


# Changes in African large carnivore diets over the past half-century reveal the loss of large prey

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## Abstract

1. Globally, large carnivores are declining due to direct persecution, habitat loss, and prey depletion. The effects of prey depletion could be amplified by changes in the composition of the herbivore (prey) community that provoke changes in carnivore diets, but this possibility has received little attention.
2. We tested for changes over the past half-century in prey selection by the large carnivore guild in Zambia's Kafue National Park (KNP).
3. Across 52 predator–prey dyads, 71% of the observed changes showed that large prey have become less important and small prey have become more important. Consequently, dietary niche breadth has decreased for KNP carnivores and niche overlap has increased.
4. We tested whether changes in the importance of prey species are related to their current abundance and uniformly found that prey that have increased in importance are now relatively common, while those that have decreased in importance are now relatively rare. We identify four potential effects of these changes for conservation (through intraguild competition, group size, the energetics of hunting, and vulnerability to snaring) that warrant investigation.
5. *Synthesis and applications.* Patterns of prey selection by the large carnivores in Kafue National Park (KNP) have changed appreciably over the past half-century. Decreased predation on large prey, which are now relatively rare, has caused niche compression and increased overlap in carnivore diets. Predation by all KNP large carnivores now concentrates on four small prey species that remain relatively abundant (impala, puku, lechwe, and warthog). Methods to detect such changes in interactions between species are well-established, but are rarely applied to large carnivore-ungulate systems. To guide conservation of ecosystem function, monitoring programmes should consider whether prey depletion alters the patterns of predation or competition within the predator guild because these interactions strongly affect the distribution and abundance of both predators and prey. If the patterns seen in KNP are general, then where carnivores are limited by prey depletion, conservation efforts will be most effective if they focus on mitigating the loss of large prey.

In KNP, targeted efforts to protect prey larger than 200 kg, particularly buffalo, should be a priority.

#### KEYWORDS

carnivore, competition, dietary niche, large herbivore, predator-prey interactions, prey depletion, prey-base homogenization

## 1 | INTRODUCTION

Current extinction rates are unprecedented in human history and are comparable to five prior mass extinctions in the earth's history (Ceballos et al., 2015). Large mammals are among the most affected taxa (Ceballos & Ehrlich, 2002), and large carnivores have experienced particularly large declines in numbers and geographic distribution (Estes et al., 2011; Ripple et al., 2014; Terborgh & Estes, 2013). Although many African ecosystems have maintained all of their large carnivores, the lion *Panthera leo*, leopard *Panthera pardus*, cheetah *Acinonyx jubatus*, and African wild dog *Lycaon pictus* are all considered vulnerable or endangered, and all show decreasing population trends (IUCN, 2017). Threats to these carnivores vary among species and populations, but common problems include habitat loss and human encroachment on protected areas (Riggio et al., 2013; Ripple et al., 2014; Watson, Becker, Milanzi, & Nyirenda, 2015), legal and illegal direct killing (Becker et al., 2013; Creel et al., 2016; Hofer, Campbell, East, & Huish, 1996; Ogada, Woodroffe, Oguge, & Frank, 2003; Packer et al., 2009; Whitman, Starfield, Quadling, & Packer, 2004), and prey depletion (Estes et al., 2011; Fa & Brown, 2009; Ripple et al., 2015; Rosenblatt et al., 2016).

These large carnivores form a coherent guild that feeds primarily on ungulates ranging from 10 to 1,000 kg and cannot persist without an ungulate prey base. Positive relationships between carnivore density and prey density have been reported for a broad range of species and ecosystems (e.g., grey wolves: Fuller & Murray, 1998; African lions: Van Orsdol, Hanby, & Bygott, 1985; tigers: Karanth & Sunquist, 1995; Ethiopian wolves: Sillero-Zubiri, Marino, Gottelli, & Macdonald, 2004). It is well-recognized that depletion of prey populations is occurring in many ecosystems, mainly due to habitat loss and illegal harvest (Bolger, Newmark, Morrison, & Doak, 2008; Fa & Brown, 2009; Ripple et al., 2015; Western, Russell, & Cuthill, 2009), and a recent review found that 65% of large carnivores have experienced an increase in the proportion of their prey that is considered vulnerable, threatened, or endangered (Wolf & Ripple, 2016). In short, it is widely recognized that prey depletion can be a strong driver of carnivore declines (Fuller & Sievert, 2001; Karanth & Stith, 1999; Midlane, 2014; Ripple et al., 2015; Rosenblatt et al., 2016). Despite this recognition, there has been little direct research on the manner in which prey depletion alters the diets of large carnivores. Logically, it is unlikely that all ungulates are equally affected by the processes driving decline,

which suggests that prey depletion might also change prey community composition. This, in turn, suggests a hypothesis that the effects of prey depletion could be amplified by a decrease in the relative frequency of carnivores' preferred prey (or mitigated by an increase). Such changes are likely to affect the persistence of large carnivore populations, to change the limiting effect of predators on prey species, and to alter competitive interactions among predators. Thus, if our goal is conserve ecosystem function, we must employ monitoring programmes that allow us to test whether prey depletion alters the patterns of interaction between species (e.g., Karanth & Sunquist, 1995).

To our knowledge, no prior studies have directly examined how long-term changes in prey selection are related to patterns of prey abundance, or how such changes have altered dietary niche partitioning within a large carnivore guild. Data from Zambia's Kafue National Park (KNP) provide an unusual opportunity to test whether the diets of a large carnivore guild have changed over a period of more than 50 years, test for changes in niche overlap, and relate the observed changes in diet to the current patterns of prey abundance. KNP is Zambia's oldest and largest National Park, protecting an area of 22,840 km<sup>2</sup> that is dominated by miombo (*Brachystegia-Julbernardia*) woodland with large floodplains. KNP supports a diverse (20 species) community of ungulates larger than 10 kg, but human encroachment on the park is substantial (Watson et al., 2015), and depletion of prey by illegal harvest has been suggested to limit KNP carnivore populations (Midlane, 2014). The KNP ungulate guild is preyed upon by lions, leopards, cheetahs, and African wild dogs. Spotted hyenas *Crocuta crocuta* are present but not common (an unusual pattern that has been true for decades: Mitchell, Shenton, & Uys, 1965). Extensive data on patterns of predation in KNP were recorded by Mitchell et al. (1965) between 1960 and 1963 and by this study between 2013 and 2016, allowing a test for changes in the composition of large carnivore diets over the past half-century. For this analysis, we ranked prey by adult body mass, determined the proportion of each carnivore's diet that was formed by each prey species in each period, examined patterns of increase and decrease, and related changes in prey selection to current relative abundance. Finally, we tested whether changes in diets affected the degree of niche overlap within the carnivore guild. The problems that large carnivore conservation faces in KNP (human encroachment, poaching, and prey depletion) are ubiquitous, suggesting that patterns found in KNP are likely to be pertinent to many ecosystems in Africa and elsewhere.

## 2 | MATERIALS AND METHODS

### 2.1 | Carnivore diets

Between 2013 and 2016, herbivore kills were recorded over an area of 3,840 km<sup>2</sup> within KNP bounded on the south by the M9 road, on the north by papyrus swamps in the Busanga Plain, on the west by the park boundary, and on the east by the Kafue and Lufupa Rivers. This area is dominated by *Brachystegia-Julbernardia* woodland broken by open floodplains and is representative of KNP with respect to vegetation types. Within this area, we recorded carnivore diets using direct observations when carnivores were located opportunistically or by radiotelemetry (of lions, African wild dogs, and cheetahs; leopards were not collared). We detected 351 carcasses, of which 288 could be ascribed to predation by an identified predator. We assigned a kill to a carnivore species if the kill was directly observed or if a single carnivore species was present at a kill that was not fully consumed and there was no sign (tracks, scats) of other carnivores at the kill site. As described in detail by Mitchell et al. (1965), parallel data were collected throughout KNP from 1960 to 1963 using opportunistic sightings. We considered whether changes in the observed diet (see Section 3) might have been affected by methodology, and four patterns in the data suggest not (see Section 4).

### 2.2 | Prey size classification

We ranked prey by adult body mass using published data (Dorst & Dandelot, 1972; Mills & Hes, 1997), taking the mean for males and females, and classified those below the median as small and those above the median as large. We used a single prey size classification (rather than separate classifications for each carnivore) because our focus is on testing for systematic changes in prey selection across the entire ungulate guild, by the entire large carnivore guild. While it is true that a species smaller than the median might be relatively large for a given carnivore, a single size classification is necessary to test for changes in prey size across the entire carnivore guild, and for valid comparison of each carnivore's use of the complete niche axis. The species in the prey set were defined by the data; that is, we included only species that were recorded in the diet of at least one carnivore and included all such species. Prey size classes were also defined by the data, using the median mass as an objective threshold. While we detected changes in the importance of single prey species, we focused our primary analysis on two objectively defined size classes because the generality of such patterns is likely to be greater than the generality of inferences from changes for single species.

### 2.3 | Species densities

We used repeated, systematic distance sampling (Buckland, Anderson, Burnham, & Laake, 2005) to measure herbivore densities in KNP with species-specific correction for the probability of detection as a function of distance and habitat type. A detailed description of these methods is available in Matandiko (2016). Briefly,

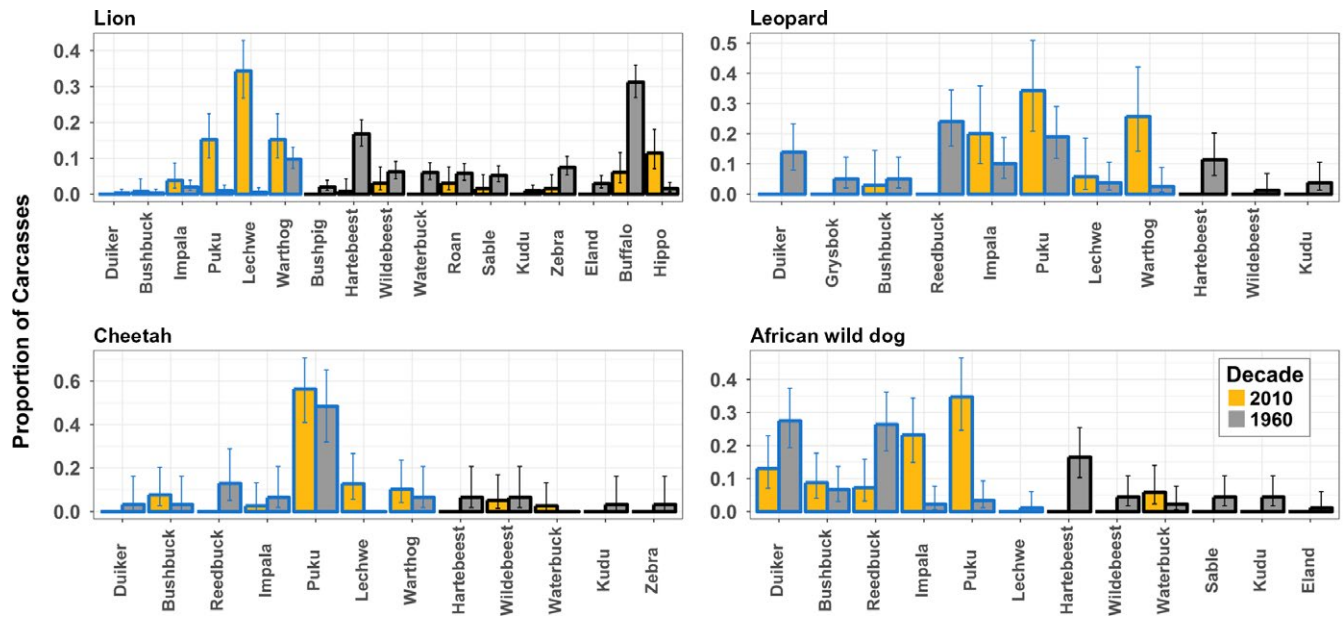
we established 18 linear transects on our study area in central KNP that ranged in length from 2 to 16 km. These transects ran in an east–west direction, with even spacing at 4 km intervals from north to south. This spacing yielded a low likelihood of double-counting herds and allowed a uniform and representative distribution of sampling effort that required 5 days on each occasion. The total length of the 18 transects summed to 119.1 km that were sampled on seven occasions. We drove transects at  $\leq 15$  km/hr, with the driver using a GPS to maintain the track while two rooftop observers scanned for herbivores. When a herd was sighted, the vehicle stopped and we recorded position, distance, and bearing to the herd using a GPS, laser rangefinder, and compass.

Our distance sampling analysis used the `distsamp` function of the unmarked package in R (Chandler, 2011; Fiske & Chandler, 2011) and required data on covariates that could affect detection, with transects as the sampling unit. To refine this analysis, we split the 18 transects into smaller segments to produce finer sampling units for which we recorded covariates. We segmented each transect based on changes in the dominant vegetation type, or at 2 km intervals if the vegetation type remained constant (range = 0.3–2 km), resulting in 77 segments. Each segment was assigned to one of four vegetation types, namely open grassland (OG—23.4%), open bushland (OB—3.96%), open woodland (OW—50.19%), and closed woodland (CW—22.45%). This distribution of sampling across vegetation types is representative for KNP. We sampled transects on seven occasions over 3 years, which resulted in data for 530 segment-sampling occasions and a total of 834 km (a few segments were inaccessible due to rain on a few occasions). For all species, detection varied by habitat type and distance. The best function to describe the effect of distance on detection varied among species (either hazard or half-normal). Matandiko (2016) provides more detailed methods and analysis of ecological and anthropogenic factors that affect the local density of each species.

Herbivore densities in KNP are low as a result of anthropogenic prey depletion (Midlane, 2014; Rduch, 2016) except for areas immediately adjacent to the Kafue River, so these surveys provided enough sightings to fit distance sampling models for only three species (impala, puku, and warthog). A set of similarly sized grazers (hartebeest, roan, wildebeest, and zebra) had too few sightings to allow for separate analysis, so we pooled these sightings to yield a total of 71 observations, which allowed a precise estimate of their collective density that corrected for the effects of vegetation type and distance on detection. All other species were sighted too infrequently to allow distance sampling models to be fit, despite repeated, intensive sampling.

### 2.4 | Niche overlap

Using the `EcoSimR` package in R, we calculated the Czekanowski index of niche overlap and its variance, following the methods recommended by Gotelli, Hart, and Ellison (2015). The Czekanowski index calculates mean overlap in resource use for all carnivores across all prey types and can range from zero (no overlap in dietary



**FIGURE 1** Changes over the last half-century in the proportion that each ungulate species formed in the diet of each large carnivore. In each panel, prey species are arranged from smallest (left) to largest (right). Bars show the proportion of a carnivore's diet comprised by each prey species and whiskers show 95% binomial confidence limits using the Wilson method (so that nonoverlapping whiskers denote differences at  $\alpha = 0.05$ ). Bar fill identifies data from the 1960s and the 2010s. Bar outline colour identifies prey species that are smaller or larger than median body mass within the KNP ungulate guild

niches) to one (identical diets). We determined Czekanowski index values separately for the data from the 1960s and the 2010s and used them to test whether niche overlap changed between the two periods.

In our results, we use the term “important” to describe the contribution of a prey species to carnivore diets and “common” to describe its relative abundance.

### 3 | RESULTS

Large prey became less important for 21 of 25 predator-prey dyads (0.84, CI = 0.65–0.94), while small prey became more important for 16 of 27 dyads (0.59, CI = 0.41–0.75) (Table 1). Overall, the direction of change for 71% of 52 dyads (CI = 58%–82%) supports the hypothesis that large prey species have become less important while small prey species have become more important over the past half-century ( $\chi^2 = 8.52$ ,  $p = 0.0035$ ). Changes in the contribution of each ungulate to the diet of each predator (Figure 1) reveal 13 cases in which a large prey species dropped out of the observed diet, but only seven cases in which small prey dropped out (five of which contributed  $\leq 5\%$  to the original diet). Particularly, notable examples of large prey that have decreased in importance are buffalo (previously the most important prey of lions, now the fifth most important) and hartebeest (previously the second most important prey of lions and taken by all four carnivores, now taken only by lions on rare occasions). More generally, large ungulates between 200 and 350 kg (hartebeest, wildebeest, greater kudu, roan, sable, and zebra) have become consistently less important in the diets of all four carnivores.

**TABLE 1** A summary of changes in the importance of small and large prey species in the diets of large carnivores in KNP over the past half-century

| Prey size | Change in contribution to large carnivore diets between 1960s and 2010s |          |
|-----------|---|----------|
|           | Decrease  | Increase |
| Small     | 11  | 16       |
| Large     | 21  | 4        |

The only large ungulate that has become appreciably more important over the last half-century is the hippo in the diet of lion.

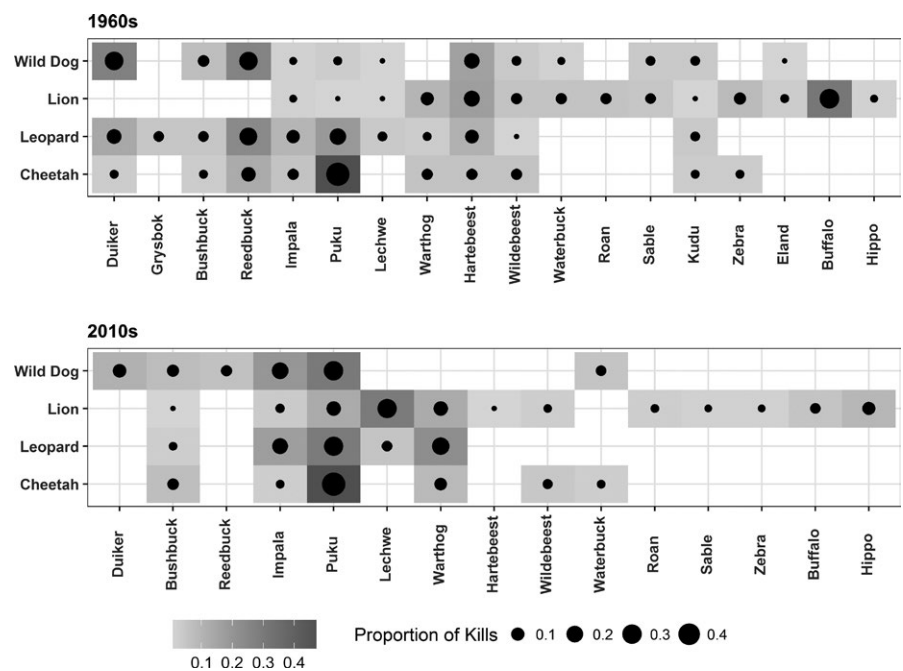
The decreasing contribution of large prey is most pronounced for the largest carnivore, the lion. Buffalo and hartebeest (both large) were the two most important prey of lions in the 1960s but have been supplanted by lechwe and warthog (both small). Increased predation on lechwe is notable because they constituted less than 1% of observed kills in the 1960s, prompting Mitchell et al. (1965) to conclude that their use of flooded plains “makes hunting very difficult, and a considerable proportion of them reach old age. There is an annual period of food stress during which their herds lose condition badly and many die of poverty”. The high current level of predation on puku (which are small) by all of the carnivores is also striking in light of Mitchell et al.'s conclusion that “the number of [puku] kills made by lions is remarkably small as is also the number made by wild dogs ... they are unexpectedly low on the list considering that they are so numerous in many areas”. In contrast to the situation

a half-century ago, puku are now the most important prey for wild dogs, leopards, and cheetahs, and the fourth most important prey for lions. Although spotted hyenas are not common in KNP, puku are now their most important prey, based on the composition of 58 scats (Rdudh, 2017).

Figure 1 is based on the number of kills that each prey species contributed to each carnivore’s diet, rather than biomass, and the decreased importance of large prey would only be strengthened if these data were weighted by differences in mass. More kills were recorded in the 1960s than in the 2010s, but this difference does not affect the proportions of large and small prey; in 100 iterations of randomly thinning the 1960s data to equal the sample size for the 2010s, all iterations confirmed that contribution of large prey decreased significantly. In addition to this broad pattern, the sample size for both periods was sufficiently large that in many cases, the observed change for a single prey species was significant (e.g., the decreased importance of buffalo and hartebeest and the increased importance of lechwe and puku for lions: Figure 1). Thinning the 1960s data appreciably weakened the observed reduction in diet breadth (mean loss of large prey dropped from 13 dyads to 8 and mean loss of small prey dropped from 7 dyads to 4). Thus, the comparison of equal-sized samples confirms that diet breadth has narrowed (by 29%, with 12 predator–prey dyads lost from the original set of 42), but also suggests that a larger sample for the 2010s might add a few observations of rarely killed species. This point does not alter the inference that large prey now comprise a smaller proportion of carnivore diets.

The currently high frequency of small prey in carnivore diets is at least partially explained by their relative abundance. Unbiased estimates of herbivore densities are not available for the 1960s, but we used herbivore densities (with correction for differences in detectability) from 2012 to 2014 (Matandiko, 2016) to test whether

prey that have become more important are those that are now most common. Seven surveys over 3 years showed that the most common herbivores in KNP are now puku, at a density of 13.0 individuals per km<sup>2</sup> (95% CI: 11.8–14.2), followed by impala at 9.6 individuals per km<sup>2</sup> (95% CI: 9.2–10.0) and warthog at 1.7 individuals per km<sup>2</sup> (95% CI: 1.5–1.8). These densities are considerably lower than past data from an ecologically similar miombo ecosystem: using comparable methods, Rogers (1979) reported densities of 28.6 impala per km<sup>2</sup>, 26.1 wildebeest per km<sup>2</sup>, 10.7 zebra per km<sup>2</sup>, and 6.4 warthog per km<sup>2</sup> in the Selous Game Reserve from 1969 to 1977. Overall, the three most abundant ungulates in Kafue now total 24.3 individuals per km<sup>2</sup>, only 37% of the 65.4 individuals per km<sup>2</sup> in Selous 40 years ago. Moreover, two of the three most abundant species in past data from Selous were large, while none are for current data from Kafue. The patterns of relative abundance we found are reinforced by data showing that puku, impala, and warthog were the three most frequently killed species on the M9 highway at the southern edge of our study site (Mkanda & Chansa, 2011) and by distance sampling by Department of National Parks and Wildlife foot patrols, which confirm that the four most abundant species are puku, impala, warthog, and common duiker, though absolute estimates of density from foot patrols were considerably lower (Schuette et al., 2018) than our data (despite correction for detection). These relatively abundant small prey have increased in importance for 10 of 12 predator–prey dyads (83%, 95% CI: 55–95). Other species were encountered too rarely to fit distance sampling models, but pooled data for a set of large obligate grazers (wildebeest, hartebeest, roan and zebra) yielded a considerably lower density of 0.20 herds per km<sup>2</sup> (95% CI: 0.15–0.25), that is, a mean of only 0.05 herds per km<sup>2</sup> per species. The importance of these four large species has decreased for 11 of 11 predator–prey dyads (100%, 95% CI: 74–100). Collectively, these results show that small prey species that remain relatively abundant have



**FIGURE 2** Niche matrices, showing changes in niche breadth and niche overlap between the 1960s (top) and 2010s (bottom). Carnivore species are rows and prey species are columns, arranged from smallest (left) to largest (right)

increased in importance for carnivore diets, while large prey that are now rare have decreased in importance ( $\chi^2 = 9.97, p = 0.0016$ ).

The systematic compression of carnivore diets towards smaller prey has increased dietary niche overlap within the carnivore guild (Figure 2). The Czekanowski Index of niche overlap for the carnivore guild increased significantly (by 15%) from the 1960s to the 2010s, from 0.39 to 0.45 (95% CI for 1960s = 0.37–0.42, 95% CI for 2010s = 0.42–0.48).

## 4 | DISCUSSION

At the scale of ecosystems, it is well-established that carnivore density often correlates with prey density (Hayward, O'Brien, & Kerley, 2007; Van Orsdol et al., 1985) and that prey depletion often contributes to carnivore decline (Estes et al., 2011; Ripple et al., 2014, 2015). Less direct attention has been given to the possibility that prey depletion might change the composition of the prey community, and thus, alter large carnivore diets as part of this relationship. Our results show that over the past half-century in KNP, the contribution of large prey to carnivore diets has systematically decreased, particularly for the lion, which often takes larger prey than the other three carnivores (Hayward & Kerley, 2005). Small species that have become more important are now relatively common, while large species that have become less important are now rare. Finally, our results show that diet breadth has narrowed, contrary to the prediction from niche theory that resource depletion should be accompanied by niche expansion. Selective depletion of large prey has caused prey-base homogenization.

Of all the predator–prey dyads we examined, the only large ungulate that became appreciably more important over time was the hippo in the diet of lion. Hippos are unusual in both size and ecology (spending most of their time in the water), and it is not clear why lions now feed on them more frequently, but it is possible that predation on megaherbivores is driven by the learnt behaviour of a few individuals. It is also possible that lion predation has shifted to hippo as a consequence of the greatly diminished role of buffalo in their diet (Figure 1).

What implications do selective prey depletion and prey-base homogenization have for large carnivore conservation? We suggest four possibilities that require further investigation. First, smaller prey might constrain carnivore group sizes to be smaller (Creel & Creel, 1995, 2002). Second, smaller prey could affect the energetics of hunting by forcing an increase in the number of kills required, and the associated costs of search, capture, and killing (Creel & Creel, 2002; Gorman, Mills, Raath, & Speakman, 1998; Speakman, Gorman, Mills, & Raath, 2015). Both of these effects could alter survival or reproduction (Creel, Mills, & McNutt, 2004), though some studies suggest that large carnivores might adapt to the use of small prey if their typical prey is not available. For example, it has been suggested that wild dogs can subsist largely on dik-diks (<7 kg) in areas where larger prey have been depleted (Woodroffe, Lindsey, Romañach, & Ranah, 2007), though other data show that this pattern is coupled with high

levels of predation on livestock (Woodroffe, Lindsey, Romanach, Stein, & Ole Ranah, 2005).

Third, both wild dogs and cheetahs are often limited by interspecific competition with larger carnivores (Creel & Creel, 1996; Durant, 2000; Mills & Gorman, 1997) and an increase in the use of small prey by the larger carnivores (particularly lions) reduces the scope for niche partitioning to reduce competition (Droge, Creel, M'soka, & Becker, 2016; Hayward, O'Brien, Hofmeyr, & Kerley, 2006).

Finally, decreases in herbivore density in African ecosystems are often driven by snaring (Becker et al., 2013; Watson, Becker, McRobb, & Kanyembo, 2013; Watson et al., 2015), which is common in KNP. A decrease in the relative frequency of large prey could provoke a decrease in snare size (as has been demonstrated for parallel cases such as the nets used to catch salmon; Allendorf & Hard, 2009). While we do not have quantitative data on this point, our observations suggest that single-stranded wires or light cables (e.g., bicycle brake cables) are often used as snares in areas dominated by small herbivores. These are braided into heavier cables where species large enough to break light snares remain common. Our observations also suggest that lighter snares are likely to cause serious injury or death, but carnivores might be able to work free from heavy snares. For example, African wild dogs were rarely snared in Tanzania's Selous Game Reserve in the 1990s (Creel & Creel, 2002), when heavy, braided snares were common and light snares were rare, but lions and wild dogs are now frequently injured in Zambia's Luangwa Valley (Becker et al., 2013; Watson et al., 2013), where light snares predominate.

One limitation of this study is that carnivore diets were described through opportunistic sightings in the 1960s and through a combination of opportunistic and telemetry-aided sightings in the 2010s. We considered the possible effect of this difference in sampling in four ways. First, if the increase in predation on small prey from the 1960s to the 2010s was due to better detection of small prey in the 2010s, then increases in importance should have been most pronounced for the smallest species and weaker for the largest species within the small size class. Contrary to this prediction, importance did not increase for the smallest species (duiker and grysbok), but increased for the largest four species within the small size class (impala, puku, warthog, and lechwe). Second, occasional predation on very small species (such as porcupines, hares, civets, and genets, not considered in our primary analysis) was detected in both the 1960s and the 2010s. In both datasets, these very small kills comprised 2% of all observations. Third, the proportions of large and small prey within the 2013–2016 data did not change when comparing the set of 288 kills described above to a subset restricted to observations made while using radiotelemetry ( $\chi^2 = 0.82, df = 3, p = 0.84$ ). Finally, data collected with identical methods (Zambian Carnivore Programme, unpublished) show that large prey remain important in the diets of large carnivores in South Luangwa National Park, particularly the buffalo, which still comprises 46% of 235 recent Luangwa lion kills (95% CI: 39–52). For Luangwa lions, 60% of the diet remains very large prey (buffalo, hippo, giraffe, and elephant). South Luangwa is the most visited and

most heavily patrolled National Park in Zambia, and the continued importance of large prey in a better-protected ecosystem suggests that the current lack of predation on large prey in KNP is accurately described by the data.

A second limitation of this study is that unbiased data on the density of prey species are not available for the 1960s. Our data show that carnivore diets have narrowed and systematically shifted to smaller species. Our data also show that changes in the importance of prey over the past 50 years are positively related to their current relative abundance, but the data do not directly establish that changes in diet were driven by changes in abundance. However, we are aware of no plausible alternative that would explain both why diets have changed and why prey that have become less important are now relatively rare.

A third limitation of this study is that we do not know whether the composition of the carnivore community itself has changed. As a consequence, we do not know whether changes in prey selection might be attributable in part to changes in the relative abundance of the carnivores.

Finally, we note that the study by Mitchell et al. (1965) in KNP is similar to other direct, observational field studies conducted in the 1960s and 1970s. As large datasets on the past carnivore diets exist for other ecosystems (e.g., Pienaar, 1969; Schaller, 1972), there are opportunities for current research to test for changes like those observed in KNP. Depletion of ungulate prey has been identified as a problem for large carnivores in many ecosystems (Karanth & Stith 1999; Western et al., 2009; Wolf & Ripple, 2016). The methods we used to test for changes in predator-prey interactions and niche partitioning within the predator guild are well-established and should be used more broadly to test whether prey depletion alters predator-prey interactions in a manner that is likely to affect the persistence of large carnivores or alter their ecological effects. If the patterns seen in Kafue prove to be general, then efforts to mitigate the effect of prey depletion on large carnivores will be most effective if focused on large prey.

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## CONFLICT OF INTEREST

The authors have no conflicts of interest.

## AUTHORS' CONTRIBUTIONS

All authors helped to refine the inferences and revise the manuscript. S.C. conceived the study, conducted the analysis, and wrote the first draft. W.M. conceived the study, initiated research in KNP, and led the data collection. P.S. conceived the study and initiated research in KNP. C.S., E.R., K.B., and M.V. collected the data. M.B. conceived the study and supervised the data collection.

## DATA ACCESSIBILITY

Data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.q448dt8> (Creel, 2018).

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