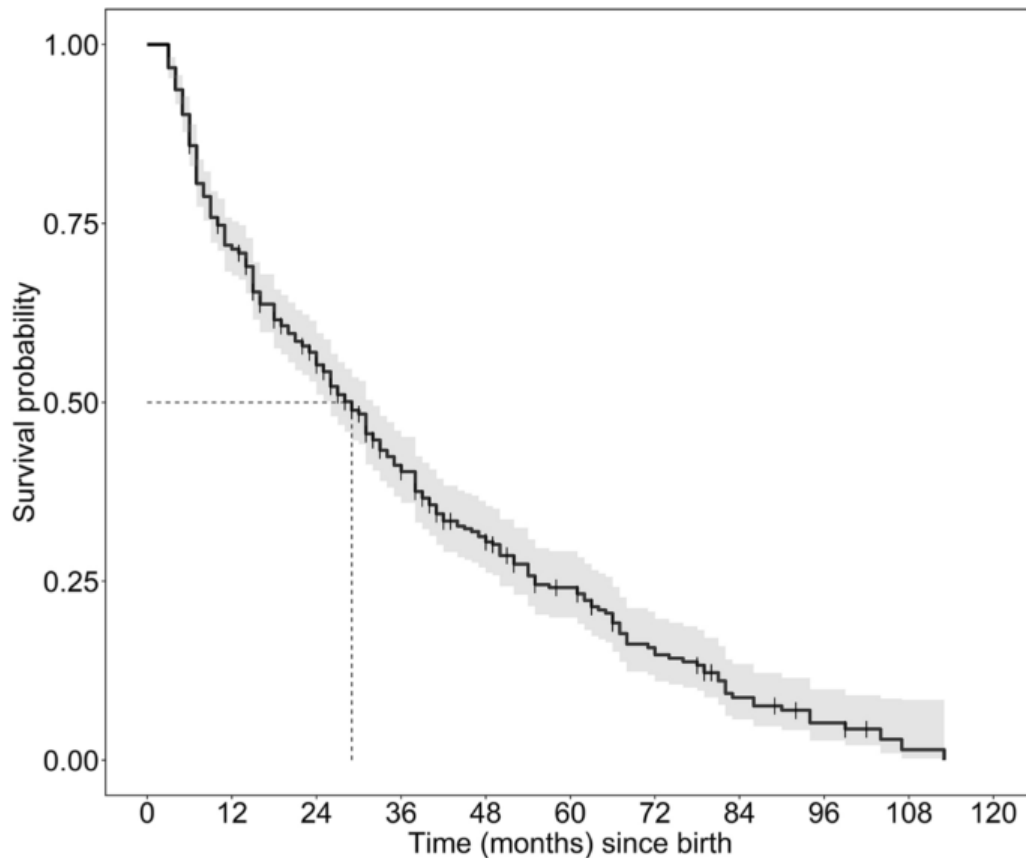


Fig. 5. Kaplan–Meier survival curve for 590 individually recognisable wild dogs born in Hluhluwe–iMfolozi Park (HiP), South Africa. Survival curves show 95% confidence intervals (grey shading), right-censored events (small black drop-down lines) and median survival probability (dashed vertical line) of 29 months

Mortality causes

We found no difference in the proportion of human-induced, natural, disease or unknown caused mortality ($\chi^2_{(3)} = 0.20$, $p = 0.98$, Table S3). We also found no difference between types within human-induced ($\chi^2_{(5)} = 5.00$, $p = 0.42$) or natural mortality ($\chi^2_{(5)} = 5.00$, $p = 0.42$). The top three natural mortality causes were interspecific competition (predation), injury and starvation (Table S3). The top three human-induced mortality causes were road accidents, fighting within a pre-release enclosure and snaring (Table S3).

Factors affecting survival probability

For both the pup and the adult and yearling age-class models, the top model for drivers of individual survival was the one including pack density, pack size, prey density and lion density (Table A2). For both age-class models, pack density had a negative effect on time to mortality (Table 2); thus, as pack density increases, so does the probability of survival (Fig. 6). Increases in pack size and prey biomass density resulted in lower individual survival for all age classes (Fig. 6). Lion density did not affect pup survival (Fig. 6), but for the adult and yearling model, increased lion density resulted in lower survival (Fig. 6).

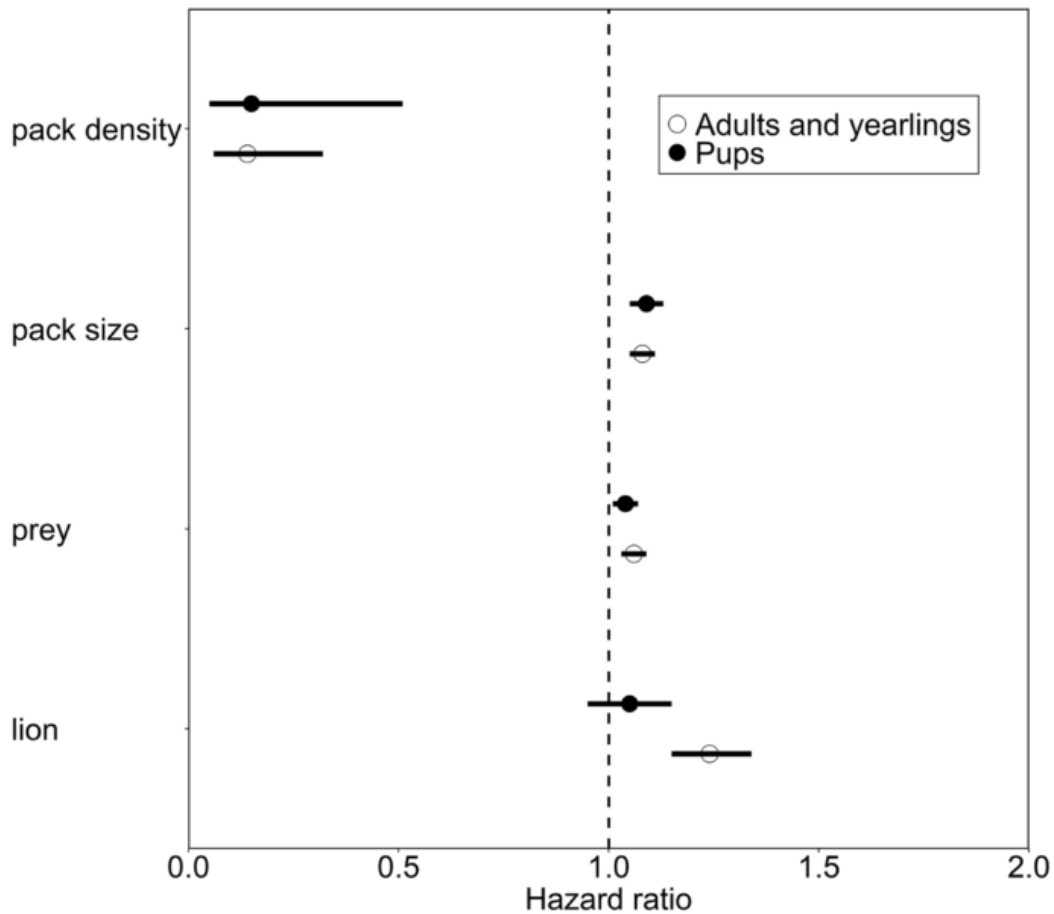


Fig. 6. Effect sizes of intrinsic and extrinsic covariates on the age-based survival of 552 individually recognisable wild dogs ($n = 389$ adults and yearlings, $n = 163$ pups) born in Hluhluwe–iMfolozi Park (HiP) between 1996 and 2018 as evaluated by semi-parametric cox-proportional hazard models. Hazard ratio (HR) and the 95% confidence intervals for each covariate are shown. A hazard ratio (HR) of 1 (dashed line) represents no effect of the covariate on survival. $HR < 1$ represents increased survival. $HR > 1$ represents decreased survival

Discussion

The initial reintroduction and ongoing supplementations and removals of wild dogs in the small and fenced ecosystem of HiP have been important in establishing this wild dog population. Aiding in this population's maintenance has also been favourable environmental conditions. The wild dog population has grown considerably since their reintroduction in 1980, and although there were periods of population decline (i.e. 1999–2001, 2006–2007 and 2011–2014; Fig. 3; Fig. S2B), in most years, the population change was positive. The average population density in HiP (mean = 3.6 dogs/100 km², Table 1) is higher than that in Gonarezhou National Park, Zimbabwe (2.5 dogs/100 km², Groom and Watermeyer 2018), the same as Selous Game Reserve, Tanzania (3.5 dogs/100 km², Creel and Creel 2002) and slightly lower than the population in Savé Valley, Zimbabwe (3.9 dogs/100 km², Groom and Watermeyer 2018). Consequently, the HiP population is among the highest population density in the species' distribution, greater than most other populations (Creel et al. 2004; Groom and Watermeyer 2018; Woodroffe 2011). That population density did not affect pack size (i.e. density-independent competition) suggests a lack of demographic Allee effects

(Somers et al. 2008). Pack sizes (mean = 10.9, Table 1) were slightly (Creel et al. 2004) or notably larger than other populations (Creel and Creel 2002; Leigh 2005; Woodroffe 2011). Collectively, demographic characteristics in HiP are synonymous with high-density population elsewhere in Africa, such as in Selous Game Reserve and Savé Valley Conservancy.

Canid populations can increase quickly under the right conditions but can also decrease rapidly, mainly due to only a single breeding pair per group (Ellgutter et al. 2020; King et al. 2014; Krofel et al. 2017). For wild dogs in HiP, the annual instantaneous population growth rate was lower than that of the entire managed metapopulation (Davies-Mostert et al. 2015). We found an interplay between extrinsic factors of lions and prey as important in predicting wild dog population change. When prey density and lion density were low, the wild dog population changed significantly. Lower lion density should result in less competition in important foraging areas. Consequently, wild dogs should be able to maximise resource acquisition in these areas with a reduced likelihood of lion competition. Considering that lions can competitively exclude wild dogs if lion density increases (Swanson et al. 2014), it is not surprising that wild dogs in HiP fared less well when lion density increased (Fig. 4). Under these increasing lion densities, wild dogs can only expand their population size if prey density also increased. When food is more readily available, capture rates and resource intake can increase (Mech et al. 1998), and wild dogs are likely to invest more heavily in reproduction (Marneweck et al. 2019b). Thus, increased recruitment in this population could result from favourable bottom-up processes found in studies on other carnivores (Carbone and Gittleman 2002; Fuller and Sievert 2001). The least favourable conditions for the wild dog population were periods of high lion density and reduced prey density. In these periods, high levels of interspecific competition could exclude wild dogs from hunting in optimal areas (i.e. high prey density areas) or raising pups in suitable den sites (i.e. rugged, dense areas with high prey density).

With food being difficult to access due to high levels of intra- and interspecific competition, combined with lower prey availability, wild dogs likely struggle to obtain enough resources for individual maintenance, which could compromise group size and lead to smaller litters (Marneweck et al. 2019b). This is a group-level demographic Allee effect (Lerch et al. 2018). That the HiP wild dog population has persisted despite this effect, suggests the lack of a population-level Allee effect, which has previously been suggested for this population (Somers et al. 2008) and one in Laikipia county, Kenya (Woodroffe et al. 2019a). In HiP, wild dogs manage to offset the costs of high levels of interspecific competition if there is high availability of preferred prey. Collectively, these results highlight the important influence of prey availability in facilitating co-existence in the large carnivore guild in this high-density ecosystem.

We are tentative to interpret the effect of low lion density and high prey density resulting in decreased wild dog rate of population change as these conditions were rarely observed (Fig. S3), likely because lions dominate prey-rich areas (i.e. high prey density). When this happens, lion populations are unlikely to decline. Inclusion of data in future periods comprising high prey density and low lion density are needed to evaluate the true direction and strength of these on wild dog rate of population change. The current direction and strength of this result is unlikely to be a driver of wild dog rate of population change because reduced lion density and high prey availability should allow wild dogs to easily offset costs of limited competition

while acquiring highly available resources. While managing genetic diversity in HiP is important through population augmentation, we did not find any statistical effects as a result of these management actions with regard to the rate at which the population changed. Due to numerous artificial introductions and removals (Davies-Mostert et al. 2015; Somers et al. 2008) (Table S1), it would have been reasonable to expect management to directly influence rate of population change, especially as these appeared to have stimulated the recoveries in 2001 and 2004 (Fig. 3, Fig. S2B). It is also possible that the increased genetic diversity had a positive impact on the population, as these individuals are better able to cope with stochastic fluctuations in their environment. Thus, there may be indirect effects of management actions on the rate of population change. Despite the reintroductions outnumbering the removals (Table S1), managers often introduced and removed individuals simultaneously to swap genetics in the population, which could explain the lack of a numerical effect on population size.

Pup survival was higher than all other populations in Africa (Burrows et al. 1994; Creel and Creel 2002; Creel et al. 2004; Frame et al. 1979; Fuller et al. 1992; Malcolm, 1979; McNutt 1995; McNutt and Silk 2008; Reich 1981). Often, wild dog pups are killed by interspecific competitors (Creel and Creel 1998, 2002), but in HiP, there was no difference between and within mortality causes (i.e. all mortality causes occurred at approximately equal proportions). Thus, mortality causes are unlikely to explain the high pup survival rates in HiP. Instead, Davies et al. (2021) found that the highly heterogeneous landscape in HiP facilitates proactive avoidance of interference competition with lions. This, along with the high availability of prey (le Roux et al. 2019), could enable high pup survival rates in HiP compared to other populations in Africa that live in more homogenous landscapes with lower food availability. Despite these high survival rates in HiP, the median survival was 29 months, and wild dogs tended to have their first litter at 24 months, suggesting a tenuous balance for most individuals to contribute to population growth, especially considering that few individuals ever breed as mating in packs is monopolised by a breeding pair (Creel and Creel 2002; Malcolm and Marten 1982).

Anthropogenic-induced wild dog mortality can occur both inside and outside protected areas (Creel and Creel 1998; Woodroffe et al. 2007). The additive effect of anthropogenic and natural mortality can degrade the persistence of populations of wild dogs (Woodroffe et al. 2007). Confirmed cases of anthropogenic, natural and disease causes of mortality were equal in proportion suggesting that human-causes of mortality are a concern in HiP. Although the proportion of disease-related deaths was equal to natural and anthropogenic causes, we observed only three disease events; rabies (one pack died; Flacke et al. 2013), canine distemper virus (one pack died; EKZNW records) and an apparent tick infection (one individual; EKZNW records). As disease-related wild dog mortalities indirectly originate from human-induced effects (Woodroffe et al. 2007), active management of both disease and anthropogenic threats are needed to limit the effect these have on this small population of wild dogs.

Individual survival was affected by intrinsic density-dependent factors. For example, survival across all ages was strongly and positively affected by high pack densities. We suggest that higher pack densities indicate an increase in the number and quality of breeding patches, which could explain higher individual survival. This may stimulate dispersal and rapid pack

formation (Marneweck et al. *in prep*), reduce the likelihood of inbreeding risk (McNutt 1996), and expose individuals to higher quality breeding and foraging patches, ultimately leading to improved individual survival. Thus, there is an important density-dependent effect on survival for all age classes that manifests at the population level. At the pack level though, larger packs were associated with lower individual survival for all ages. In packs, only alphas and new pups are prioritised at kills (Creel and Creel 1995, 2002), and the rest of the subordinates and previous offspring have to compete for limited remaining food. As alphas and new pups make up small proportions in packs relative to the subordinates and previous offspring, there is a disproportionately high number of yearlings and subordinate adults struggling to obtain enough food resources, which could compromise yearling and adult survival in packs. This could also lead to early dispersal by subordinates and previous year's offspring (McNutt 1996; Woodroffe et al. 2019b), which increases mortality risk as dispersers have lower survival than residents (Bonnet et al. 1999; Bonte et al. 2012; Woodroffe et al. 2019b). This suggests that at the pack level, the benefits of group living could be outweighed by the costs of reduced resource intake for subordinates as they relate to per capita survival.

Unexpectedly, we found pup survival decreased in larger packs (hazard ratio > 1 in Fig. 6). This is contrary to previous findings that pup survival increased as pack size increased, as found in other populations (McNutt and Silk 2008; Woodroffe et al. 2017) and the HiP population (Marneweck et al. 2019b). This observation could be due to increasing levels of competition for food as pack size increases. However, this interactive effect of litter size and pack size on pup survival needs to be tested. Alternately, our unusual observation could be due to differences in statistical analyses. For example, McNutt and Silk (2008) and Marneweck et al. (2019b) modelled factors influencing pup survival using Poisson generalised linear mixed effects models, and Woodroffe et al. (2017) used logistic regression, whereas we used cox-proportional hazard models. It is important to note that the hazard ratios for the effect of pack size on survival for all ages is only marginally > 1 in our study (Fig. 6). Considering that most other studies found positive effects of pack size on pup survival (Marneweck et al. 2019b; McNutt and Silk 2008; Woodroffe et al. 2017), we are tentative to conclude that pack size has negative effects on pup survival.

Individual survival was also affected by extrinsic factors of lions and prey, although the manifestation of their effects were dependent on wild dog age class. High lion density can exert strong direct and indirect top-down effects on wild dog survival due to high levels of interspecific competition. This showed as reduced survival for adults and yearlings but had no effect on pup survival. While packs in HiP use landscape features to proactively avoid detection by lions (Davies et al. 2021), during direct encounters, adult and yearling wild dogs defend pups from lions (Creel and Creel, 2002) and likely increase the probability of a fatal interaction. This could result in an age-class discrepancy in lion-induced mortality (Table S3). Surprisingly, the extrinsic effect of higher prey density resulted in lower survival. The effect size of this relationship is small and we are tentative to interpret this effect too closely. A potential, but tentative, explanation could be that higher prey densities might positively influence other intraguild competitors (i.e. cheetahs, leopards, spotted hyenas), which could have slightly negative effects on wild dog survival as wild dogs compete with these species (Creel et al. 2001; Vanak et al. 2013). However, no long-term data are available for these species in HiP, and this conclusion remains tentative.

Our study provides important insights into the regulatory drivers of rate of population change and survival in a high-density, enclosed population of wild dogs. This population has performed well across multiple generations, highlighting that effective conservation of functional populations of wild dogs in small, fenced reserves is possible. Moreover, these managed populations can exhibit patterns in demographics, survival and mortality similar to free-roaming populations. Additionally, our results highlight the critical importance of extrinsic effects of prey that mediate rate of population change irrespective of the density of dominant interspecific competitors. In the same study area, Davies et al. (2021) showed that small-scale variation in woody cover also contributes to the co-existence of wild dogs and lions. The high density of lions in HiP, and the fact that metapopulation intervention did not influence rate of population change, highlight that wild dogs are adaptable to living under high levels of interspecific competition. High prey availability, in addition to high habitat heterogeneity (Davies et al. 2021), facilitates this unique example of co-existence for this subordinate predator at high levels of interspecific competition.

Data availability

The datasets generated during and/or analysed during the current study are available in the figshare repository <https://doi.org/10.6084/m9.figshare.14368043.v1>.

Code availability

The code generated during and/or analysed during the current study are available in the figshare repository <https://doi.org/10.6084/m9.figshare.14368043.v1>.

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Conflict of interest

The authors have no relevant financial or non-financial interests to disclose.

Ethical approval

All applicable international, national and institutional guidelines for the care and use of animals were followed. All procedures performed in studies involving animals were in accordance with the ethical standards of The University of Pretoria under the approved Animal Ethics Committee project number EC006-14.

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Appendix

Table A1. The seven a priori candidate regression models used to investigate factors affecting the wild dog rate of population change in Hluhluwe–iMfolozi Park, South Africa

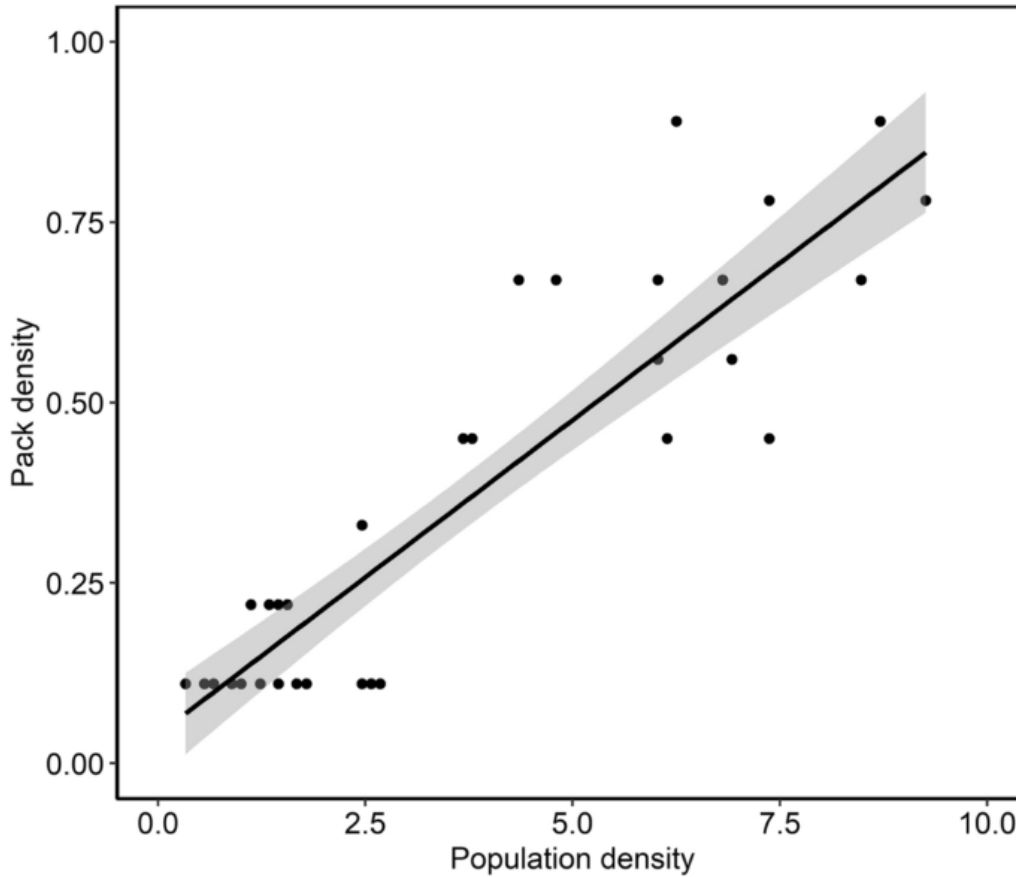


Fig. A1. Relationship between the annual population density (number of adults and yearlings/100 km²) and annual pack density (number of packs/100 km²) fitted with a linear regression model. Grey shaded region illustrates the 95% confidence intervals

Table A1. The seven a priori candidate regression models used to investigate factors affecting the wild dog rate of population change in Hluhluwe–iMfolozi Park, South Africa

Rank	Form of regression	<i>df</i>	loglikelihood	AICc	Δ AICc	w_i
1	Prey density + lion population density + prey density: lion population density	4	- 94.83	199.89	0.00	0.46
2	Prey density	2	- 98.09	200.78	0.90	0.29
3	Pack density	2	- 99.50	203.61	3.72	0.07
4	Lion population density	2	- 99.65	203.90	4.02	0.06
5	Anthropogenic	2	- 99.74	204.08	4.19	0.06
6	Prey density + pack density + prey density: pack density	4	- 96.96	204.15	4.26	0.05
7	Lion population density + pack density + lion population density: pack density	4	- 99.48	209.19	9.30	0.00

Top models are indicated in bold where Δ AICc \leq 2

Table A2. Predictive power of each model set of covariates on individual wild dog survival for different age classes

Model covariate(s)	Concordance (SE)	Likelihood ratio test
<i>Pup survival model</i>		
Pack density	0.569 (0.03)	$\chi^2_{(1)}=4.88; p=0.03$
Pack density + group size	0.662 (0.03)	$\chi^2_{(2)}=24.98, p<0.001$
Pack density + group size + prey density	0.664 (0.03)	$\chi^2_{(3)}=34.44, p<0.001$
Pack density + group size + prey density + lion density	0.664 (0.03)	$\chi^2_{(4)}=35.43, p<0.001$
<i>Adult and yearling survival model</i>		
Pack density	0.540 (0.02)	$\chi^2_{(1)}=2.57; p=0.1$
Pack density + group size	0.620 (0.02)	$\chi^2_{(2)}=12.82, p=0.002$
Pack density + group size + prey density	0.643 (0.02)	$\chi^2_{(3)}=31.41, p<0.001$
Pack density + group size + prey density + lion density	0.697 (0.02)	$\chi^2_{(4)}=62.29, p<0.001$

Higher concordance indicates higher predictive power and that model should be considered most important. Top supported models are highlighted in bold. Likelihood ratio test gives the global statistical significance of the model