

Estimating lion population variables: prey and disease effects in Kruger National Park, South Africa

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Abstract

Context. Lion (*Panthera leo* Linnaeus, 1758) populations experience a range of ecological and human influences that affect their demography. Few lion populations have reliable estimates of population size, trends in these, or demographic profiles. Threats such as those imposed by diseases are thus hard to evaluate and respond to.

Aims. To calibrate call-up stations and define survey effort required to achieve estimates with known precision, and extract age structures and estimate survival rates, to estimate lion numbers, sex and age structure and survival rates, and then to evaluate the effect of bovine tuberculosis (bTB) on estimates of lion density and survival.

Methods. By using call-up stations, we developed a statistically robust approach to estimate selected population variables and evaluated the perceived threat of bTB in landscapes of varying prey biomass in the Kruger National Park.

Key results. The size of the lion population was stable, although long intervals between present and historical estimates limit this conclusion. Density and survival rates associated positively with prey biomass, and a positive association was detected between the survival rate and bTB prevalence, with survival being higher in areas that had high prevalence of bTB. Male survival was lower than female survival, disregarding the effects of prey biomass or bTB prevalence. Body condition of lions was high, with scores lower at low to medium prey density.

Conclusions. The effect of an exotic disease on the Kruger lion population may be negligible at present. Intra-specific competition in areas where lions live at high densities affects survival rate. However, droughts could disrupt the hierarchical influences of prey biomass and bTB prevalence on lion densities and survival.

Implications. To evaluate the effect of an exotic disease on lion demography, population surveys should include age- and sex-structure assessments, complemented with focal studies of fecundity. This reflects the importance of understanding host–disease dynamics to inform management options.

Additional keywords: bovine tuberculosis, call-up surveys, demography, monitoring, *Panthera leo*, population size.

Introduction

Biodiversity, ecosystem function and services depend on integrity of ecological processes (Midgley and Thuiller 2005). Several factors may impose on these (Daszak *et al.* 2001) and carry undesirable consequences for human society (Daszak *et al.* 2000). Invasive species and infectious diseases affect biodiversity, ecosystems and human health (Crowl *et al.* 2008). Responding to these concerns carries challenges. Ecological change and disease emergence often associate with complex and large-scale processes difficult to pinpoint (Plowright *et al.* 2008), and attempts at disease control may carry unpredictable outcomes both for disease dynamics and also for the host species (e.g. McDonald *et al.* 2008).

Several approaches address the above complexities. Sentinel species, often carnivores, form a focus in providing insight into the health of an ecosystem (Aguirre 2009). However, ecological monitoring and disease screening provide challenges in

evaluating (1) threats and (2) how well the system responds to management actions (Woodford 2009). It thus seems paramount that conservationists embark on certainty of the potential effects of a disease on ecosystem dynamics, before embarking on the uncertainties of how to respond to such risks.

The numbers and density of the lion (*Panthera leo* Linnaeus, 1758) vary considerably across Africa (Bauer and van der Merwe 2004), and may decline as their prey decrease as a result of competition with livestock (Ogutu and Dublin 2002; Ogutu *et al.* 2005), retribution killing of stock-raiding lions (Woodroffe and Frank 2005) and excessive trophy hunting (Loveridge *et al.* 2007) or poaching. Although such disturbances threaten lion's persistence, prey biomass usually determines lion density (van Orsdol *et al.* 1985; Packer *et al.* 2005; Hayward *et al.* 2007). Whereas extrinsic factors, such as disease, could modulate the responses of the lion population; in severe cases, they may lead to dramatic local declines (Kissui and Packer 2004).

Although estimates vary, a minimum of 16 000 African lions are extant in 66 lion-conservation units (Chardonnet 2002; Bauer and van der Merwe 2004). Nineteen of these units are viable, with only six having >1000 adults (IUCN SSC Cat Specialist Group 2006). Some units have populations exposed to disease that could place them at risk (Mollel 1977; Brown *et al.* 1994; Roelke-Parker *et al.* 1996; Keet *et al.* 1997; Packer *et al.* 1999; Cleaveland *et al.* 2005), especially when such populations are small and isolated (Kissui and Packer 2004).

As a rule, researchers use concerted efforts or surveys to estimate lion numbers (e.g. Smuts 1976; Castley *et al.* 2002), and calculate population growth rate from repeated estimates in the same area (e.g. Maddock *et al.* 1996). Variance in the estimates leads to uncertainty in growth rates, which can be overcome by using long time series (Gerrodette 1987). However, such time series exist only for a few populations (e.g. Stander 1991; Castley *et al.* 2002; Packer *et al.* 2005). In addition, variables other than population size (e.g. sex and age structure, birth and death rates) are demanding to estimate (e.g. Ogutu and Dublin 2002). Paucity of information is thus common for most lion populations (Bauer and van der Merwe 2004).

Several methods can help estimate the numbers of a carnivorous species in a specific area (e.g. Wilson and Delahay 2001; Thorn *et al.* 2009). Call-up stations are popular for lions and spotted hyaenas (*Crocuta crocuta*) (e.g. Smuts *et al.* 1977; Ogutu and Dublin 1998, 2002; Mills *et al.* 2001), although they are constrained by response rates not having been measured in most areas (Ogutu and Dublin 1998; Mills *et al.* 2001). Here, we calibrate call-up stations and define the survey effort required to achieve estimates with known precision. We also extract age structures and estimate survival rates.

The lions living in the Kruger National Park (hereafter Kruger) epitomise the issues that lion conservationists and disease managers in general face. Up to 2000 lions may live in the Greater Limpopo Transfrontier Park, which includes Kruger (Bauer and van der Merwe 2004). The invasion of an exotic disease, bovine tuberculosis (bTB), into Kruger may affect species directly, one of these being the lion (Keet *et al.* 1996). In addition, the incidence of bTB in key prey species (e.g. African buffalo, *Syncerus caffer*, Funston *et al.* 1998) varies from region to region (Rodwell *et al.* 2000). Bovine tuberculosis may thus affect lions through effects on their prey and these effects may vary regionally.

Even though data exist for the lion population in Kruger, none of these earlier surveys (Smuts 1976, 1978; Mills 1995; Funston *et al.* 2003) was conducted at a park-wide scale. Thus, the potential direct or indirect impact of bTB on the lion population remains unmeasured. We apply our technique to estimate the numbers, and the sex and age structure of the lion in Kruger from call-ups conducted during 2 years. We then use our results to evaluate the effect of bTB on the estimates of lion density and survival, once the effect of prey biomass has been accounted for.

Materials and methods

Study area

The Kruger National Park is situated in the low-lying savannas of the eastern parts of the Limpopo and Mpumalanga provinces

of South Africa (Fig. 1), adjacent to Mozambique in the east, and Zimbabwe in the north. The Park covers an area of 19 485 km². Mean annual rainfall varies from 750 mm in the south to 450 mm in the north, with ~80% of the rain falling during October–March (Gertenbach 1980). Granite and gneiss soils dominate the western half of Kruger whereas nutrient-rich basalt soils dominate the eastern half, with a narrow band of Karoo sediment occurring at the junction of the granite and basalt (Schutte 1986).

The vegetation on the southern basalts is largely wooded savanna, with *Sclerocarya caffra* and *Acacia nigrescens* dominating the tree canopy. Mixed *Combretum* spp. and *Acacia* spp. dominate the southern granites. In the north, *Colophospermum mopane* dominates both the basalt and granite substrates. However, taller *C. mopane* as well as *Combretum* spp. and *Acacia* spp. occur more often on the granites, whereas stunted or shrub-like *C. mopane* sparsely interspersed with *S. caffra* are found on the basalts (Gertenbach 1983).

Bovine tuberculosis apparently invaded Kruger in the early 1960s (Bengis *et al.* 1996) and remained undetected until 1990 (Caron *et al.* 2003). Buffalo is the primary host (Rodwell *et al.* 2000; Bengis *et al.* 2003), with herd prevalence varying across Kruger, as follows: 38.0%, 16.0% and 1.5% in the southern, central and northern regions respectively (Rodwell *et al.* 2000). The body condition of the buffalo in herds with high prevalence of bTB is lower than in herds with low bTB infection (Caron *et al.* 2003; Cross *et al.* 2009). The disease has been found in lions, leopards (*Panthera pardus*), cheetahs (*Acinonyx jubatus*), kudus (*Tragelaphus strepsiceros*) and baboons (*Papio ursinus*) (Keet *et al.* 1996; Keet *et al.* 2000, 2001). Vaccination has not been attempted because long-term vaccination programs need to be combined with other control measures to eradicate the disease from buffalo (Cross and Getz 2006).

The substrate and vegetation patterns define zones that are closely matched by large herbivore densities. Herbivores live at higher densities on the fertile basalts than on the granites, and at much lower densities in the dry north, irrespective of substrate (Gertenbach 1983) (Fig. 1). Stratified distance sampling along aerial transects annually provides population estimates of the larger mammals in Kruger (Viljoen 1989; Whyte 2001). We used data from the 2006 census (Judith Kruger, Scientific Services, SANParks, unpubl. data) to calculate the biomass of eight key prey species that make up >95% of the lion's prey in Kruger (Mills and Shenk 1992; Radloff and du Toit 2004). We multiplied each species' estimated abundance by the average adult female body mass (Skinner and Smithers 1990). These served as indices to illustrate that prey biomass differed among zones.

The Olifants River is the boundary between the northern and southern regions (Fig. 1). It is also the boundary between the northern low and central medium bTB-prevalence zones (Rodwell *et al.* 2000). The Sabie River separated the southern half of Kruger into medium and high bTB-prevalence zones. We thus defined the following six zones with varying levels of prey biomass and prevalence of bTB in prey: low prey + low disease, medium prey + low disease, high prey + medium disease, very high prey + medium disease, high prey + high disease, and very high prey + high disease (Fig. 1).

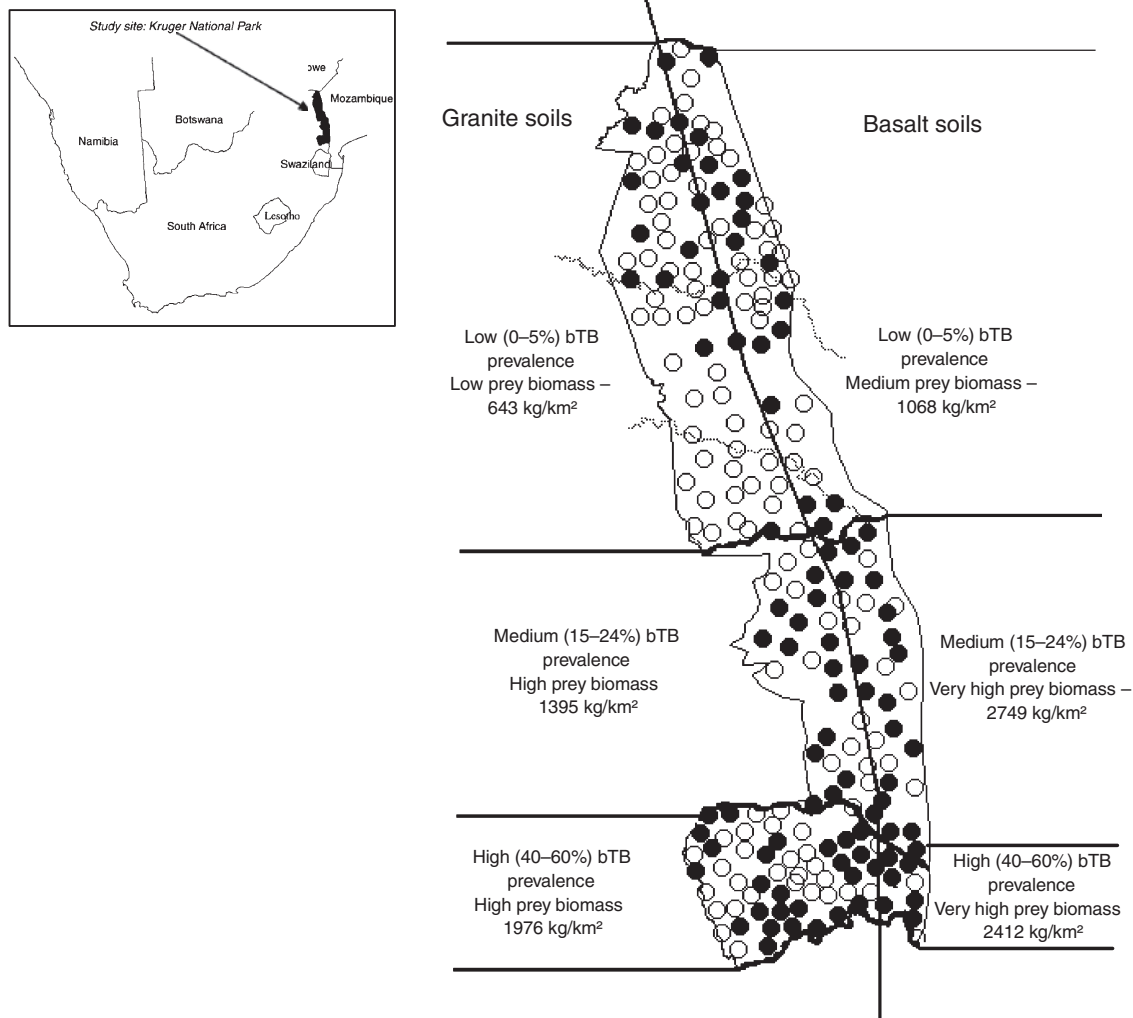


Fig. 1. The localities where we sampled lions by using calibrated call-up stations in Kruger National Park during 2005 and 2006. The open symbols indicate localities where we recorded no lions during sampling. Closed symbols indicate localities where lions responded to our call-ups. We also show the approximate boundaries of the six different zones defined by prey biomass (kg km⁻²) in 2006 (J. M. Kruger, unpubl. data) and the incidence of bTB in buffalo (Rodwell *et al.* 2000).

Data collection

To calibrate the technique, we opportunistically located 37 lion groups comprising 170 individuals in the central region of Kruger during June–July 2005 by driving and searching for lions. For each of these groups, an observer stayed with it while we set-up a calling station at a known distance away. We played a 4.25-min recording of a buffalo calf in distress repeatedly for 1 h on a LG MF-FM12 MP3 player (LG Electronics Inc., Seoul, Korea). This was connected to a 12-V 60-W Jedia Mobile 60 Mixing Power Amplifier (Jedia Co. Ltd, Kyung Gi-Do, Korea) powered by the vehicle's 12-V battery, which was connected to two Show 40-M 4-ohm horn speakers (Show Co. Ltd, Kyung Gi-Do, Korea, diameter 40 cm), with Show TU-35 M4 40 W driver units (Show Co. Ltd, Kyung Gi-Do, Korea) connected in a series and facing 180° direction from each other. The vocalisations were broadcast at full volume from the speakers mounted on a steel tripod 2.5 m above the ground. The tripod was pegged to the ground and placed in the

middle of a road 20 m away from the observation vehicle to facilitate sex determination and visual assignment of arriving individuals into broad age classes. The speakers were rotated every 15 min to get an all-round sound distribution. No bait was provided at a calling station.

For population surveys, our placement of call-up stations focussed on the following six study zones within Kruger (Fig. 1): low prey + low disease ($n=58$ call-up stations); medium prey + low disease ($n=45$); high prey + medium disease ($n=27$); very high prey + medium disease ($n=18$); high prey + high disease ($n=70$); and very high prey + high disease ($n=14$). To minimise any chance of double-counting individuals, stations were at least 10 km apart. We sampled three or four stations per night during August–September 2005 (the northern regions with low bTB prevalence), and May–August 2006 (the southern regions with medium and high bTB prevalence) by playing a recording of a buffalo calf in distress for 1 h. All call-ups were conducted a minimum of half an hour

after dark in the evening from 1800 hours to 0100 hours because lions are most active during this period (Schaller 1972; Stander 1992; Hayward and Hayward 2007).

We recorded each group that arrived during the hour, with more than one group arriving on only seven occasions ($n=232$ call ups). We sexed and assigned age to each lion from shoulder heights on the basis of parameter values from a known population, by using a modified von Bertalanffy growth equation, as follows (Sam M. Ferreira and Paul J. Funston, unpubl. data):

$$\begin{aligned}\text{♀: } h_i &= 14.56 + (95.81 - 14.56)(1 - e^{-1.18x}), \quad \text{and} \\ \text{♂: } h_i &= 14.71 + (108.68 - 14.71)(1 - e^{-1.09x}),\end{aligned}$$

estimated from known-age lions where h_i (cm) is shoulder height and x is the age. Shoulder heights came from digital photogrammetry (Shrader *et al.* 2006). We used a 20D Canon digital camera (Canon Inc., Tokyo, Japan) with a Canon 100–400-mm image-stabilised zoom lens and a Canon 580 Ex speedlight to make images of individual lions. We calculated lion shoulder heights from

$$h_i = \frac{\varphi_i}{(1.5174f)d^{-1}},$$

where h_i is shoulder height in centimetres, φ_i is the number of pixels represented by a lion's front leg between its shoulder and foot, f is the focal length of the lens and d is the distance to the lion measured by a rangefinder (Impulse 200, ASC Scientific, Carlsbad, CA).

When possible, lions were assigned a body-score by using the following criteria: 1, extremely emaciated, unlikely to survive, with a very poor coat; 2, very thin with backbone ribs and hip bones showing clearly, and a flat, compressed stomach, often with a poor coat condition; 3, thin and showing signs of muscle loss, may have blotches on the coat; 4, relatively thin, sometimes with a poor coat condition; and 5, a very healthy looking animal, with good muscular development and a good coat condition.

Data analysis

Two primary constraints affect the use of call-up stations to count lions, namely the probability that lions appear at a station and the chance of sampling the same lion more than once (Ogutu and Dublin 1998; Mills *et al.* 2001). The probability that lions may appear depends on whether a group reacts and whether all individuals in a responding group react in the same way. Lion groups containing cubs are likely to be more cautious when approaching call-up stations than are other types of groups (Ogutu and Dublin 1998; Mills *et al.* 2001). Our analysis separated groups into those with ($n=9$) and those without ($n=28$) cubs. We did not separate male groups from female groups, because males often accompanied females. We thus assumed that sexes responded in the same way. We reasoned that by finding groups and following them when a call-up is made at a known distance from them, we could calculate the proportion responding at intervals of 0.5-km distance. Fitting an inverse sigmoid to these data by using a maximum likelihood approach (Edwards 1972; Microsoft Excel macro provided by

Hood 2005) allowed us to estimate the radius (r_e) and area (\bar{A}) that call-up stations sampled. The response function was fitted separately for groups with and without cubs.

If there were no distance effects of call-ups, all lions within the sample area should respond, giving a theoretical response function of $y=1$. By dividing the integral (limits set between 0 and the radius) of the fitted response function by that of the theoretical response function over the same interval (0 to the radius), we could estimate the probability (P_p) that a group will react to a call-up. We estimated $\text{var}[r_e]$, $\text{var}[\bar{A}]$ and $\text{var}[P_p]$ through Monte Carlo simulation (Gentle 1943), using the distributions of the parameters of the inverse sigmoid function defined by their values and variances estimated through maximum likelihood as before.

To estimate the probability (P_i) that an individual within a responding group will respond itself, we focussed on responding groups and expressed P_i as the proportion of responding lions to the total number of lions in a group. We estimated $\text{var}[P_i]$ as $P_i(1 - P_i)$ (Sokal and Rohlf 1995).

By noting the number of times that lions with clear natural markings responded to call-ups, we could estimate the probability (P_r) that a lion will be noted more than once in a survey. We estimated $\text{var}[P_r]$ as $P_r(1 - P_r)$ (Sokal and Rohlf 1995).

To estimate lion population size (N_j) in a study zone j , we defined

$$N_j = \frac{A_T \sum_{s=1} f_{nc,s}}{n \bar{A} P_{nc,p} P_{nc,i} (1 - P_{nc,r})} + \frac{A_T \sum_{s=1} f_{c,s}}{n \bar{A} P_{c,p} P_{c,i} (1 - P_{c,r})},$$

where A_T is the total area of zone j , n is the number of call-up stations here and \bar{A} is the effective area sampled by a station. $\sum_{s=1} f_{nc,s}$ and $\sum_{s=1} f_{c,s}$ are the total number of lions in groups with and without cubs, respectively, that appeared at the stations. The parameters $P_{c,p}$ and $P_{nc,p}$ are the probabilities that groups with (c) or without cubs (nc) will respond, and $P_{c,i}$ and $P_{nc,i}$ are the probabilities that an individual within a responding group will appear at a station, and $P_{c,r}$ and $P_{nc,r}$ are the probabilities that an individual will respond more than once. Note that A_T does not contribute to the variance of the estimate, $\text{var}[N_j]$, so that

$$\text{var}[N_j] = N_j^2 \left[\frac{\text{var}[\bar{A}]}{\bar{A}^2} + \frac{X_{nc}^2 \text{cv}^2[X_{nc}] + X_c^2 \text{cv}^2[X_c]}{(X_{nc} + X_c)^2} \right],$$

where

$$X_{nc}^2 = \frac{\sum_{s=1}^n f_{nc,s}}{P_{nc,p} P_{nc,i} (1 - P_{nc,r})} \quad \text{and} \quad X_c^2 = \frac{\sum_{s=1}^n f_{c,s}}{P_{c,p} P_{c,i} (1 - P_{c,r})},$$

with s = call-up stations and CV = the coefficient of variance of a variable. We defined

$$\begin{aligned}CV^2[X_{nc}] &= \frac{\frac{n}{n-1} \sum_{s=1}^n (f_{nc,s} - \bar{f}_{nc})^2}{(\sum_{s=1}^n f_{nc,s})^2} + \frac{\text{var}[P_{nc,p}]}{P_{nc,p}^2} \\ &\quad + \frac{1 - P_{nc,i}}{P_{nc,i}} + \frac{P_{nc,r}}{1 - P_{nc,r}}\end{aligned}$$

and

$$CV^2[X_c] = \frac{\frac{n}{n-1} \sum_{s=1}^n (f_{c,s} - \bar{f}_c)^2}{(\sum_{s=1}^n f_{c,s})^2} + \frac{\text{var}[P_{c,p}]}{P_{c,p}^2} + \frac{1 - P_{c,i}}{P_{c,i}} + \frac{P_{c,r}}{1 - P_{c,r}}.$$

For each zone, we converted the estimated population size and its confidence intervals to density by using the area covered by that zone.

We studied the influence of the survey effort on population estimates and randomly drew subsamples for a specific survey effort (n stations per 1000 km²), 50 times from our total sample of call-up stations, and recalculated a population estimate and its confidence limits. We calculated a standardised index of precision (percentage confidence limit, PCL, is the confidence limit range expressed as a percentage of the estimate, Barnes 2002) and plotted these against the number of call-up stations per 1000 km². We assumed a reasonable sample size if PCLs were <20%.

We derived zone-specific age distributions by grouping responding lions into 1-year age classes up to 4 years for females and 5 years for males. Older lions were grouped into one large adult age class. We corrected frequencies by using the probabilities of responding as before. We then smoothed these observed age distributions by using Ferreira and van Aarde's (2008) expansion method and maximum likelihood (Edwards 1972; Microsoft Excel macro provided by Hood 2005) to obtain a decay rate a (Eberhardt 1988) and $\text{var}[a]$. The decay rate a , describes the shape of an age distribution.

We collated previous estimates of lion numbers for the Central District (Smuts 1976) and the Lower Sabie Plains (Smuts 1976; Funston *et al.* 2003) and calculated an estimate for these two areas from our own data. Fitting exponential models ($N_t = N_0 e^{rt}$) to the combined data by using maximum likelihood (Edwards 1972; Microsoft Excel macro provided by Hood 2005) allowed us to estimate exponential growth r and $\text{var}[r]$, which we converted to a finite growth rate λ ($\lambda \approx 1 + r$). We assumed a stable age distribution (Michod and Anderson 1980) and estimated survival rate s for each of the regions from $s = a\lambda$ (Eberhardt 1988). We estimated $\text{var}[s]$ by using 50 values drawn from the distributions of a and λ , defined by their estimates and variances.

We extracted 30 values of population estimates and survival rates for each zone from the respective distributions of the estimates determined before. We used these in two-way ANOVAs (Sokal and Rohlf 1995) to evaluate whether zones with different prey biomass and bTB prevalence in prey differed in lion densities or survival.

We also related density estimates and survival rates to prey biomass. We used Mann–Whitney U -tests (Sokal and Rohlf 1995) to find out whether the residuals of these relationships were associated with bTB prevalence. To test for any social constraints on survival, we calculated a relative lion-density index as the number of lions per unit prey biomass ($n \text{ kg}^{-1}$ prey biomass) and related sex-specific survival rates to this index.

For our final analysis, we expressed the relative frequency (percentage) of lions for each condition score within zones

separately and used χ^2 -tests (Sokal and Rohlf 1995) to evaluate whether body conditions differed among zones.

Results

Calibration of call-up stations

We could estimate the response only for lion groups without cubs. The response decayed with distance. The fitted inverse-sigmoid model predicted that lions responded up to 4.3 ± 0.9 km (mean \pm s.d.; 95% confidence interval (CI): 2.5–6.1 km) away from call-up stations (Fig. 2a). This means that call-up stations sampled 57.7 ± 24.9 km² (mean \pm s.d.; 95% CI: 8.9–106.6 km²). We assumed that the area sampled by a call-up station was the same for groups with cubs than that for groups without cubs.

Approximately 73% of the 28 lion groups without cubs within the sampling area responded to a call-up (0.734 ± 0.076 , mean \pm s.e.). We estimated that nearly 29% of those nine groups that did have cubs would respond (0.286 ± 0.079 , mean \pm s.e.). However, nearly all individuals within a

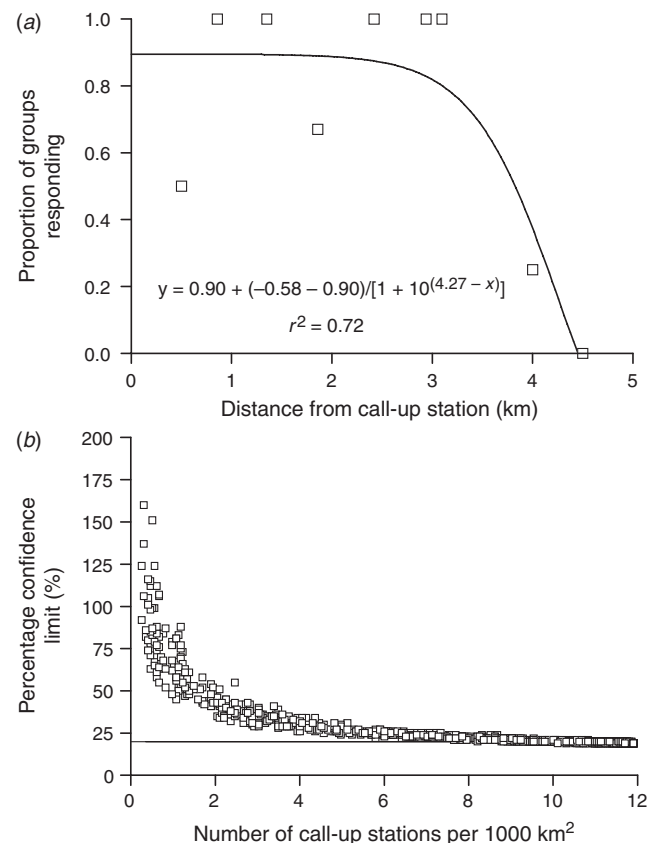


Fig. 2. (a) The decay of responses of lion groups without cubs to call-ups conducted in the Kruger National Park. The model suggests that groups respond to call-ups up to 4.28 km away. A call-up station thus samples 57.71 km². (b) The effect of sampling effort on the precision (percentage confidence limit, PCL, is the confidence limit expressed as a percentage of the estimate; Barnes 2002) of estimates recorded in the Kruger National Park. The simulation suggests that PCLs <20% (horizontal line) can be achieved at eight call-ups per 1000 km².

responding group turned up at a call-up station. Nearly 96% of the lions in a responding group with cubs would appear at a call-up station (0.957, 95% CI: 0.555–1.000) and ~90% of those in a group with no cubs (0.902, 95% CI: 0.320–1.000) would appear. The above probabilities suggest that the number of lions observed at a call-up station needs correction by a factor of 1.51 and 3.66 for groups without ($[P_{nc,p} P_{nc,i}]^{-1}$) and with cubs ($[P_{c,p} P_{c,i}]^{-1}$) respectively.

Survey effort

The percentage confidence limits declined exponentially as the number of call-up stations per 1000 km² increased (Fig. 2b). At eight call-up stations per 1000 km², PCLs were <20%. Our sample sites were distributed across Kruger (Fig. 1), with varying densities in the six zones (low prey+low disease: 9.54 call-up stations per 1000 km²; medium prey+low disease: 11.33 call-up stations per 1000 km²; high prey+medium disease: 13.16 call-up stations per 1000 km²; very high prey+medium disease: 6.66 call-up stations per 1000 km²; high prey+high disease: 19.05 call-up stations per 1000 km²; and very high prey+high disease: 33.33 call-up stations per 1000 km²). With the exception of one (very high prey+medium disease), all zones were sampled at intensities larger than eight call-up stations per 1000 km². This suggests that our sampling was appropriate for most of the zones.

The high density of call-up stations in the very high prey+high disease zone was a concern because we could have potentially sampled individual lions more than once. However, during calibration we found that in all cases ($n=5$) where we repeated the call-up to a known group of lions that had responded previously, the next time they did not respond. Double-sampling was thus unlikely in this zone.

Densities

Lion densities varied considerably across the study zones (Table 1). Within the zones that had a low bTB prevalence in northern Kruger, the lion density was higher in the zone that had a higher prey biomass ($t_{58}=14.17$, $P<0.01$). The zones in the southern parts of Kruger had generally higher lion densities

than those in the north. Here, we tested the relative contribution of prey biomass and the level of bTB prevalence in prey to the variance in lion densities noted among the zones. The four zones differed in lion density; however, this was primarily due to prey biomass ($F_{1,116}=307.89$, $P<0.01$). Lion densities also varied as a result of bTB prevalence in prey ($F_{1,116}=55.38$, $P<0.01$), and were the highest in zones with medium rather than high bTB prevalence.

Disregarding zones, lion densities were positively associated with prey biomass (Fig. 3a). Once the effect of prey biomass was removed, we found no significant differences among the areas that had different bTB prevalences in prey (Fig. 3b).

Population estimates and trends

The regional differences in density that related primarily to prey biomass resulted in zonal variance in population sizes (Table 1). Disregarding zonal differences, we estimated a population size of 1684 (95% CI: 1617–1751) lions for Kruger as a whole. No previous similar estimates were found. Smuts (1978) estimated 708 lions in the Central District during 1976. We estimated 632 for the same area (Table 2), predicting an exponential growth rate of -0.4% (95% CI: -1.1–0.3%). Smuts (1978) also estimated lion numbers for the Lower Sabie Plains at 67 in 1976. Funston *et al.* (2003) reported a time series of estimates from 1986 to 1995 for the same area, ranging from 52 to 67. Our estimate of 48 (Table 2) predicted an exponential growth rate of -0.3% (95% CI: -2.5–1.9%) for these plains.

Age distributions and survival rates

Age distributions differed among zones (Table 3). We corrected observed values by the calibration factors for groups with and without cubs previously estimated. We could also not reliably sex lions younger than 1 year. We estimated values for the rate at which the number of individuals in an age distribution decays (α) for males in each zone (low prey+low disease: 0.41 ± 0.01 , mean \pm s.e.; medium prey+low disease: 0.58 ± 0.04 ; high prey+medium disease: 0.73 ± 0.07 ; very high prey+medium disease: 0.63 ± 0.04 ; high prey+high disease: 0.71 ± 0.03 ; and

Table 1. Areas surveyed, number of calling stations (N), observations (n_{lc} – lions with cubs, n_l – lions without cubs), population estimates (\hat{N}) and densities (\hat{D}) of lions in six different zones within the Kruger National Park for 2005/2006
All regions combined resulted in a population estimate of 1684 lions for the whole park (95% CI: 1617–1751)

Location and zone	Area (km ²)	Habitat	N	n_{lc}	n_l	\hat{N}	\hat{D}
Northern Kruger National Park							
Low bTB prevalence							
Low prey biomass	6810	Granites, sand veld, rugged veld	58	35	26	340 (280–400)	5.0 (4.1–5.9)
Medium prey biomass	3442	Basalts/Lebombos	45	26	80	286 (239–333)	8.3 (6.9–9.7)
Southern Kruger National Park							
Medium bTB prevalence							
High prey biomass	2502	Granites/bottom lands	27	23	20	183 (137–230)	7.3 (5.5–9.2)
Very high prey biomass	3016	Basalts/Lebombos	18	40	23	525 (353–698)	17.4 (11.7–23.1)
High bTB prevalence							
High prey biomass	3675	Granites/bottom lands/mountains	70	59	75	299 (255–344)	8.1 (6.9–9.4)
Very high prey biomass	460	Basalts/Lebombos	14	16	21	51 (34–68)	11.2 (7.5–14.9)

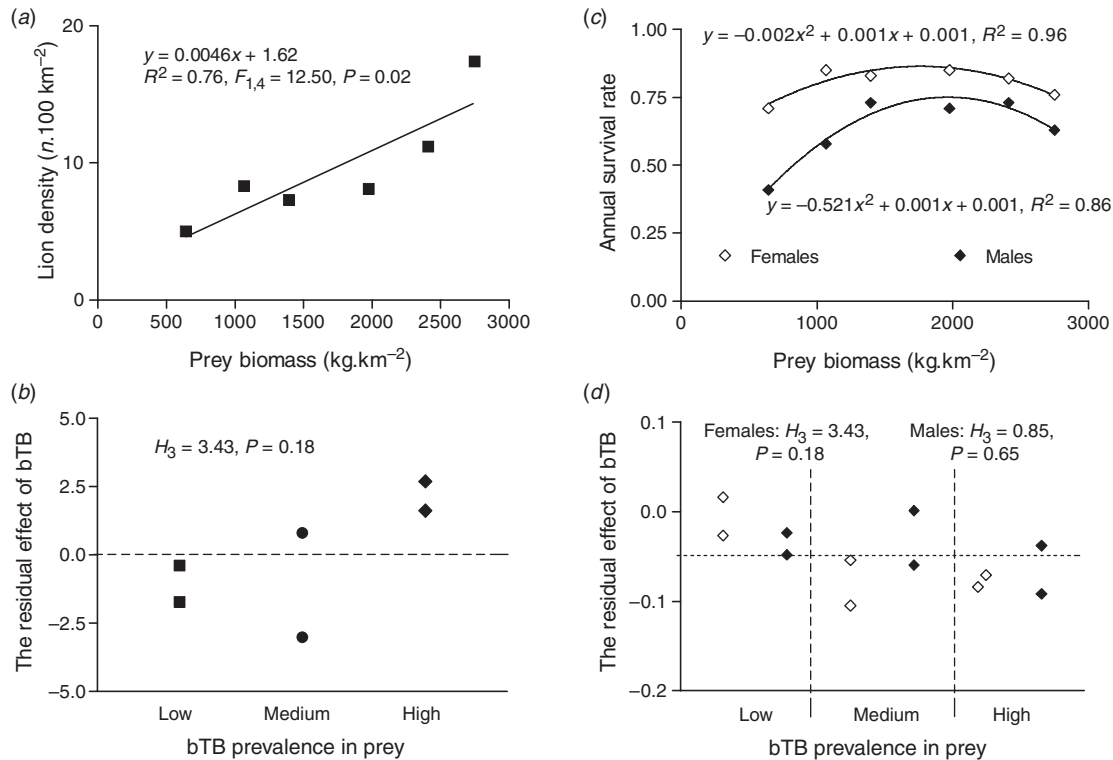


Fig. 3. The effects of prey biomass and bTB prevalence in prey on lion density and sex-specific survival recorded in the Kruger National Park. (a) Lion density increased linearly with prey biomass. (b) The residuals of the relationship between the lion density and prey biomass were not associated with bTB prevalence in prey. (c) Sex-specific survival increased non-linearly with prey biomass. (d) The residuals of the relationships between sex-specific survival and prey biomass were not associated with bTB prevalence in prey.

Table 2. Estimates of lion numbers collated for two regions within the Kruger National Park

We also include estimates (\pm s.e.) for these regions calculated from our own survey. We estimated exponential growth rate from estimates since 1976. Before that, the lion population was recovering from previous management control (Smuts 1976). Our results suggest that lion numbers have been stable during the past 30 years. The population in the Central District had an exponential growth of -0.4% (95 CI: -1.1 – 0.3%), whereas that of the Lower Sabie Plains changed at -0.3% (95% CI: -2.5 – 1.9%)

Year	Central District	Reference	Lower Sabie Plains	Reference
1925	205	Smuts (1978)	–	–
1956	454	Smuts (1978)	27	Smuts (1978)
1976	708	Smuts (1978)	67	Smuts (1978)
1986	–	–	52	Funston <i>et al.</i> (2003)
1987	–	–	56	Funston <i>et al.</i> (2003)
1988	–	–	62	Funston <i>et al.</i> (2003)
1989	–	–	67	Funston <i>et al.</i> (2003)
1993	–	–	62	Funston <i>et al.</i> (2003)
1994	–	–	64	Funston <i>et al.</i> (2003)
1995	–	–	62	Funston <i>et al.</i> (2003)
2006	632 \pm 64	Present study	48 \pm 17	Present study

very high prey + high disease: 0.73 ± 0.03). We also estimated values of a for females in each zone (low prey + low disease: 0.71 ± 0.03 , mean \pm s.e.; medium prey + low disease:

0.85 ± 0.03 ; high prey + medium disease: 0.83 ± 0.03 ; very high prey + medium disease: 0.76 ± 0.04 ; high prey + high disease: 0.85 ± 0.02 ; and very high prey + high disease: 0.82 ± 0.03).

On the basis of the CIs of the estimated changes in lion numbers we assumed a finite growth rate of $\lambda = 1$. If this is true, then estimates of a are also estimates of survival rate. Within the zones of low bTB prevalence in the northern parts of Kruger, females had higher survival than males ($F_{1,116} = 3747.89$, $P < 0.01$), and lions irrespective of sex survived better in the zone with higher prey biomass ($F_{1,116} = 1060.11$, $P < 0.01$). In contrast, variability of survival rates in the southern parts of Kruger was mostly associated with sex ($F_{1,232} = 530.31$, $P < 0.01$), with females surviving better than males, although in this comparison, survival rates were lower at areas of very high prey biomass ($F_{1,232} = 89.93$, $P < 0.01$). Variance in the survival rate was also associated with the prevalence of bTB within a region ($F_{1,232} = 69.00$, $P < 0.01$), with the highest survival rates occurring in the regions with high bTB prevalence.

Sex-specific survival increased non-linearly with prey biomass, disregarding zones (Fig. 3c). Survival was not related to bTB prevalence in prey for each sex, once the effect of prey biomass was removed (Fig. 3d). However, when lion density was high relative to prey biomass, survival rate was lower for males (Fig. 4).

Table 3. Age structures of male and female lions recorded in six zones within the Kruger National Park during 2005 and 2006

n_{lc} , the number of lions recorded in groups with cubs. n_l , the number of lions recorded in groups without cubs. \hat{n} , the corrected frequency using the appropriate correction factors (see text). The values in parentheses are percentages

Location and zone	Age class	Males			Females		
		n_{lc}	n_l	\hat{n}	n_{lc}	n_l	\hat{n}
Northern Kruger National Park							
Low bTB prevalence							
Low prey biomass	<1	6	—	40 (63) ^A	16	—	40 (38) ^A
	1–2	3	2	14 (22)	2	3	12 (11)
	2–3	0	2	3 (5)	2	3	12 (11)
	3–4	0	1	2 (3)	—	—	—
	4–5	0	0	0 (0)	—	—	—
	Adults	0	3	5 (7)	6	12	40 (38)
Medium prey biomass	<1	7	—	46 (37) ^A	18	—	46 (14) ^A
	1–2	12	2	47 (38)	7	2	29 (8)
	2–3	0	2	3 (2)	16	16	83 (24)
	3–4	0	2	3 (2)	—	—	—
	4–5	0	1	2 (1)	—	—	—
	Adults	0	17	26 (20)	34	38	182 (54)
Southern Kruger National Park							
Medium bTB prevalence							
High prey biomass	<1 ^A	3	—	20 (59) ^A	8	—	20 (27) ^A
	1–2	0	1	2 (4)	1	0	4 (5)
	2–3	0	0	0 (0)	1	3	8 (11)
	3–4	0	0	0 (0)	—	—	—
	4–5	0	1	2 (4)	—	—	—
	Adults	2	7	18 (43)	8	8	41 (57)
Very high prey biomass	<1 ^A	6	—	16 (24) ^A	3	—	16 (15) ^A
	1–2	4	5	22 (34)	3	6	20 (19)
	2–3	3	3	16 (24)	8	2	32 (30)
	3–4	1	1	5 (8)	—	—	—
	4–5	0	0	0 (0)	—	—	—
	Adults	1	2	7 (10)	9	4	39 (36)
High bTB prevalence							
High prey biomass	<1 ^A	9	—	26 (30) ^A	5	—	26 (15) ^A
	1–2	4	6	24 (27)	2	4	13 (8)
	2–3	0	1	2 (2)	6	11	39 (22)
	3–4	0	2	3 (3)	—	—	—
	4–5	0	1	2 (2)	—	—	—
	Adults	0	21	32 (36)	13	29	91 (54)
Very high prey biomass	<1 ^A	1	—	6 (15) ^A	2	—	6 (13) ^A
	1–2	3	2	14 (33)	2	0	7 (15)
	2–3	2	0	7 (17)	1	5	11 (23)
	3–4	0	0	0 (0)	—	—	—
	4–5	1	0	4 (9)	—	—	—
	Adults	0	7	11 (26)	4	6	24 (49)

^AWe could not sex all cubs <1-year old. We thus assumed equal sex ratios for those of unknown sex.

Body-condition scores

We noted no lions with scores of 1 or 2 (Table 4). We could not detect a bTB effect in the high ($\chi_4^2 = 6.76$, $P = 0.15$) or very high ($\chi_4^2 = 0.47$, $P = 0.98$) prey zones. When we combined these zones, the frequencies of the body-condition scores differed ($\chi_4^2 = 61.99$, $P < 0.01$) from those in the zones in the north of Kruger that had low bTB incidence in prey and low to medium prey densities. In the north, the lion body-condition scores were nearly evenly distributed between Score 4 (relatively thin, sometimes with a poor coat condition)

and Score 5 (a very healthy looking animal, with good muscular development and a good coat condition). Lions living in zones of high and very high prey biomass were mostly scored 5.

Discussion

The number of lions living in Kruger National Park is likely to be variable; however, it has not changed directionally over the past 30 years, despite the invasion of bTB and the resultant high prevalence in prey species. Variation in lion densities among zones was associated with prey biomass and less so

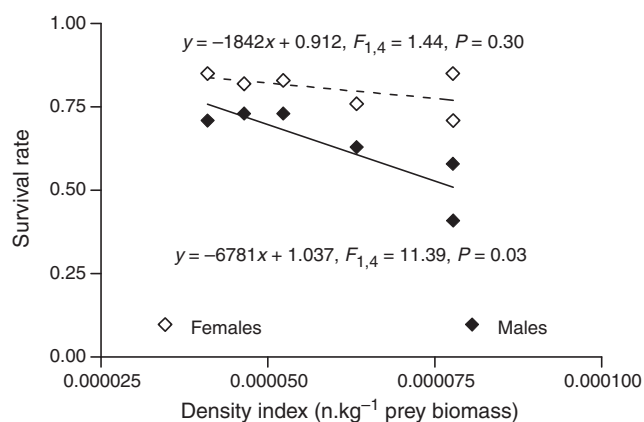


Fig. 4. Survival rate related to a lion density index. The index expressed the number of lions relative to the amount of prey. Survival declined as the number of lions per unit prey increased.

Table 4. Number of lions in different body condition score categories observed in six zones within the Kruger National Park during 2005 and 2006

n, the number of lions observed. We present the percentage of lions for each body-condition score (see text)

Zone	Body-condition score					
	<i>n</i>	1	2	3	4	5
Low bTB						
Low prey biomass	60	0	0	8	52	40
Medium prey biomass	106	0	0	3	55	42
Medium bTB						
High prey biomass	43	0	0	0	2	98
Very high prey biomass	63	0	0	0	5	95
High bTB						
High prey biomass	104	0	0	0	12	88
Very high prey biomass	37	0	0	0	3	97

with bTB prevalence in prey. The association of lion density with prey biomass is in accordance with the results of studies elsewhere (van Orsdol *et al.* 1985; Hayward *et al.* 2007). In addition, prey biomass influenced the lion survival rate, assuming the population vital rates were stationary within zones for some time before our survey. Lion survival was best in zones with high prey biomass. Zones with very high biomass had high lion densities but lower survival, most likely because of intra-specific competition (Bertram 1973; Hanby *et al.* 1995). Survival was the lowest in the northern regions of Kruger, with low to medium prey biomass and low bTB prevalence. When the effects of prey biomass were accounted for, the survival was higher in zones with the highest level of bTB prevalence in prey, contrary to what we expected. This could have been a result of bTB leading to higher vulnerability of prey to predation and, hence, increased lion survival. Caron *et al.* (2003), however, noted that bTB had negligible ecological effects on buffalo, a key prey item of lions (Mills *et al.* 1995; Funston *et al.* 1998). When we checked the body condition of lions, we could not find differences in scores that associated with bTB prevalence. These results contrast those of other studies on how disease can influence carnivore populations

(Alexander and Appel 1994; Roelke-Parker *et al.* 1996; Sillero *et al.* 1996; Kissui and Packer 2004).

There are several possible reasons as to why our results contradicted the conventional wisdom on the effect of diseases on wildlife populations. The first of these is that our survey method was biased. We assumed that a 1-h continuous play back would result in a high response probability and a large effective sampling area (Ogutu and Dublin 1998). Lion surveys often target large areas that may need intense surveys that could be limited by the sampling area of each calling station. However, at densities such as those in Kruger, call-up stations placed at a frequency of eight stations per 1000 km² would have provided accurate and precise estimates. In most zones, we surveyed with a much higher sampling intensity.

Intense surveys such as ours carry alternative risks of bias in their estimates. Lions usually responded within 30 min, with 15% arriving within 45–60 min of calling. Such 1-h sampling maximises the number of groups observed and reduces the duration of the survey; 1000 km² will take two evenings at four call-ups per night, given the optimal survey effort for densities similar to those in Kruger. By conducting surveys at night in winter, we further limited the potential influence of diurnal- and seasonal-specific lion activity on our estimates. Night call-ups in winter also increase the response because sound travels better during cold, still nights (Garstang *et al.* 1995). However, double-sampling is likely, even though we noted no repeat responses for lions. Even so, it is unlikely that survey bias in our estimates would mask long-term trends associated with disease effects. However, we caution that in areas of a lower lion density it may be necessary to increase the sampling intensity, although never to the point where sample plots start to overlap. At lower densities, the potential bias of double-counting may be reduced substantially. The effects of varying survey effort with prey density on population estimators need further evaluation, given that lion home ranges vary with prey density (Hayward *et al.* 2007).

Given that sampling has negligible effects on the results we have noted, we consider four biological explanations for the lack of disease effects. First, the effect of bTB may not be linear. We restricted the factor analyses of the relative importance of prey biomass and disease to zones with medium or high bTB prevalence. In these zones, much of the bTB effects may have been realised at these prevalence levels in prey. If so, we simply did not detect it in the demography of lions because we did not include a comparable zone with high prey density and low bTB prevalence. Intuitively, however, one would expect asymptotic behaviour of disease effects that comes through an indirect mechanism to be at the high prevalence end of the scale rather than at the low one (e.g. Cleaveland *et al.* 2001). It is thus likely that our results are real and not confounded by non-linear bTB effects on lion demography at low prevalence in prey. In addition, our analyses of the effect of bTB once the effect of prey biomass had been accounted for suggest negligible or non-detectable bTB effects.

Second, the effects of bTB on a predator as reflected by prevalence in prey are not clear. Few studies have focussed on associations between predator survival and disease infections in their prey, and those that have, have not recorded strong effects

(Murray *et al.* 1999). In our case, the effect of bTB in prey on lions could have been negligibly small, which our techniques were not sensitive enough to detect. However, the consistency with which densities, survival and body condition varied, disregarding bTB prevalence, suggests that it is unlikely that the bTB effects were hidden. We do, however, concede that our assumption of a stable age distribution may constrain our conclusions on survival rates.

Third, the low disease influence is further confounded by the prediction that lion demography is primarily associated with prey biomass (van Orsdol *et al.* 1985; Hayward *et al.* 2007) rather than with bTB prevalence. It is thus likely that the strong influence of prey biomass on lion demography that we noted conceals disease effects. We stress that we interpret our results cautiously because we assessed the relative importance of only two variables, namely prey biomass and bTB prevalence in prey. In doing so, we could not separate the interactions for the northern parts of Kruger where we had only one disease treatment. In the south, however, we could separate the interactions, although one of our study zones was small, which could have influenced our analyses.

The final explanation relates to the effects of bTB on prey dynamics itself. For instance, the survival of buffalo, a key prey species, appears not to be affected by bTB prevalence (Cross *et al.* 2009). Prey availability to lions may thus not be enhanced by prey having bTB and thus leading to indirect effects of bTB on lion survival or fecundity. However, even with these constraints and variably potential mechanisms, our results are compelling. It appears that at present, bTB in prey has little detectable influence on lion demography in Kruger.

This conclusion is, however, reserved because the demographic signals that we detected in lions were generated during a relatively wet period with high-quality prey biomass. During wet periods, lions in Kruger predate mostly wildebeest (*Connochaetes taurinus*) and zebra (*Equus burchellii*), and fewer buffalos (Mills *et al.* 1995). During dry periods, prey switching occurs, with buffalo becoming more important (Mills *et al.* 1995). Because buffalo is the key maintenance host of bTB in the Park (Keet *et al.* 1996), the effects of the disease could be substantially different in dry periods because of cascade effects of several stressors on a lion population. Either the lions themselves may have higher infection rates because of high level of contact with infected prey, or the prey biomass may decline. In both instances, lion survival and density may reduce accordingly. Given that no study has confirmed an association between direct bTB infection and lion demography (Keet *et al.* 1997), it is unlikely that bTB prevalence in prey will affect lion demography indirectly, much like what we observed in the present study.

We also have little guidance from other studies with respect to the demographic responses of lion populations exposed to similar disease effects. Most reported disease events in lions are epidemics and the disease effects are dramatic and short lived (Roelke-Parker *et al.* 1996; Kissui and Packer 2004). In these instances, population recovery has tended to be quite rapid, and, although not reported, was probably due to higher rates of juvenile survival. The effects of bTB in populations are likely to be chronic in that they are

slower and more lingering, which may then induce other population responses.

The dominant association of lion demography with prey biomass (van Orsdol *et al.* 1985; Hayward *et al.* 2007; the present study) provides further insights into the dynamics of lions. We were surprised at survival rates being lower in zones with higher prey biomass than in comparable zones with lower prey biomass in Kruger. These zones with lower lion survival had higher lion densities. This was the same for both males and females, even though sex-specific survival differed, as has been found elsewhere (Schaller 1972). Male survival was particularly affected by lion density relative to the amount of available prey, with survival reducing when the number of lions per unit prey increased. Intra-specific interactions, most likely due to other limitations than prey, could lead to a density-dependent reduction in survival at high densities. The observation provides a mechanism through which lion numbers may have remained relatively constant for 30 years.

In the Serengeti, lion numbers were also remarkably stable for extended periods, although major shifts in prey biomass changed the equilibrium population sizes of the lion (Packer *et al.* 2005). However, once the shift has taken place, our study suggests that density-dependent social mechanisms may limit lion numbers (e.g. Bertram 1973; Packer *et al.* 2005). Our finding is significant because it predicts that prey biomass and social constraints may limit lion numbers in some areas; healthy lion populations are expected to be mostly stable in numbers and densities, even though large spatial variation is expected to occur.

What are the implications of our findings for conservationists? First, our results do not justify laissez-faire approaches to the detection of new exotic diseases in a National Park. However, our results reflect the historic consequences of actions that allowed the disease to spread – a consequence that lion managers have to deal with now. At least in Kruger, the persistence of lions is not threatened; however, these dynamics could change in different climatic conditions and with additional stressors such as the presence of other diseases. We thus propose that monitoring is essential, and now have a technique that allows relatively efficient monitoring of demography, in addition to density. However, we concede that our assumptions require complementary focal monitoring directed at estimating fecundity and survival independently.

In a broader context, our results allow some wider implications. Often species respond to an emerging disease through rapid evolution that leads to resistance or tolerance (Råberg *et al.* 2007). Slow or lingering disease dynamics, as may be the case for the bTB-infected lion population in Kruger, may mask these evolutionary responses. Uncertain management actions induced at the detection of a new disease may result in unpredictable outcomes or inefficient approaches (e.g. Donnelly *et al.* 2006). Our study highlights the importance of understanding host and disease ecology when planning and informing future scenarios and management options.

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References

- Aguirre, A. A. (2009). Wild canids as sentinels of ecological health: a conservation medicine perspective. In 'Parasites and Vectors (Supplement 1). Proceedings of the 4th Symposium on Canine Vector-borne Diseases'. (Seville, Spain.)
- Alexander, K. A., and Appel, M. J. G. (1994). African wild dogs (*Lycaon pictus*) endangered by a canine-distemper epizootic among domestic dogs near the Masai-Mara National Reserve, Kenya. *Journal of Wildlife Diseases* **30**, 481–485.
- Barnes, R. F. W. (2002). The problem of precision and trend detection posed by small elephant populations in West Africa. *African Journal of Ecology* **40**, 179–185. doi:10.1046/j.1365-2028.2002.00376.x
- Bauer, H., and van der Merwe, S. (2004). Inventory of free-ranging lions *Panthera leo* in Africa. *Oryx* **38**, 26–31. doi:10.1017/S0030605304000055
- Bengis, R. G., Grant, C. C., and de Vos, V. (2003). Wildlife diseases and veterinary controls. In 'The Kruger Experience: Ecology and Management of Savanna Heterogeneity'. (Eds J. T. du Toit, H. C. Biggs and K. H. Rogers.) pp. 349–369. (Island Press: Washington, DC.)
- Bengis, R. G., Kriek, N. P. J., Keet, D. F., Raath, J. P., de Vos, V., and Huchzermeyer, H. F. K. A. (1996). An outbreak of bovine tuberculosis in a free-living African buffalo (*Syncerus caffer* – Sparman) population in the Kruger National Park – A preliminary report. *Onderstepoort Journal of Veterinary Research* **63**, 15–18.
- Bertram, B. C. R. (1973). Lion population regulation. *East African Wildlife Journal* **11**, 215–225.
- Brown, E. W., Yuhki, N., Packer, C., and O'Brien, S. J. (1994). A lion lentivirus related to feline immunodeficiency virus: epidemiological and phylogenetic aspects. *Journal of Virology* **68**, 5953–5968.
- Caron, A., Cross, P. C., and du Toit, J. T. (2003). Ecological implications of bovine tuberculosis in African buffalo herds. *Ecological Applications* **13**, 1338–1345. doi:10.1890/02-5266
- Castley, J. G., Knight, M. H., Mills, M. G. L., and Thouless, C. (2002). Estimation of the lion (*Panthera leo*) population in the southwestern Kgalagadi Transfrontier Park using a capture-recapture survey. *African Zoology* **37**, 27–34.
- Chardonnet, P. (2002). 'Conservation of the African Lion: Contribution to a Status Survey.' (International Foundation for the Conservation of Wildlife, France, and Conservation Force, USA.)
- Cleaveland, S. C., Hess, G., Laurenson, M. K., Swinton, J., and Woodroffe, R. M. (2001). 'The Ecology of Wildlife Diseases.' (Oxford University Press: Oxford, UK.)
- Cleaveland, S., Mlengeya, T., Kazwala, R. R., Michel, A., Kaare, M. T., Jones, L., Eblate, E., Shirima, G. M., and Packer, C. (2005). Tuberculosis in Tanzanian wildlife. *Journal of Wildlife Diseases* **41**, 446–453.
- Cross, P. C., and Getz, W. M. (2006). Assessing vaccination as a control strategy in an ongoing epidemic: Bovine tuberculosis in African buffalo. *Ecological Modelling* **196**, 494–504. doi:10.1016/j.ecolmodel.2006.02.009
- Cross, P. C., Heisey, D., Bowers, J., Hay, C. T., Wolhuter, J. *et al.* (2009). Disease, predation and demography: assessing the impacts of bovine tuberculosis on African buffalo by monitoring at individual and population levels. *Journal of Applied Ecology* **46**, 467–475. doi:10.1111/j.1365-2664.2008.01589.x
- Crowl, T. A., Crist, T. O., Parmenter, R. R., Belovsky, G., and Lugo, A. E. (2008). The spread of invasive species and infectious disease as drivers of ecosystem change. *Frontiers in Ecology and the Environment* **6**, 238–246. doi:10.1890/070151
- Daszak, P., Cunningham, A. A., and Hyatt, A. D. (2000). Emerging infectious diseases of wildlife: threats to biodiversity and human health. *Science* **287**, 443–449. doi:10.1126/science.287.5452.443
- Daszak, P., Cunningham, A. A., and Hyatt, A. D. (2001). Anthropogenic environmental change and the emergence of infectious diseases in wildlife. *Acta Tropica* **78**, 103–116. doi:10.1016/S0001-706X(00)00179-0
- Donnelly, C. A., Woodroffe, R., Cox, D. R., Bourne, F. J., Cheeseman, C. L. *et al.* (2006). Positive and negative effects of widespread badger culling on cattle tuberculosis. *Nature* **439**, 843–846. doi:10.1038/nature04454
- Eberhardt, L. L. (1988). Using age structure data from changing populations. *Journal of Applied Ecology* **25**, 373–378. doi:10.2307/2403829
- Edwards, A. W. F. (1972). 'Likelihood.' (Cambridge University Press: Cambridge, UK.)
- Ferreira, S. M., and van Aarde, R. J. (2008). A rapid method to estimate population variables for African elephants. *Journal of Wildlife Management* **72**, 822–829. doi:10.2193/2007-151
- Funston, P. J., Mills, M. G. L., Biggs, H. C., and Richardson, P. R. K. (1998). Hunting by male lions: Ecological influences and socioecological implications. *Animal Behaviour* **56**, 1333–1345. doi:10.1006/anbe.1998.0884
- Funston, P. J., Mills, M. G. L., Richardson, P. R. K., and van Jaarsveld, A. S. (2003). Reduced dispersal and opportunistic territory acquisition in male lions (*Panthera leo*). *Journal of Zoology* **259**, 131–142. doi:10.1017/S0952836902003126
- Garstang, M., Larom, D., Raspet, R., and Lindeque, M. (1995). Atmospheric controls on elephant communication. *Journal of Experimental Biology* **198**, 939–951.
- Gentle, J. E. (1943). 'Random number generation and Monte Carlo methods.' (Springer-Verlag: New York.)
- Gerrodette, T. (1987). A power analysis for detecting trends. *Ecology* **68**, 1364–1372. doi:10.2307/1939220
- Gertenbach, W. P. D. (1980). Rainfall patterns in the Kruger National Park. *Koedoe* **23**, 35–43.
- Gertenbach, W. P. D. (1983). Landscapes of the Kruger National Park. *Koedoe* **26**, 9–121.
- Hanby, J. P., Bygott, J. D., and Packer, C. (1995). Ecology, demography and behaviour of lions in two contrasting habitats: Ngorongoro Crater and the Serengeti Plains. In 'Serengeti II: Dynamics, Management and Conservation of an Ecosystem'. (Eds A. R. E. Sinclair and P. Arcese.) pp. 315–331. (University of Chicago Press: Chicago, IL.)
- Hayward, M. W., and Hayward, G. J. (2007). Activity patterns of reintroduced lion *Panthera leo* and spotted hyaena *Crocuta crocuta* in Addo Elephant National Park, South Africa. *African Journal of Ecology* **45**, 135–141. doi:10.1111/j.1365-2028.2006.00686.x
- Hayward, M. W., O'Brien, J., and Kerley, G. I. H. (2007). Carrying capacity of large African predators: predictions and tests. *Biological Conservation* **139**, 219–229. doi:10.1016/j.biocon.2007.06.018
- Hood, G. M. (2005). 'Poptools. Version 2.6.6.' Available at <http://www.cse.csiro.au/poptools> [accessed 1 July 2005].
- IUCN SSC Cat Specialist Group (2006). 'Regional Conservation Strategy for the Lion *Panthera leo* in Eastern and Southern Africa.' Available at www.felidae.org [accessed December 2006].

- Keet, D. F., Kriek, N. P. J., Penrith, M. L., Michel, A., and Huchzermeyer, H. (1996). Tuberculosis in buffaloes (*Syncerus caffer*) in the Kruger National Park: spread of the disease to other species. *Onderstepoort Journal of Veterinary Research* **63**, 239–244.
- Keet, D. F., Kriek, N. P. J., Penrith, M. L., and Michel, A. (1997). Tuberculosis in lions and cheetahs. In 'Proceedings of a Symposium on Lions and Leopards as Game Ranch Animals. Onderstepoort'. (Ed. J. van Heerden.) pp. 151–156. (Wildlife Group of the South African Veterinary Association: Onderstepoort, South Africa.)
- Keet, D. F., Kriek, N. P. J., Bengis, R. G., Grobler, D. G., and Michel, A. (2000). The rise and fall of tuberculosis in a free-ranging chacma baboon troop in the Kruger National Park. *Onderstepoort Journal of Veterinary Research* **67**, 115–122.
- Keet, D. F., Kriek, N. P. J., Bengis, R. G., and Michel, A. (2001). Tuberculosis in kudus (*Tragelaphus strepsiceros*) in the Kruger National Park. *Onderstepoort Journal of Veterinary Research* **68**, 225–230.
- Kissui, B. M., and Packer, C. (2004). Top-down population regulation of a top predator: lions in the Ngorongoro Crater. *Proceedings of the Royal Society of London* **271**, 1867–1874. doi:10.1098/rspb.2004.2797
- Loveridge, A. J., Searleb, A. W., Murindagomob, F., and Macdonald, D. W. (2007). The impact of sport-hunting on the population dynamics of an African lion population in a protected area. *Biological Conservation* **134**, 548–558. doi:10.1016/j.biocon.2006.09.010
- Maddock, M. E., Anderson, A., Carlisle, F., Galli, N., James, A., Verster, A., and Whitfield, W. (1996). Changes in lion numbers in Hluhluwe–Umfolozo Park. *Lammergeyer* **44**, 6–18.
- McDonald, R. A., Delahay, R. J., Carter, S. P., Smith, G. C., and Cheeseman, C. L. (2008). Perturbing implications of wildlife ecology for disease control. *Trends in Ecology & Evolution* **23**, 53–56. doi:10.1016/j.tree.2007.10.011
- Michod, R. E., and Anderson, W. W. (1980). On calculating demographic parameters from age frequency data. *Ecology* **61**, 265–269. doi:10.2307/1935184
- Midgley, G. F., and Thuiller, W. (2005). Global environmental change and the uncertain fate of biodiversity. *New Phytologist* **167**, 638–641. doi:10.1111/j.1469-8137.2005.01522.x
- Mills, M. G. L. (1995). Notes on wild dog (*Lycaon pictus*) and lion (*Panthera leo*) population trends during a drought in the Kruger National Park. *Koedoe* **38**, 95–99.
- Mills, M. G. L., and Shenk, T. M. (1992). Predator–prey relationships: the impact of lion predation on wildebeest and zebra populations. *Journal of Animal Ecology* **61**, 693–702. doi:10.2307/5624
- Mills, M. G. L., Biggs, H. C., and Whyte, I. J. (1995). The relationship between lion predation, population trends in African herbivores and rainfall. *Wildlife Research* **22**, 75–88. doi:10.1071/WR9950075
- Mills, M. G. L., Juritz, J. M., and Zucchini, W. (2001). Estimating the size of spotted hyaena (*Crocuta crocuta*) populations through playback recordings allowing for non-response. *Animal Conservation* **4**, 335–343.
- Mollet, C. L. (1977). A probable case of anthrax in a Serengeti lioness. *East African Wildlife Journal* **15**, 331.
- Murray, D. L., Kapke, C. A., Evermann, J. F., and Fuller, T. K. (1999). Infectious disease and the conservation of free-ranging large carnivores. *Animal Conservation* **2**, 241–254. doi:10.1111/j.1469-1795.1999.tb00070.x
- Ogutu, J. O., and Dublin, H. T. (1998). The response of lion and spotted hyaenas to sound playbacks as a technique for estimating population size. *African Journal of Ecology* **36**, 83–95. doi:10.1046/j.1365-2028.1998.113-89113.x
- Ogutu, J. O., and Dublin, H. T. (2002). Demography of lions in relation to prey and habitat in the Maasai Mara National Reserve, Kenya. *African Journal of Ecology* **40**, 120–129. doi:10.1046/j.1365-2028.2002.00343.x
- Ogutu, J. O., Bhola, N., and Reid, R. (2005). The effects of pastoralism and protection on the density and distribution of carnivores and their prey in the Mara ecosystem of Kenya. *Journal of Zoology* **265**, 281–293. doi:10.1017/S0952836904006302
- Packer, C., Altizer, S., Appel, M., Brown, E., Martenson, J., O'Brien, S. J., Roelke-Parker, M., Frederick, M. D., Hofmann-Uhmann, R., and Lutz, H. (1999). Viruses of the Serengeti: patterns of infection and mortality in African lions. *Journal of Animal Ecology* **68**, 1161–1178. doi:10.1046/j.1365-2656.1999.00360.x
- Packer, C., Hilborn, R., Mosser, A., Kissui, B., Borner, M., Hopcraft, G., Wilmshurst, J., Mduma, S., and Sinclair, A. R. E. (2005). Ecological change, group territoriality, and population dynamics in Serengeti lions. *Science* **307**, 390–393. doi:10.1126/science.1105122
- Plowright, R. K., Sokolow, S. H., Gorman, M. E., Daszak, P., and Foley, J. E. (2008). Causal inference in disease ecology: investigating ecological drivers of disease emergence. *Frontiers in Ecology and the Environment* **6**, 420–429. doi:10.1890/070086
- Råberg, L., Sim, D., and Read, A. F. (2007). Disentangling genetic variation for resistance and tolerance to infectious diseases in animals. *Science* **318**, 812–814. doi:10.1126/science.1148526
- Radloff, F. G. T., and du Toit, J. T. (2004). Large predators and their prey in a southern African savanna: a predator's size determines its prey size range. *Journal of Animal Ecology* **73**, 410–423. doi:10.1111/j.0021-8790.2004.00817.x
- Rodwell, T. C., Kriek, N. P., Bengis, R. G., Whyte, I. J., Viljoen, P. C., De Vos, V., and Boyce, W. M. (2000). Prevalence of bovine tuberculosis in African buffalo at Kruger National Park. *Journal of Wildlife Diseases* **37**, 258–264.
- Roelke-Parker, M. E., Munson, L., Packer, C., Kock, R., Cleaveland, S. et al. (1996). A canine distemper virus epidemic in Serengeti lions (*Panthera leo*). *Nature* **379**, 441–445. doi:10.1038/379441a0
- Schaller, G. B. (1972). 'The Serengeti Lion.' (University of Chicago Press: Chicago, IL.)
- Schutte, I. C. (1986). The general geology of the Kruger National Park. *Koedoe* **29**, 13–38.
- Shrader, A. M., Ferreira, S. M., and van Aarde, R. J. (2006). Digital photogrammetry and laser rangefinder techniques to measure African elephants. *South African Journal of Wildlife Research* **36**, 1–7.
- Sillero, Z. C., King, A. A., and McDonald, D. W. (1996). Rabies and mortality in Ethiopian wolves (*Canis simensis*). *Journal of Wildlife Diseases* **32**, 80–86.
- Skinner, J. D., and Smithers, R. H. N. (1990). 'The Mammals of the Southern African Subregion.' (University of Pretoria: Pretoria.)
- Smuts, G. L. (1976). Population characteristics and recent history of lions in two parts of the Kruger National Park. *Koedoe* **19**, 153–164.
- Smuts, G. L. (1978). Responses of free-ranging lions (*Panthera leo*) to experimental cropping operations. *Carnivore* **1**, 61–72.
- Smuts, G. L., Whyte, I. J., and Dearlove, T. W. (1977). A mass capture technique for lions. *East African Wildlife Journal* **15**, 81–87.
- Sokal, R. R., and Rohlf, F. J. (1995). 'Biometry: The Principles and Practice of Statistics in Biological Research.' (W.H. Freeman & Co.: New York.)
- Stander, P. E. (1991). Demographics of lions in the Etosha National Park. *Madoqua* **18**, 1–9.
- Stander, P. E. (1992). Foraging dynamics of lions in a semi-arid environment. *Canadian Journal of Zoology* **70**, 8–21. doi:10.1139/z92-002
- Thorn, M., Scott, D. M., Green, M., Bateman, P. W., and Cameron, E. Z. (2009). Estimating brown hyaena occupancy using baited camera traps. *South African Journal of Wildlife Research* **39**, 1–10. doi:10.3957/056.039.0101
- Van Orsdol, K. G., Hanby, J. P., and Bygott, J. D. (1985). Ecological correlates of lion social organization (*Panthera leo*). *Journal of Zoology* **206**, 97–112.

- Viljoen, P. C. (1989). 'Ecological Aerial Survey in the Kruger National Park: Objectives and Methods.' (South African National Parks: Skukuza, South Africa.)
- Whyte, I. J. (2001). 'Information and Instructions to Pilots and Observers Participating in the Kruger National Park's Aerial Line Transect Surveys (ALTs) in the Partenavia P-68 Observer.' (South African National Parks: Skukuza, South Africa.)
- Wilson, G. J., and Delahay, R. J. (2001). A review of methods to estimate the abundance of terrestrial carnivores using field signs and observation. *Wildlife Research* **28**, 151–164. doi:[10.1071/WR00033](https://doi.org/10.1071/WR00033)
- Woodford, M. H. (2009). Veterinary aspects of ecological monitoring: the natural history of emerging infectious diseases of humans, domestic animals and wildlife. *Tropical Animal Health and Production* **41**, 1023–1033. doi:[10.1007/s11250-008-9269-4](https://doi.org/10.1007/s11250-008-9269-4)
- Woodroffe, R., and Frank, L. G. (2005). Lethal control of African lions (*Panthera leo*): local and regional population impacts. *Animal Conservation* **8**, 91–98. doi:[10.1017/S1367943004001829](https://doi.org/10.1017/S1367943004001829)

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