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The impact of lions on the demography and ecology of endangered African wild dogs

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Abstract

It has long been recognized that superior carnivores can impact on the demography and ecology of smaller members of the guild, although exact mechanisms remain unclear. Here we use original data from a unique natural experiment to study some of the mechanisms by which African lions *Panthera leo* impact on African wild dogs *Lycaon pictus*. Using a study site where wild dogs outnumbered lions for several years prior to lion population recovery, we aimed to investigate whether or not, and by which means, wild dog populations are regulated and influenced by lions. We used 38 pack-years of demographic and behavioural data across two 4-year periods where lion density differed 20-fold (pre-lion era: 1996–1999 and lion era: 2010–2013) to assess how lions may affect wild dog pack size and age structure, litter size and pup survival (n = 329 pups), as well as den site selection (n = 46 dens). Pack size was significantly greater during the pre-lion era. The pup to adult ratio was lower during the lion era and the change in pack composition was directly attributable to significantly greater lion-induced pup mortality. We also demonstrate a behavioural shift, with locations selected for the vulnerable denning period being in more rugged terrain and in areas with lower prey densities during the lion era, as compared with the pre-lion era. Lower adult recruitment into a population of an obligate cooperative breeder like the African wild dog can have complex consequences, including on feeding and defence of young, and mate finding.

Introduction

Populations of apex carnivores not only play a key role in the regulation of prey populations, but also have significant effects on smaller members of predator guilds – the mesopredators (Ritchie & Johnson, 2009; Ripple *et al.*, 2014). Mesopredator suppression can play a major role in structuring ecosystems (Sergio & Hiraldo, 2008; Ritchie & Johnson, 2009; Estes *et al.*, 2011) and is driven by costly competitive interactions between co-occurring carnivore species. This top-down process exerts strong selective pressures, influencing mesopredator distributions and abundances (Palomares & Caro, 1999; Creel, 2001; Caro & Stoner, 2003; Ritchie & Johnson, 2009). Apex predators frequently account for more than 50% of mesopredator mortality (Thurber *et al.*, 1992; Moseby *et al.*, 2012) and this form of interspecific competition ultimately decreases a species' fitness (Creel & Creel, 1996; Linnell & Strand, 2000) and heightens its likelihood of local extinction (Polis, Myers & Holt, 1989).

The large carnivore assemblage in African savannas is species-rich and forms a critical component of the continent's biodiversity (Winterbach *et al.*, 2013). The large carnivore guild consists of lions *Panthera leo*, leopards *Panthera pardus*, cheetahs *Acinonyx jubatus*, spotted hyenas *Crocuta crocuta* and African wild dogs *Lycaon pictus* (hereafter wild dogs). Lions are the largest (120–180 kg) and most dominant species within the guild, while wild dogs are the smallest (18–28 kg) and are often greatly suppressed by lion populations where the two co-exist (Creel & Creel, 1996; Swanson *et al.*, 2014). Across several studied populations, predation by lions was the single most important cause of wild dog mortality (Woodroffe & Ginsberg, 1999) accounting for significant proportions of recorded adult and pup mortality. Over five different study populations, lions accounted for an average of 12% of adult and 31% of pup deaths with a maximum of 47% adult mortality in Moremi, Botswana (Woodroffe & Ginsberg, 1999), while 43% of wild dog pup deaths were attributed to lions in Selous Game Reserve (Ginsberg, Mace & Albon, 1995).

Wild dogs attempt to avoid lions at all times (Webster, McNutt & McComb, 2012) and their large territories have been reasoned to facilitate avoidance of high-risk lion habitats (Creel & Creel, 2002). However, due to wild dog breeding behaviour, lions are able to exert a large influence on wild dog pup survival. Wild dog packs usually have a short, synchronous, annual breeding season (Frame *et al.*, 1979; Reich, 1981) during which large litters are born (Fuller *et al.*, 1992; Woodroffe, Ginsberg & Macdonald, 1997). The young are altricial and vulnerable to direct predation, and are confined to a den for 3 months. This curtails the pack's usual wide-ranging behaviour, also making the adults more vulnerable to lions.

Spatial and temporal avoidance of dominant carnivores constitute vital strategies which facilitate coexistence and the persistence of multi-predator guilds (Caro & Stoner, 2003; Harrington *et al.*, 2009). Wild dogs employ strategies such as habitat partitioning whereby prey-rich areas, associated with higher lion densities, are avoided (Mills & Gorman, 1997), selection of den sites less vulnerable to encountering lions (Jackson *et al.*, 2014), or restricting their range of movements in general, as do cheetahs (Durant, 1998). Highly cooperative group-living behaviour can also be considered a strategy to minimize interspecific competition (Fanshawe & Fitzgibbon, 1993). Demographic adaptations to living with lions might include maintaining larger pack sizes to allow babysitters to remain with the young during hunting (Courchamp & Macdonald, 2001) or producing larger litters to sustain a certain amount of mortality (Creel, Mills & McNutt, 2004).

Understanding how mesopredator suppression might translate into population-level effects is particularly challenging. Lions significantly outnumber wild dogs in most ecosystems where the lion–wild dog ratio may range from 3:1 to 21:1 (Creel & Creel, 1996). Elucidating the effects of mesopredator suppression on behaviour, habitat use, den site selection and survival are consequently challenging due to a lack of control sites devoid of top-down lion regulation. In the present study, we use a study site where wild dogs outnumbered lions for several years prior to lion population recovery, providing a rare study opportunity to quantify how wild dog populations may be regulated and influenced by lions. We assessed how lions may affect wild dog pack size and age structure, litter size and pup survival. We hypothesized that den site selection would include a shift to areas of lower prey density and into more rugged terrain, while home ranges would increase to facilitate spatial avoidance of preferred lion habitats.

Materials and methods

Study area

The 3440 km^2 Savé Valley Conservancy (SVC) is located in the semi-arid south-east lowveld of Zimbabwe and was created in 1991 from an amalgamation of 18 former cattle *Bos taurus* ranches. The natural land cover is deciduous woodland savanna dominated by *Colophospermum mopane*, *Acacia–Combretum* woodland and *Acacia tortillis* woodland (Pole, 1999). During the cattle ranching era (*c.* 1921–1992), almost all predators as well as most large herbivores were eradicated. This included wild dogs, lions, cheetahs and spotted hyenas, with only leopards managing to exist at reasonable densities (du Toit, 1994; Pole, 1999). The only predator reintroduction into SVC was a total of 13 lions, 3 in 1995 and 10 in 2005. Even so, lion densities remained low and only began increasing significantly in 2008. The population of African wild dogs, which naturally recolonized SVC, started to pick up in the early 1990s, reaching record densities in 2004; the species has been intensively studied since 1996.

The variation in the rate of wild dog and lion population recovery resulted in a rare situation where wild dogs outnumbered their superior competitors by a considerable margin [an estimated 6 lions to 62 wild dogs by 1999 (a 10:1 ratio)] and provides a unique opportunity to empirically assess the impact of lions on the behaviour and demography of wild dogs. In order to investigate the impact of lions on the wild dog population we defined two distinct 4-year study periods, one in the 'pre-lion era' (1996–1999) and one in the 'lion era' (2010–2013).

Lion numbers

Having been locally extirpated during the cattle era, three lions were introduced to SVC in 1995. Variations in the size of the extremely small lion population during the pre-lion era (see Results) were thus easily established by direct monitoring and the continual recording of all lion sightings (Pole, 1999). The interest shown by landowners was high and frequent reports were sufficient for monitoring group sizes and the total lion population (Pole, 1999).

In the lion era (2010–2013), lion densities in SVC were estimated by an annual spoor survey, conducted in October every year. Spoor surveys have been shown to be an effective and efficient means to assess wildlife densities (Stander, 1998; Funston *et al.*, 2001, 2010; Davidson & Romañach, 2007) as there is a strong correlation between spoor density and true density. Validation of the technique has confirmed its accuracy for censusing lion populations (Midlane *et al.*, 2015). The SVC spoor survey used the methods pioneered in SVC by Davidson & Romañach (2007), based on those used by Stander (1998) in Namibia. The same methodology has been used annually since 2008. A call-up survey for lions in SVC was conducted in 2011 and verified the spoor survey results for lions (Funston, 2011). During the pre-lion era, the SVC covered 3440 km^2 (Pole, 1999), but after a land reform programme in 2001, the effective area of the conservancy, and the land available to wild dogs, decreased to 2439 km^2; these figures were used to calculate lion and wild dog densities (details below).

Wild dog demographics

Wild dogs have been intensively monitored in SVC since 1996. Methods include locating packs through traditional spoor tracking, use of VHF and GPS collars, following up on sighting reports and compiling photographic identification kits for each pack. Data for the pre-lion era were collected during 1996–1999 (Pole, 1999), while that for the lion era was collected from 2010 to 2013 (this study). The number of packs and pack sizes were recorded and wild dog densities calculated.

In addition to competition from lions, wild dog populations could potentially be influenced by variability in prey availability. Impala *Aepyceros melampus* accounted for 74% of the wild dogs' diet during both the pre-lion and lion eras (Pole *et al.*, 2004; Mbizah, Marino & Groom, 2012), and were also the dominant species in the lions' diets at 43% (Mbizah *et al.*, 2012). Census data for the entire SVC were not available for both the time periods. However, data were available for a section comprising approximately a quarter of SVC. Impala densities were available for 1998, 1999 and 2000 and for 2010–2013 and were, respectively, used to estimate impala densities during pre-lion and lion eras.

Wild dog pack sizes and age structure [the relative proportion of adults, sub-adults (yearlings) and pups] differs over the course of a year, particularly due to the annual synchronized denning season (usually starting between late April and June). Data from April of each year, immediately prior to the onset of the denning season or at least before any pups emerged from the den were used to investigate total pack sizes and age structure.

Litter sizes were recorded by direct observations at den sites, more recently assisted by use of camera traps at the dens. It is not possible to know how many pups were born, or whether pup mortality occurred prior to first emergence of the pups at approximately 3 weeks of age. However, a good count of the pups at first emergence, either through direct observation or use of camera traps, and subsequent close monitoring of packs allowed us to calculate litter sizes and pup survival by month for the first 12 months.

In addition to total pack size, we were particularly interested to assess the potential effect of lions on pup survival for each of the first 12 months following birth, and potential shifts in the population's age structure. To facilitate such a detailed analysis, study packs that had not produced pups the preceding season (e.g. newly formed packs), or packs for which good pup survival data for each of the first 12 months following birth were not available, were excluded from analyses. While this reduced sample sizes, valuable insights into pup survival and age structure were facilitated. Sample sizes for pup survival to the age of 12 months were calculated from monthly survival data for 329 pups spanning 38 pack-years (n = 126 pups and 14 pack-years during pre-lion era, n = 203 pups and 24 pack-years during lion era).

Kaplan–Meier survival plots and Cox proportional hazard models with mixed effects, which analyse survival data by regression models, were used to analyse pup survival during the pre-lion and lion eras. Wild dog pack identity was used as a random factor in the Cox model. These analyses were conducted in R using the 'Coxme' package (Therneau, 2012; R Core Team, 2013).

Den site selection

As the dominant carnivore, lion densities are positively correlated with prey densities (Mills & Gorman, 1997). To assess whether wild dogs may have avoided denning in habitats with higher prey densities during the lion era as a risk avoidance strategy, we used impala density distribution from aerial censuses. Total aerial counts were conducted annually since 2004, during the dry season; the same season in which wild dogs den. The distribution of water-dependent herbivores, such as impala, during the dry season is restricted to areas with water and forage and these water-near habitats represent the greatest threat from lion predation (de Boer *et al.*, 2010; Davidson *et al.*, 2013). The annual distribution of dry season water sources is similar such that, despite inter-annual variations in the impala/herbivore populations, certain areas are consistently associated with greater prey densities (see Fig. S1). Since the area covered by the census was reduced in size in 2011, we used the 7 years of complete census data (2004–2010) to calculate mean impala herd densities across the SVC during the dry season. The 'point density' tool in ArcMap (ESRI, Redlands, CA, USA) was used to calculate and map mean impala density in SVC. Den site locations were thereafter overlaid onto the map and impala densities extracted to each den location.

Wild dogs have been reported to select den sites in rugged terrain as a potential lion avoidance strategy (Jackson *et al.*, 2014; Davies *et al*., 2016). To determine whether wild dog den sites were located in habitat that differed in terrain ruggedness during the pre-lion and lion eras, terrain ruggedness was assessed within a 500-m radius around each den site (pre-lion era: n = 16 dens; lion era: n = 30 dens). A terrain ruggedness index was derived from a 90-m digital elevation model in ArcMap. A spatial filter was then applied to calculate the standard deviation around each focal grid cell. This was calculated from a kernel of 3 × 3 grid cells around each focal grid cell. The highest values thus correspond to areas with the greatest altitudinal variation between neighbouring grid cells, identifying the most rugged terrain. The terrain ruggedness values for each grid cell within a 500-m radius of each den site were extracted in ArcMap for statistical analysis.

It was not possible to record data blind because our study involved focal animals in the field.

Results

Lion numbers

During the pre-lion era, there were estimated to be an average of eight lions in the SVC (0.0024 lion per km^2, N = 58 records, Pole, 1999). Recorded group sizes varied from one to seven (mean = 3.42 ± 0.9). The mean lion population size during the lion era was 123 (0.05 lions per km^2), with a maximum of 143 in 2010.

Wild dog demographics

Pack size and age structure for reproductively active packs prior to the onset of the annual denning period indicated that pack size was significantly greater during the pre-lion era (Table 1). There was no difference in the adult and sub-adult age group during the two periods and the difference in pack size was directly attributable to significantly fewer pups during the lion era (Table 1). The recruitment of pups to yearlings was halved between the pre-lion and lion eras which resulted in a drastic shift in the population's age structure. During the pre-lion era, packs were comprised of more pups than adults for the majority of the year (adult–pup ratio = 1:1.5) (Fig. 1). Following the recovery of the lion population the inverse was true, with a greater number of adults than pups in every month (adult–pup ratio = 1:0.65) (Fig. 1). These changes could not be linked to a decrease in prey availability, as impala densities increased significantly from a mean of 2.5 ± 0.4 to 7.4 ± 0.7 (*t*-test, $t = -10.3$, d.f. = 5, $P = <0.001$).

The significant difference in pup numbers between the two periods did not result from lower litter sizes (mean litter size during pre-lion era = 9.6 ± 0.59; lion era = 8.3 ± 0.64; $t(40) = 1.35$, $P = 0.18$). Instead, pup survival rates were significantly lower in the lion era than the pre-lion era (Fig. 2). Pup survival was very similar for the first 2 months, but deviated sharply after 2 months of age.

A log-rank test (Table 2) indicated that pup survival was significantly lower during the lion era compared to the pre-lion era ($\chi^2 = 15.2$, d.f. = 1, $P < 0.001$).

The Cox proportional hazard models were fitted by maximum-likelihood (log-likelihood, null = −864.86; integrated = −823.51; fitted = −795.73; see Table 3) and corroborated the significantly lower pup survival during the lion era (coef = 1.34, Exp = 3.83, ±SE = 0.59, $Z = 2.26$, $P = 0.024$; Pack ID as random effect: SD of intercept = 1.14, variance = 1.29).

The inference that the significant decline in pup survival is directly attributable to lions is substantiated by mortality data. During the pre-lion era, no recorded adult or pup mortality resulted from lions ($n = 31$ carcasses). During the lion era, 26% of adult mortality ($n = 31$ carcasses with known cause of death) and 69% pup mortality ($n = 29$ carcasses with known cause of death) were due to lions.

Den site selection

Compared to the pre-lion era ($n = 16$), wild dog den sites were located in areas of significantly lower mean impala density during the lion era ($n = 30$) (Mann–Whitney rank sum test, Mann–Whitney U statistic = 113.0, $T = 384.0$, $P = 0.028$; Fig. 3).

During the lion era, terrain ruggedness within 500 m of den sites was significantly greater than during the pre-lion era (Mann–Whitney rank sum test, Mann–Whitney U statistic = 1 207 953.0, T = 20 944 12.0, $P = 0.023$; Fig. 4).

Discussion

Mesopredator suppression is perhaps one of the least understood aspects of carnivore biology, partly due to the scarcity

Table 1 The composition of reproductively active wild dog packs in Savé Valley Conservancy in April of each year (before the new litters are born) in the pre-lion ($n = 14$ pack-years) and lion eras ($n = 24$ pack-years)

	Pre-lion era 1996–1999	Lion era 2010–2013	Statistical test results
Mean pack size (April)	13.4 ± 1.2	9.8 ± 1.1	Mann–Whitney U Statistic = 89.0; $T = 352.0$; $P = 0.017$
Mean number of adults and sub-adults per pack (April)	5.4 ± 0.9	6.0 ± 0.6	Mann–Whitney U Statistic = 147.5; $T = 252.5$; $P = 0.54$
Mean number of pups per pack (April)	8.1 ± 0.6	3.9 ± 0.7	$t(36) = 4.28$, $P < 0.001$
Ratio adults:pups	1:1.5	1:0.65	–

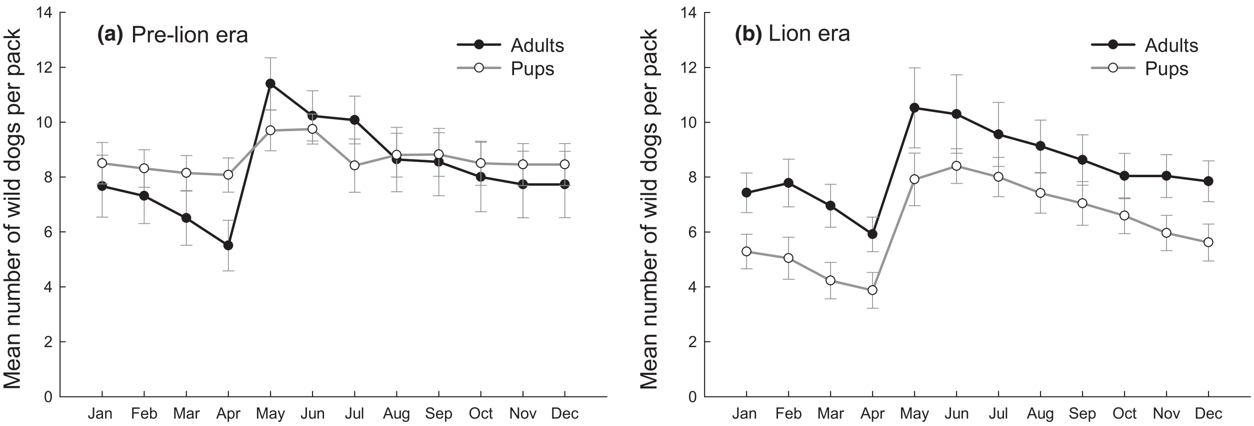

Figure 1 The mean number of adults and pups, by month, in wild dog packs in Savé Valley Conservancy during (a) the pre-lion era and (b) the lion era. Error bars represent standard error.

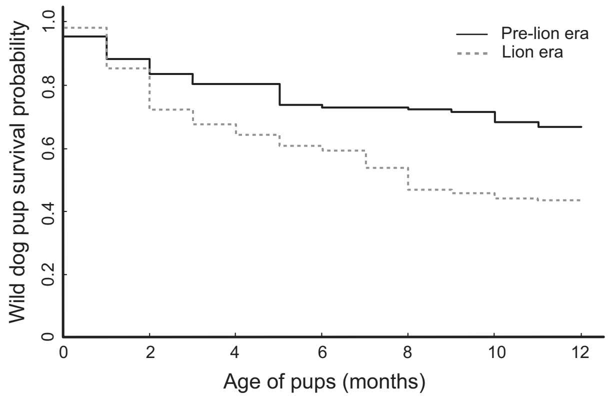

Figure 2 Kaplan–Meier curves illustrating age-specific wild dog pup survival probability for the first 12 months after birth. The solid line depicts pup survival probability during the pre-lion era (n = 126 pups; 14 litters) and the dashed line for the lion era (n = 203 pups; 24 litters).

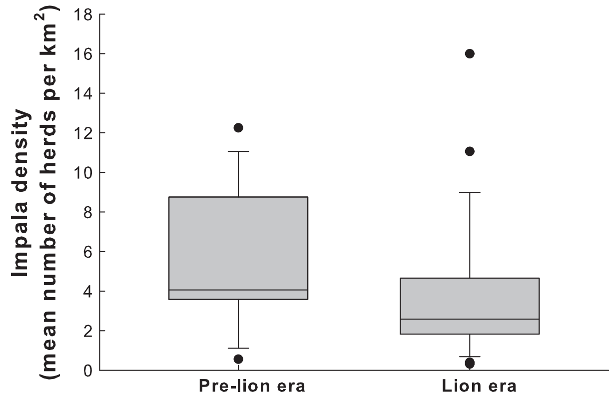

Figure 3 Mean impala density at wild dog den sites in Savé Valley Conservancy during the pre-lion (n = 16 den sites) and lion (n = 30 den sites) eras.

Table 2 Results from the log-rank test testing for differences between the survival curves of wild dog pups born during the pre-lion era and lion era

	n	Observed	Expected	$(O - E)^2/E$	$(O - E)^2/V$
Pre-lion era	126	42	65.1	8.19	15.2
Lion era	203	115	91.9	5.80	15.2

Table 3 Maximum likelihood fitting of the Cox mixed effects model

	χ^2	d.f.	P	AIC	BIC
Integrated log-likelihood	82.70	2.00	0.00	78.70	72.59
Penalized log-likelihood	138.25	16.11	0.00	106.02	56.77

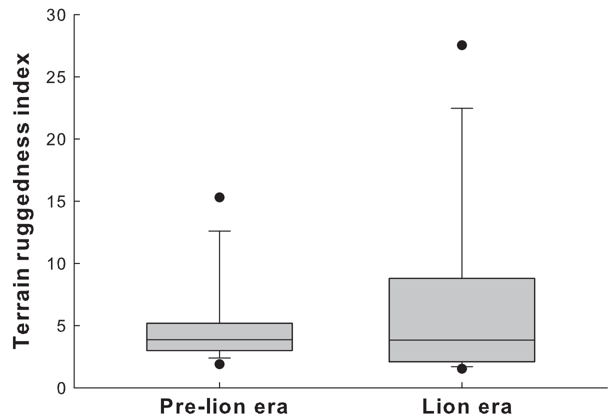

Figure 4 Box plot showing the terrain ruggedness index values within 500 m of wild dog dens in the pre-lion (n = 16) and lion eras (n = 30). Median values are indicated by the line in the boxes, error bars represent the range, while outliers (dots) represent 5th and 95th percentiles.

of natural experiments necessary to test hypotheses. We used a unique study opportunity to investigate how the behaviour and population dynamics of a subordinate large carnivore are influenced by a competitively superior carnivore. African wild dogs are the most threatened of the large African carnivores and have been extirpated from 25 of the 39 countries they formally occurred in (Woodroffe *et al.*, 1997), now occupying only 9.4% of their historical range (Woodroffe & Sillero-Zubiri, 2012). The entire global population is estimated to consist of <1400 mature individuals in as few as 660 packs and the species is listed as endangered on the IUCN red list (Woodroffe & Sillero-Zubiri, 2012). Protected areas play a vital part in conservation efforts, yet wild dog (and other inferior carnivore) populations within protected areas may be severely limited by interspecific competition (Ginsberg *et al.*, 1995; Woodroffe & Ginsberg, 1999; Creel, 2001; Swanson *et al.*, 2014). Conservation efforts for large carnivores generally are therefore complicated by mesopredator suppression, and there is a dearth of information on detailed spatial and temporal avoidance strategies and ecological factors facilitating coexistence. For endangered wild dogs, it is therefore of considerable importance to understand the impact from lions, themselves listed as vulnerable (Bauer, Nowell & Packer, 2012), in order to enhance our ability to optimally conserve both species.

The ever-increasing threats posed by rapidly increasing human populations have resulted in the fencing-off of several protected areas, specifically to protect conflict-prone large carnivores such as lions (Packer *et al.*, 2013). This also allows dominant carnivores, e.g., lions, to attain greater densities (Snyman, Jackson & Funston, 2015), potentially further compromising subordinate carnivores', e.g., wild dogs', ability to coexist.

The SVC lion population increased rapidly and exponentially between 2002 and 2010. For wild dogs unfamiliar with sustained and heightened levels of competition, the rapid change resulted in several population-level impacts. Lions do not merely impact wild dogs through direct predation, but also by reducing their fitness through competition for resources and spatial avoidance which excludes them from optimal hunting areas (Mills & Gorman, 1997; Davies-Mostert, 2010; Swanson *et al.*, 2014).

Here, we demonstrate that wild dogs are able to partially alter their behaviour during their most vulnerable time, the denning season, to reduce contact with lions. Jackson *et al.* (2014) found that wild dogs in four different populations selected areas that were significantly more rugged than available on average when denning, postulating that this was an attempt to minimize the probability of encountering lions (see also Davies *et al.*, 2016). Our findings support this hypothesis, as den sites were located in significantly more rugged terrain during the lion era when lion density was 20 times greater than the pre-lion era. This cannot be accounted for by human disturbance in the south of SVC as 78.3% of all dens were located north of the human-influenced area.

Following the recovery of the lion population, den sites were located in areas with significantly lower impala densities compared to den site locations during the pre-lion era. This illustrates a behavioural change to avoid lions which, as the dominant carnivore, frequent habitats close to water with greater prey availability (Mills & Biggs, 1993; Creel & Creel, 1996). This has been observed before in SVC (Romañach & Lindsey, 2008), and further examined by Mbizah *et al.* (2012), who found that the wild dogs were in fact selecting areas with lower impala densities, rather than consuming or scaring away sufficient prey to cause the reduced density of impalas observed around their dens. The change in den site selection in response to the risk of predation is a spatial avoidance strategy. However, this strategy is dependent on spatial variability in lion densities. Conservation managers thus need to ensure that protected areas designed to conserve the threatened species have heterogeneous habitat that would allow wild dogs to seek refuge in areas with lower lion densities.

Despite these behavioural shifts in den site selection, pup mortality was significantly higher during the years that lions were present. Wild dogs remain at the den for *c.* 2½–3 months. Our results (Fig. 2) showed that pup survival during the two periods were very similar for the first 2 months, but deviated sharply from 3 months of age. While some mortality may have occurred when pups left the den just prior to 3 months, observations (RJG), camera trap records and data confirm lion predation of pups at dens. Of 31 carcasses found in the pre-lion era, none were attributable to lions, whereas 69% of the 29 pup carcasses found in the lion era were.

While discussions of threats to wild dogs have tended to focus on causes of adult mortality (Woodroffe *et al.*, 1997; Creel & Creel, 2002), more recent analyses suggest that pup mortality may be as important as, or even more important than, adult mortality (Cross & Beissinger, 2001; Creel *et al.*, 2004), and hence the high mortality inflicted on pups by lions could have serious population-level consequences. This is because for obligate cooperative breeders, an annual single litter of pups per pack is usually their only opportunity for recruitment. It has been widely shown in the literature that juveniles are the most susceptible age class to any negative influences, so the wild dogs are not only putting all their eggs in one basket, they are also investing their future (i.e. pack growth and persistence) in the least viable age class. As such, when this vulnerable age class is heavily impacted, this can have significant consequences for the pack, and potentially the population as well (Courchamp & Macdonald, 2001; Creel *et al.*, 2004).

What has not been seen in this study is a compensatory increase in litter sizes in the lion era. This may be because it is still too early to see such an effect, or because of the various confounding factors that influence litter sizes (Creel *et al.*, 2004). As such, in time, it is likely that pack sizes will decrease (as we have seen in this study), which will have important repercussions for pack survival as it influences hunting efficiency (Fuller *et al.*, 1992; Creel *et al.*, 2004), guarding of kills (from spotted hyenas particularly), as well as pup care and provisioning (Courchamp & Macdonald, 2001).

Our analyses indicated that during the pre-lion era there were on average twice as many pups per pack. This was in April every year, when pups were *c.* 11 months old. The analysis also revealed, however, that the number of adults per pack was the same during the two eras. Given the significantly higher rates of pup survival during the pre-lion era, dispersal is likely to have been significantly higher, without which the number of adults would also have been significantly higher during the pre-lion era. The data thus suggest that considerably fewer wild dogs entered the dispersal phase during the lion era. The potential indirect effects of pup predation by lions on wild dog dispersal rates are considerable and have received little attention in the literature to date.

Wild dog pack formation is critical to population persistence and is severely curtailed due to the mate-finding Allee effect (Somers *et al.*, 2008). Assuming that significantly fewer dispersing individuals left their natal packs in search of mates during the lion era, the effect of the mate-finding Allee effect would be exacerbated as the probability of encountering suitable mates would be far lower. As such, an important finding from this study is that the impact of lions on wild dogs, or indeed any other factor that significantly reduces pup survival, inhibits wild dog population viability in a number of complex ways, both directly and indirectly. Wild dog population viability would be inhibited both by reduced pack sizes and by reduced pack formation.

These findings indicate the complex and potentially far reaching effects apex carnivores may have on mesopredators, and thus have broader implications for mesopredators in general, not just the mammalian carnivore guild. While mesopredator suppression by apex predators is a widespread phenomenon, both taxonomically and geographically, the findings are particularly relevant for social species, both terrestrial and aquatic, where group size impacts survival and dispersal, and where recruitment of young may be compromised by a dominant predator. As such there would be great value in future work aiming to elucidate to what extent and through what mechanisms indirect effects influence population persistence for other mesopredators, particularly when such species are already threatened.

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Conflict of interest

The authors declare that they have no conflict of interest.

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Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Figure S1. Mean impala herd density in Savé Valley Conservancy between 2004 and 2010.