RESEARCH ARTICLE

African large carnivore population changes in response to a drought

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African lions (*Panthera leo*) and spotted hyaenas (*Crocuta crocuta*) play key roles in savanna ecosystems. Habitat change, overharvesting and retaliatory killing may threaten the persistence of some populations. Climate may cause further disturbance that accentuate negative effects. Droughts weaken the ability of prey to avoid predators resulting in larger carnivore populations. We thus expected populations of African lions and spotted hyaenas to increase during a drought in Kruger National Park (Kruger). Prey that is easier to hunt during droughts may also influence age and sex structures through impacts on survival and fecundity schedules. We tested these predictions by collating information from previous studies and conducting a field call-up survey in Kruger. A severe drought in Kruger during the summer of 2015/2016 allowed pre- and post-drought comparisons. Before the drought, lion and spotted hyaena numbers increased in response to increasing prey biomass. During the drought, lions maintained their numbers, while spotted hyaena numbers increased further. There were substantially more subadult male lions after than before the drought. The abundant subadult males may induce higher incidences of human–carnivore conflict through more dispersing males in future. Our analyses highlighted immediate and lag effects of carnivores in response to droughts.

Keywords: climate change, drought, lions, spotted hyaenas, age and sex structure, abundance, Kruger National Park.

INTRODUCTION

Large carnivores play important facilitating roles within ecological dynamics (Atkins *et al*., 2019) in relatively intact African ecosystems, as is the case in Kruger National Park (Kruger), South Africa (Owen-Smith & Mills, 2008). Here, lion (*Panthera leo*) and spotted hyaena (*Crocuta crocuta*) populations recently increased in response to prey biomass changes (Ferreira & Funston, 2020). The leopard (*Panthera pardus*) population is also relatively robust at 2188 (95% CI: 1633–2862; Maputla, 2014). Cheetah (*Acinonyx jubatus*) and wild dog (*Lycaon pictus*) populations declined, mostly in the northern parts of Kruger, but the Park still had 412 (329–495) and 151 (144–157), respectively, by 2009 (Marnewick *et al*., 2014). By 2017, the wild dog population was 163 (115–262) adults and yearlings (Nicholson, Marnewick, Lindsey, Marnewick & Mostert, 2020).

Lions and spotted hyaenas formed part of predator control operations in Kruger at intermittent intervals between 1912 and 1961 to allow recovery of over-hunted antelope species (Joubert, 1986). By the early 1970s, management noted in some areas in central Kruger and around Crocodile Bridge a doubling of lion numbers over a 50-year period (Smuts 1976) and initiated a short period in the mid-1970s of controlling predators again (Joubert, 1986). Since then, lion numbers have fluctuated (Ferreira & Funston 2010a) until recently when the number of adult lionesses increased (Ferreira & Funston, 2020). The recovery of spotted hyaenas after predator control stopped was much slower and most likely only reached pre-control abundances by the 2000s (Ferreira & Funston, 2016). Recently, however, spotted hyaena numbers have also increased (Ferreira & Funston, 2020).

Lions can influence prey dynamics (Pienaar, 1969; Mills *et al*., 1995; Funston & Mills, 2006) as do spotted hyaenas (Owen-Smith & Mills, 2008). Both these species' dynamics, however, are associated with prey biomass (Ferreira & Funston, 2010a; Ferreira & Funston, 2016; Ferreira & Funston 2020). Perturbations that influence prey availability may thus have important conse-

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quences for apex predators such a lions and spotted hyaenas in African systems.

The response of carnivores to perturbations are important for persistence. For instance, emergence of bovine tuberculosis in lions in Kruger carries few consequences for lion population persistence (Ferreira & Funston, 2010a) with lions acting as a spill over host (Kosmala *et al*., 2016). Lions, however, do respond to some environmental perturbations by switching prey (Maruping-Mzileni, Funston & Ferreira, 2017). A previous analysis did not find that lion and spotted hyaena populations responded to the poaching of rhinoceroses (Ferreira & Funston, 2020), which theoretically provided them with access to atypical prey (Everatt, Andresen, Ripple & Kerley, 2016).

Climate is a key global environmental change driver that should have additional perturbation impacts on carnivores (Pandey & Papes, 2018). Most climate change scenarios reflect some increase in temperature, but consistently also predict more variable rainfall expected in future (Déqué et al., 2017). Incidences of droughts are likely to increase (Gizaw & Gan, 2017). The drought in the summer of 2015/2016 in Kruger (Swemmer *et al*., 2018) provided an opportunity to evaluate carnivore responses to climate variability. Within Kruger, prey dynamics dictate large carnivore dynamics (Owen-Smith & Mills, 2008). Prey accessibility typically improves during droughts, simply because many poorer conditioned animals may have weaker predator defence mechanisms (Knight, 1995). Indeed, wild dog and lion numbers increased in some areas in Kruger during dry periods between 1989 and 1993 (Mills, 1995). Such a scenario predicts that spotted hyaena and African lion populations should remain stable or increase in the short term through a drought.

Abundant prey was one of the factors that improved survival of spotted hyaenas in Zambia's Liuwa Plain National Park (M'soka, Creel, Becker & Droge, 2016), while prey availability also improved fecundity and survival in the Masai Mara National Reserve, Kenya, once researchers accounted for competition with lions (Watts & Holekamp, 2009). Prey availability also has a key influence on lion survival (*e.g*. Ferreira & Funston, 2010a) and cub recruitment rates in older age classes (*e.g*. Vinks *et al*., 2021). Readily accessible prey during droughts should thus improve fecundity as well as sex- and age-specific survival that translates into changes in the age and sex structure of populations. We tested these predictions by collating published information and conducting an African lion and spotted hyaena survey in Kruger after the drought of 2015/2016.

MATERIAL AND METHODS

Study area

The study took place in Kruger, a large, protected area (19 485 km^2) in the northeastern region of South Africa (Fig. 1). The focal southern area comprises granite and gneiss soils in the western half, while nutrient-rich basalt soils dominate the eastern half. A narrow band of Karoo sediment joins the granite and basalt (Schutte, 1986). The southern part of Kruger covers an area of 9653 km^2 with mean annual rainfall ranging from 750 mm in the south to 450 mm in the north (Gertenbach, 1980). Winter daily temperatures can reach 26.8°C with minimums as low as 5.6°C. In mid-summer, daily temperatures typically reach 34.9°C with daily minimums of 19.2°C (Venter & Gertenbach, 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 (Gertenbach, 1983).

Data collection

Several prey species for lions and hyaenas have varied in abundance over time (Table 1). We collated and converted these to prey biomass by extracting the average female body mass of focal species from Skinner & Chimimba (2005) and multiplied these by the estimates and their confidence intervals for each species for each year that had an available estimate. Adding these values provided an estimate of available prey biomass during any particular year (Fig. 2). In addition, herbivore species that make up most of the prey of large carnivores live at higher densities on the fertile basalts than on the granites (Gertenbach, 1983) (Fig. 1). Previously, prey densities and prevalence of bovine tuberculosis in prey species defined six zones (Ferreira & Funston, 2010a).

Most rainfall is during summer months from October to March in Kruger. Kruger experienced an intense drought during the summer of 2015/2016 (*i.e*. October 2015 to March 2016; Swemmer *et al*., 2018) similar to that in the summers of 1982/1983 and 1991/1992 (Smit, Peel, Ferreira, Greaver & Pienaar, 2020). During 2015/2016, the southern and central parts of Kruger experienced

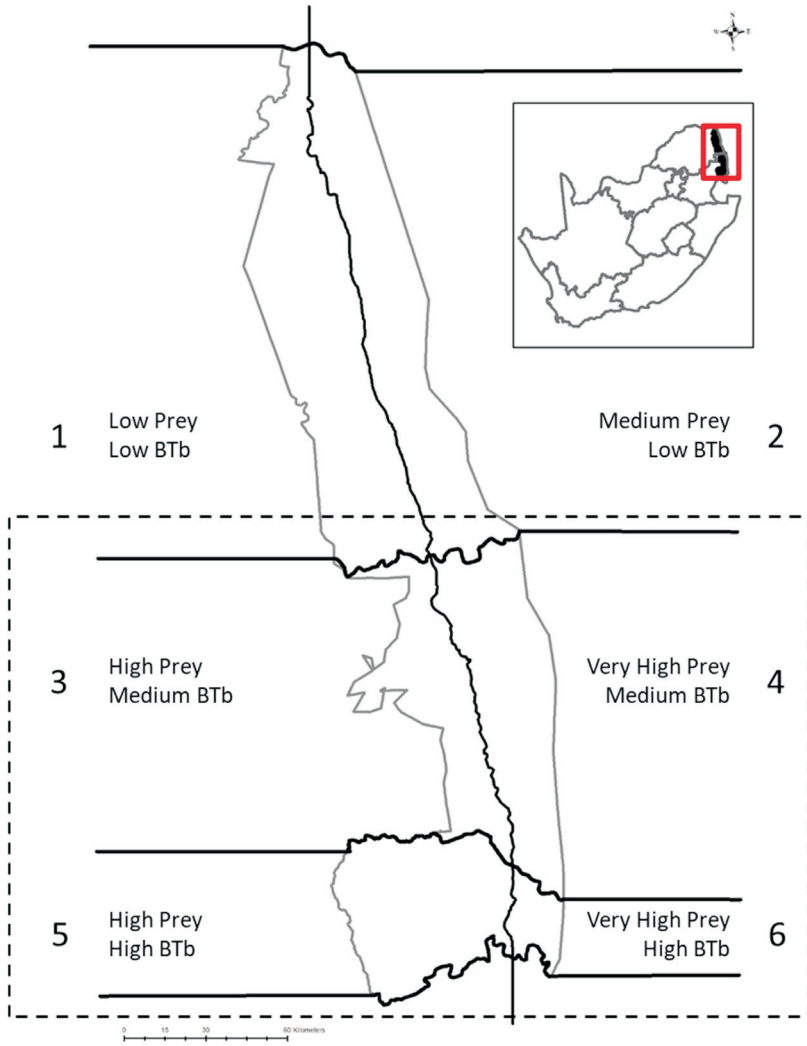

Fig. 1. Map of Kruger National Park showing the six zones. Researchers sampled all these zones during 2005/2006, 2008 and 2015, with only zones 3 to 6 sampled during 2017. Samples during 2017 focused on southern Kruger where the drought was most severe during the summer of 2015/2016. BTb = bovine tuberculosis.

the most intense drought effects. The southern region of Kruger only received 57.7% of its normal annual rainfall of 638 mm. The central region had the worst and only received 37.2% of its normal annual rainfall of 532 mm. Contrast that to the far northern region of Kruger that only received 62.6% of its 487 mm annual rainfall (Smit *et al.*, 2020). We focused on the four zones of southern Kruger (Fig. 1) to evaluate predictions associated with drought impacts on lions and spotted hyaenas.

Previous surveys focused on lions and spotted hyaenas across the whole of Kruger. We extracted lion estimates for the four zones constituting southern Kruger from the data of surveys for 2005/2006 (Ferreira & Funston, 2010a), 2008 (Young-Overton, Funston & Ferreira, 2014) and 2015 (Ferreira & Funston, 2020). For spotted hyaenas, we extracted estimates for the four zones from the data for surveys in 2005/2006 and 2008 (Ferreira & Funston, 2016) and 2015 (Ferreira & Funston, 2020). The estimates during 2015 served as measures shortly before the drought. For the 2015 survey, we also extracted the overall sex and age frequencies for lions.

During 2017, we used the same protocol as that used during previous surveys (Ferreira & Funston, 2010a; Young-Overton *et al.*, 2014; Ferreira & Funston, 2016; Ferreira & Funston, 2020) that

Table 1. Population estimates of prey species that lions and spotted hyaenas typically feed on in the Kruger National Park. Values in brackets represent 95% confidence intervals estimated through distance sampling. Note that buffalo represent the minimum known to be alive at the time of a survey in a specific year. Note that the 2017 prey survey took place after the lion survey in 2017. Data extracted from the SANParks Data Repository*.

Year	Impala	Giraffe	Zebra	Wildebeest	Kudu	Waterbuck	Warthog	Buffalo
1998	**106 103** (84 636–133 026)	**7263** (5515–9566)	**22 425** (17 973–27 980)	**10 179** (6586–15 731)	**3437** (2412–4899)	**1369** (708–2646)	**1432** (878–2335)	**21 095**
1999	**77 575** (59 274–101 530)	**4178** (3152–5539)	**14 296** (11 117–18 385)	**6373** (4458–9109)	**3021** (2167–4211)	**739** (385–1418)	**1625** (736–3585)	**20 395**
2000	**89 921** (71 946–112 390)	**4981** (3769–6582)	**19 620** (14 471–26 600)	**5102** (3109–8373)	**4961** (3603–6831)	**2866** (1657–4959)	**1727** (1098–2715)	**22 264**
2001	**91 742** (74 213–113 410)	**6754** (5421–8414)	**29 016** (21 912–38 422)	**17 994** (11 993–26 996)	**4705** (3607–6136)	**2288** (1301–4023)	**2260** (955–5350)	**25 155**
2002	**79 492** (64 509–97 955)	**5655** (4363–7329)	**21 598** (16 651–28 011)	**9331** (5981–14 557)	**3764** (2945–4812)	**4663** (2269–9583)	**3840**	**23 263**
2003	**85 869** (67 462–109 280)	**5144** (4010–6521)	**17 797** (13 792–22 965)	**9612** (5993–15 418)	**5798** (4422–7602)	**2951** (1805–4825)	**697**	**23 778**
2004	**61 433** (49 929–75 589)	**4140** (3235–5298)	**12 177** (9631–15 396)	**9574** (6330–14 483)	**4614** (3552–5992)	**2517** (1411–4491)	**1126** (686–1850)	**28 489**
2005	**100 947** (88 986–111 452)	**6692** (5626–7960)	**21 102** (17 753–25 083)	**12 018** (8104–17 822)	**6705** (5403–8320)	**3213** (2066–4996)	**2283** (1442–3615)	**31 062**
2006	**98 003** (80 451–119 380)	**7698** (6155–9627)	**32 879** (26 565–40 694)	**8122** (5659–11 658)	**13410** (10 939–16 440)	**4997** (3062–8127)	**5457** (3832–7771)	**33 308**
2007	**90 065** (74 563–108 791)	**6497** (5352–7885)	**25 562** (20 385–32 060)	**9726** (6778–13 935)	**8727** (6268–12 152)	**2521** (1649–3855)	**2250** (1547–3273)	**30 907**
2008	**127 788** (99 831–163 574)	**8812** (7091–10 950)	**26 337** (20 868–33 239)	**11 110** (8963–13 770)	**10 297** (8045–13 179)	**4949** (3210–7629)	**3210** (2316–4449)	**36 321**
2010	**152 726** (132 257–176 363)	**8332** (6771–10 253)	**28 938** (23 691–35 348)	**9178** (6424–13 112)	**13 894** (11 157–17 304)	**4900** (3072–7815)	**4197** (3100–5684)	**37 133**
2012	**189 937** (158 220–228 012)	**8987** (7427–10 876)	**35 630** (29 161–43 450)	**8125** (6058–10 896)	**10 453** (8239–13 490)	**5790** (3763–8907)	**3170** (2096–4795)	**34 202**
2014	**128 617** (108 495–152 471)	**7678** (6400–9211)	**24 411** (19 851–30 020)	**10 003** (6600–15 163)	**7846** (6048–10 168)	**2348** (1409–3910)	**4158** (2877–6009)	**38 323***
2016	**124 140** (100 603–153 186)	**9883** (8180–11 940)	**30 263** (25 677–35 668)	**12 944** (9342–17 936)	**9109** (6891–12 039)	**3613** (1892–6898)	**2917** (1919–4433)	**41 617***
2017								

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*Interpolated from surveys done in 2012, 2015 and 2017.

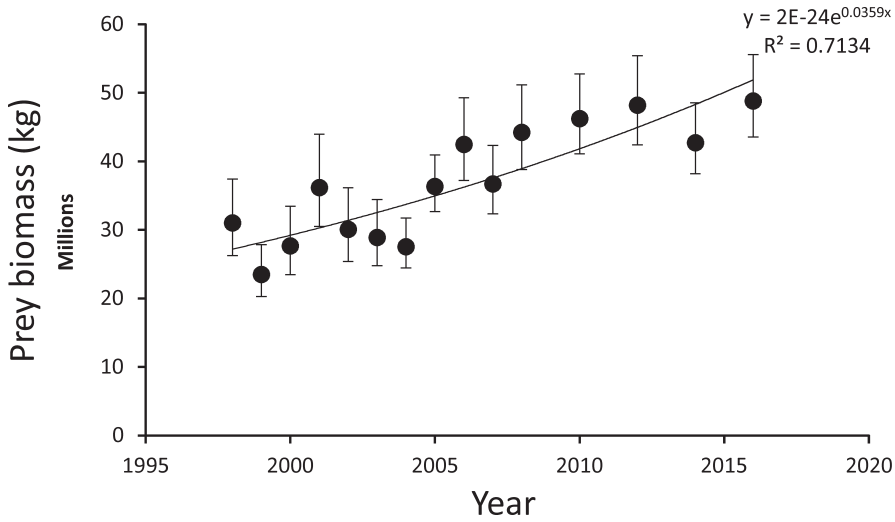

Fig. 2. Estimates of the annual biomass of prey that lions and spotted hyaenas typically feed on in Kruger National Park. The error bars represent 95% confidence intervals.

comprised a 4.25-min recording of a buffalo (*Syncerus caffer*) calf in distress repeatedly for 1 h on a LG 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. The amplifier 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 degrees direction from each other. During the survey, we broadcasted the vocalizations at full volume.

For population surveys, we placed call-up stations in the four focal zones (Fig. 1) as follows: Zone 3, 29 call-up stations; Zone 4, 28; Zone 5, 56; and Zone 6, 21. Stations were at least 10 km apart to minimize any chance of double-counting individuals (Ferreira & Funston, 2010a; Ferreira & Funston, 2016). Sampling took place during the dry season towards the end of winter from August–September 2017, at a similar time to previous surveys (Ferreira & Funston, 2010a; Young-Overton *et al*., 2014; Ferreira & Funston, 2016; Ferreira & Funston, 2020), by playing the 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 18:00 to 01:00 because lions are most active during this period (Hayward & Hayward, 2007; Schaller, 1972; Stander, 1992). Spotted hyaenas are active through most of the night (Kolowski, Katan, Theis & Holekamp, 2007). We recorded each group of lions or spotted hyaenas that arrived during the hour. For lions, we also assigned sexes and ages using relative size criteria (Ferreira & Funston, 2010b). At most, we surveyed four call-up stations a night.

Data analysis

We used previously developed lion (Ferreira & Funston, 2010a) and spotted hyaena estimators (Ferreira & Funston, 2016) making use of the recorded data collated through call-up stations. These approaches treat call-up stations as sample units with the area sampled by each unit defined by the distance away from which individuals will respond (lions: 4.3 ± 0.9 km, mean ± S.D., sampling 57.7 ± 24.9 km^2, Ferreira & Funston, 2010a; spotted hyaenas: 2.12 ± 0.4 km, mean ± S.D., sampling 14.12 ± 5.47 km^2, Ferreira & Funston, 2016).

Note that not all individuals respond where a response is defined as a visual observation of an individual lion. Biases evaluated previously noted that 73.4 ± 7.6% (mean ± S.E.) of lion groups without cubs and 28.6 ± 7.9% of lions groups with cubs within the effective sampling areas of a call-up station responded (Ferreira & Funston, 2010a). Typically 95.7% (95% CI: 55.5–100.0%) of the lions in a group with cubs will appear while 90.2% (95% CI: 32.0–100.0%) of the lions in a group without cubs will appear (Ferreira & Funston, 2010a). For spotted hyaenas, previous evaluated biases noted that 68% (95% CI: 48–87%) of individuals within the effective sampling area of a call-up

station responded (Ferreira & Funston, 2016). We used these previously estimated probabilities to correct for lions and spotted hyaenas observed at call-up stations using the estimators of Ferreira & Funston (2010a) and Ferreira & Funston (2016), respectively.

We concluded that there were population changes in southern Kruger as a whole if the 95% confidence intervals did not overlap. This approach allowed us to evaluate the first prediction of expected increases in lion and spotted hyaena populations.

To evaluate predictions associated with age and sex distributions of lions, we conducted chi-square tests (Fisher, 1922) to evaluate parity of male and female frequencies in cub (<1 year old), juvenile (1–<2 years old), subadult (2–<4 years old) and adult (4 years and older) age classes (see Ferreira *et al.*, 2020). We also calculated binomial proportion confidence intervals (Wallis, 2013) to evaluate age-specific sex ratio differences.

RESULTS

Population estimates for lions in the four focal zones varied among survey periods (Table 2). Lion abundances, however, were higher during 2015 and 2017 than approximately ten years before (Fig. 3). Spotted hyaenas were also more abundant than ten years before, but the increase noted in 2015 (Ferreira & Funston, 2020) may have continued during 2017 (Fig. 3). Such increases appeared to be in Zones 4 and 5 (Table 2).

The age and sex structures during 2015, prior to the drought, were typical of those expected for normal lion populations that have differential sex- and age-specific survival rates. Females dominated the adult age class (Fig. 4). Just before the drought, adult lions comprised 61.3% (95% CI: 53.7–68.8%) females. Post-drought, the adult age class was also dominated by females (Fig. 4), with females comprising 72.9% (95% CI: 60.7–85.1%) of adult lions.

Note that we did not find significant differences in the frequencies of sexes encountered in the juvenile age classes during 2015 and 2017 (Fig. 4) even though it changed from 46.8% (95% CI: 29.2–64.3%) to 59.1% (95% CI: 30.0–88.1%) being male. We found, however, substantial changes in the subadult age group (Fig. 4). Prior to the drought males made up 47.0% (95% CI: 38.5–55.5%) of the subadults, but after the drought that increased to 65.3% (95% CI: 52.0–78.6%).

DISCUSSION

Lion populations maintained their abundances following the increase previously noted (Ferreira &

Table 2. Zone-specific population estimates of spotted hyaenas and lions in southern Kruger National Park where drought was most severe during the summer of 2015/ 2016. The values in brackets reflect 95% confidence intervals.

a) Spotted hyaenas Year	Zone 3	Zone 4	Zone 5	Zone 6
2005	**424** (285–563)	**861** (521–1201)	**1056** (852–1260)	**48** (24–72)
2008	**399** (314–484)	**755** (613–897)	**962** (818–1106)	**243** (131–355)
2015	**1318** (912–1724)	**1476** (1022–1930)	**1400** (1095–1705)	**430** (248–612)
2017	**1309** (754–1864)	**1549** (892–2206)	**1889** (1104–2674)	**430** (243–617)
b) African lions Year	Zone 3	Zone 4	Zone 5	Zone 6
2005	**183** (137–230)	**525** (353–698)	**299** (255–344)	**51** (34–68)
2008	**337** (201–473)	**284** (215–353)	**120** (95–145)	**20** (–)
2015	**299** (223–375)	**850** (625–1075)	**213** (181–245)	**37** (24–50)
2017	**582** (357–807)	**680** (404–956)	**96** (63–129)	**52** (34–70)

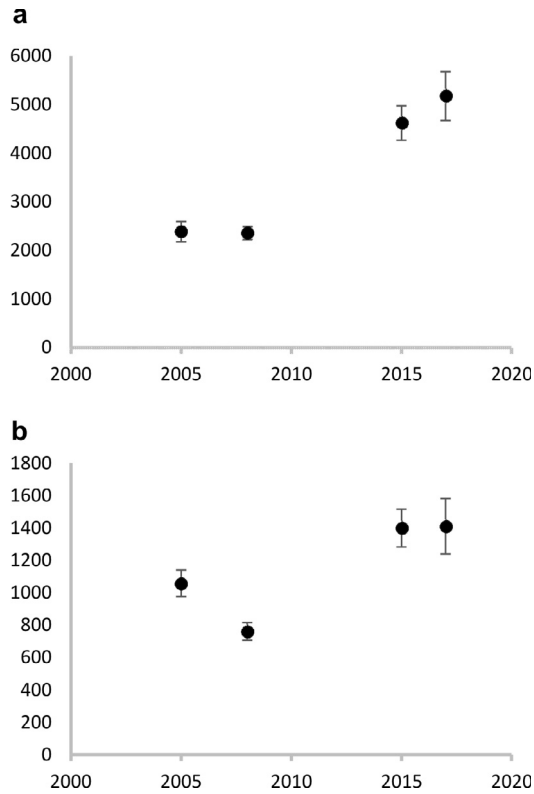

Fig. 3. Population estimates for southern Kruger National Park for (**a**) spotted hyaenas and (**b**) African lions. The error bars represent 95% confidence intervals.

Funston, 2020). Contrary to expectations, however, lions did not increase in the focal study area. The dynamics we noted align with saltatory equilibrium dynamics previously noted in the Serengeti (Packer *et al*., 2005). Prey increases facilitate changes, but other social requirements impose constraints and limitations, particularly on highly social species (Bertram, 1973; Bertram, 1975). It is likely that the southern part of Kruger as a whole is displaying similar saltatory dynamics as noted elsewhere (Packer *et al*., 2005).

Nevertheless, a substantial amount of variation exists at the local scale – lion trends varied from year to year in the different zones that we studied. We acknowledge that response rates of lions and spotted hyaenas to distress calls may be lower if prey is more accessible during droughts (Knight, 1995). For lions, a previous study highlighted that response rates associated largely with distance to water in the landscape (Young-Overton *et al*., 2014). Variation in trends from year to year in different zones is also likely because of spatial responses by individual lions, some of which may not be loyal to existing home ranges (Loveridge *et al*., 2009), in response to the distribution of prey. During the drought, several large grazers like hippos (*Hippopotamus amphibius*), buffaloes and white rhinos (*Ceratotherium simum*), re-distributed substantially and this changed again after the drought (Smit *et al*., 2020). Spatial responses to varying prey distributions could thus influence estimates and generate the variance we noted.

Spotted hyaenas appeared to have further increases through the drought following the initial increase noted between 2005 and 2015 (Ferreira & Funston, 2020). Spotted hyaenas are slow at recovering following major population disruptions. Indeed, the recovery of spotted hyaenas following culling in Kruger has been significantly slower than that of lions (Ferreira & Funston, 2016). This trend may associate with the clan social structure, with females being the dominant individuals (Engh, Esch, Smale & Holekamp, 2000), accentuated by social relationships inherited from their mothers (Ilany, Holekamp & Akçay, 2021). Female dispersal seldom takes place (Henschel &

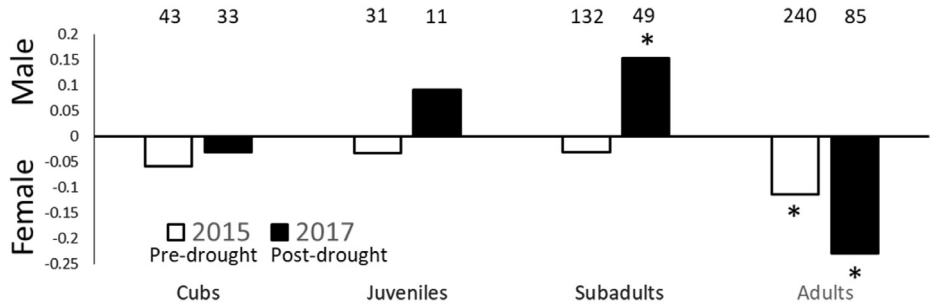

Fig. 4. Age-specific sex biases for lions in southern Kruger National Park. The numbers reflect the number of individuals encountered during a specific survey – note that for 2015, we extracted all observations including those made in northern Kruger National Park. The horizontal line reflects when the number of males and females are exactly equal. The asterisks indicate when sex ratios differed significantly from parity.

Skinner, 1987), with males leaving natal territories at 2 to 5 years of age (van Horn, McElhinny & Holekamp, 2003). This scenario suggests that once a clan has disappeared from a territory, other spotted hyaenas may take a long time to permanently occupy vacant space because it depends on females colonizing available areas. Once colonized, however, increases in clan size could be rapid under conditions of high prey abundance and availability (Holekamp & Dloniak, 2010). The increases in southern Kruger, specifically during the drought, most likely resulted from increases in clan sizes rather than more clans occupying vacant spaces. Increases in clan size would most likely associate with a combination of higher reproductive outputs and better survival of clan members because of more readily and easily available prey.

During droughts, prey are predictably easier to catch than in wet periods (Owen-Smith & Mills, 2008). The responses of herbivores during the drought (Smit *et al.*, 2020) provide a premise that the drought increased prey availability to the carnivores. Access to easy prey should translate into better food availability, improved body conditions, and hence increased survival and fecundity. Survival effects could also be differential. For instance, better survival during the drought of male lion offspring born shortly before the drought may result in dominating female siblings at carcasses, with consequent effects of female survival. If realized, such influence on vital rate schedules should translate into changes in the age and sex structure of populations. For lions, we noted changes in the standing age and sex structures of lions, with many more subadult male lions than expected after the drought compared to before. Lionesses with good body condition may produce litters that have a male-favoured sex bias (Trivers & Willard, 1973). Although survival of male and female lion cubs may vary during the first year after birth (*e.g.* Ferreira, Beukes, Haas & Radloff, 2020), most studies make no distinction between sex-specific survival of cubs (*e.g.* Stander, 1991; Funston, Mills, Richardson & van Jaarsveld, 2003). Lion sociology (Orsdol, Hanby & Bygott, 1985) typically induces substantial male-biased mortalities during the subadult stages (Stander, 1991; Ferreira *et al.*, 2020). If male-biased cub mortalities are negligible, male-biased litters induced by droughts should result in male-biased juveniles in the one to two years after the drought. Our results, however, noted no differences in juvenile sex ratios before and after the drought.

Subadult male lions have low survival when they disperse from natal prides (van Hooft, Keet, Brebner & Bastos, 2018). Dispersing young males do successfully hunt (Lehmann, Funston, Owen & Slotow, 2008), but encounter increased incidences of intraspecific aggression especially from adult males (Loveridge, Hemson, Davidson & Macdonald, 2010). Prey abundance is key to the coexistence of lions and spotted hyeanas despite their strong potential for prey competition (Périquet, Fritz & Revilla, 2015). Access to easy prey during a drought may thus allow better survival of subadult male lions. This survival predicts strong male-biased frequencies in the subadult and young adult age classes of the lion population one to two years after the drought. We noted that sex ratios prior to the drought had no significant male bias, but 18 months after the drought, subadult males were more abundant than subadult females. Young lions find it difficult competing for food at kills, often leading to reduced survival, particularly in the lean season (Orsdol *et al.*, 1985). Part of this competition most likely originates from the stress experienced by juvenile and subadult males when pride males or other adult lions harassed them. Having abundant food is likely to reduce these incidences, alleviating influences that typically impact subadult survival including reduced hunting success (Funston, Mills & Biggs, 2001) and opportunities to acquire territories (Funston *et al.*, 2003) when emigrating from natal areas (Hanby & Bygott, 1987). The observations that there were relatively more abundant subadult males 18 months post-drought suggest that juvenile and subadult males survived better during the drought.

Our results highlighted that lions and spotted hyaenas have maintained or increased abundances; and, there were relatively more subadult males 18 months after a drought compared to before. Male lions disperse from natal territories when three to four years old (Hanby & Bygott, 1987). The higher abundances of lions compared to a decade prior (Ferreira & Funston, 2020) and the likely play out of saltatory dynamics due to social constraints (Packer *et al.*, 2005) has implications for lion management. Specifically, authorities could expect more dispersing male lions exploring while seeking territories and/or refuge in areas outside Kruger where lions, and in particularly adult males, are absent or densities are low. Indeed, the incidence of reports on transgressing

lions from Kruger increased substantially during the dry season of 2019 (SANParks, Unpublished data*), four years after the drought of 2015/2016. In this context, authorities could consider proactive responses and remove young male lions within peripheral prides.

Higher spotted hyaena abundances, most likely because of large clan sizes, should also result in more dispersing males of 2 to 5 years of age (van Horn, McElhinny & Holekamp, 2003). This scenario thus predicts substantive increases in spotted hyaena males exploring beyond clan territories, some areas of which would be outside Kruger. Spotted hyaenas are particularly good at acquiring new diets (Abay, Bauer, Gebrihiwot & Deckers, 2011). Authorities should thus also expect delayed increases in reports of transgressing spotted hyaenas because of drought influences on their population dynamics. Managers in Kruger reported substantial increases during 2019 and 2020 (four to five years after the drought) in spotted hyaena depredation of livestock in areas abutting the Park (SANParks, Unpublished data*).

It is likely that responses of apex carnivores to droughts may have variable effects on ecosystem resilience through various cascade effects (Atkins *et al*., 2019; Ripple *et al*., 2014) such as release or suppression of mesocarnivore dynamics, or increased predation pressures that alter herbivore top–down regulating mechanisms. The cascade influences on other species and critically binding ecosystem keystone effects of lions and spotted hyaenas may enhance biological diversity as illustrated by wolves (*Canis lupus*) in the Americas and Europe (Linnell *et al*., 2005; Ripple & Beschta, 2012).

Mesopredator interactions with large carnivores (Ritchie & Johnson, 2009), however, may degrade some other species' resilience in the face of responses of large carnivores to incidences of drought. Similarly, human–carnivore conflict may also be variable, but intensified under conditions following droughts. Our results highlight key contributions that carnivores can make. Authorities, however, would do well to consider the consequences of environmental variability such as droughts when developing policies aimed at enhancing benefits that humans may carry from biological diversity, while minimizing costs and risks to people and wildlife species alike.

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