Prey depletion and the effect of group size on cooperative hunting in African wild dogs

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Abstract: Cooperative hunting can favor group living by increasing the probability that a hunt will end with a kill, increasing the size of prey that can be taken, increasing the probability of killing multiple prey, or decreasing the distance moved and energy expended. Across a broad range of taxa, environments and hunting behaviors, one of the most consistent benefits of cooperation is an increase in the mass of prey that can be killed. African wild dogs (*Lycaon pictus*) are cursorial hunters that cooperatively search for, capture and kill prey that are typically ~1.5X – 2X their own mass (and sometime as much as 10X). Prior research with wild dogs has shown that cooperative hunting favors group living though all of these mechanisms. However, most ecosystems with appreciable wild dog populations are now affected by prey depletion due to bushmeat poaching, which disproportionately reduces the density of large prey such as wildebeest (*Connochaetes taurinus*), relative to smaller prey such as impala (*Aepyceros melampus*) or puku (*Kobus vardonii*). Here, we applied a Bayesian structural equation model to data from high frequency triaxial accelerometers in 13 wild dog packs in two ecosystems to test whether prey depletion altered the effect of group size on hunting movements and energy expenditure. Contrary to prior results from an ecosystem with abundant prey of all sizes, we found that larger packs made larger movements and expended more effort when hunting. Also contrary to prior results, we found that large packs did not kill larger prey. Our results suggest that prey depletion reduces the benefit of hunting in large groups by reducing opportunities to kill large prey, thereby necessitating increased movement and energy expenditure. Anthropogenic effects are now altering fundamental ecological relationships such as the costs and benefits of variation in group size. Although the behavioral consequences of shifting ecological baselines will often be difficult to detect, understanding these effects is increasingly important for the conservation of endangered species like the African wild dog.

Many taxonomic groups show considerable variation in social organization. For example, ~85% of carnivore species are solitary and associate with other adults only to reproduce, but the remaining ~15% include some of the most highly cooperative societies among the vertebrates (Rood 1986, Gittleman 1989, Clutton-Brock 2002). Many factors can favor the evolution of gregariousness and sociality (Waser and Jones 1983), including intraspecific competition for space or mates (Caro and Collins 1987), intraspecific and interspecific defense of food (Lamprecht 1978, Fitzgibbon and Fanshawe 1989, Durant 2000), and cooperative detection of or defense from predators (Rood 1986, Bshary and Noe 1997). Among large carnivores and other active hunters, cooperative hunting can also favor group living through several mechanisms.

Cooperative hunting usually (but not always) increases hunting success, *i.e.*, the proportion of hunts that end with a kill. Spotted hyenas (*Crocuta crocuta*) hunting wildebeest (*Connochaetes taurinus*) calves in the Ngorongoro Crater succeeded in only 15% of solitary hunts, but in 74% of group hunts (Kruuk 1972). In the Masai Mara, spotted hyenas' hunting success (across all prey types) increased as group size rose from one to three, and then leveled off (Holekamp et al. 1997). In Serengeti, the hunting success of lions (*Panthera leo*) in groups (82 kills in 273 hunts was twice that of solitary hunters (37 kills in 249 hunts) (Schaller 1972). In Etosha, lions' hunting success increased significantly as group size increased from one to seven, for each of their five most important prey species (Stander & Albon 1993). The success of Harris's hawks (*Parabuteo unicinctus*) hunting lagomorphs increased as group size increased from one to six (Bednarz 1988). Similar patterns have been found in experimental studies; for example, hunting success more than tripled as flock size rose from one to seven for black headed gulls (*Larus ridibundus*) hunting schools of bleak (*Alburnus alburnus*) (Götmark et al. 1986). This patterns is not universal, and some studies with equally good data have detected no increase in hunting success as hunting group size increases. For example, hunting success was constant across group sizes for spotted hyenas hunting gemsbok (*Oryx gazella*) and wildebeest in Kalahari (Mills 1990).

Hunting in groups often increases the likelihood of killing multiple prey, in both observational and experimental studies (Packer & Ruttan 1990). Examples come from a broad range of taxa, including jacks (*Caranx ignobilis*) hunting Hawaiian anchovies (*Stolephorus purpureus*) (Major 1978), ravens (*Corvus corax*) hunting kittiwakes (*Rissa tridactyla*) (Montevecchi 1979), great blue herons (*Ardea herodias*) hunting fish and amphibians (Krebs 1974), and African wild dogs (*Lycaon pictus*) hunting impala (*Aepyceros melampus*), wildebeest or warthogs (*Phaecocoerus africanus*) (Creel & Creel 2002). For large carnivores, multiple kills are usually several juveniles from the same herd, or an adult female and her offspring (Estes & Goddard 1967, Kruuk 1972).

Relative to the two benefits just described, less is known about the effect of group size on the effort that must be expended in hunting (Creel & Creel 1995, Jordan et al. 2023), but cooperation can reduce individual effort. For African wild dogs, the distance of chases decreased significantly as pack size increased, particularly in successful chases (Creel & Creel 1995, 2002). For social spiders, shared webs can decrease the individual cost of construction (Yip et al. 2008). Individual lions adopt unique roles in hunts, with some the flanking a prey herd and others catching prey that flees the flankers, so that single lions do not have to undertake all of these actions (Schaller 1972, Stander 1992).

One of the most common benefits of cooperative hunting, across a broad range of taxa, hunting behaviors and environments, is an increase in the size of prey that can be killed. Colonies of social spiders (*Anelosimus eximius*) capture larger prey (Yip et al. 2008) as group size increases, over a range from dozens to thousands of spiders. Prey mass increased eight-fold as group size increased from one to seven for chimpanzees (*Pan troglodytes*) hunting monkeys (Boesch 1994). Using highly coordinated attacks, large groups (up to 35 individuals) of killer whales (*Orcinus orca*) are capable of killing prey as large as sperm whales (*Physeter macrocephalus*) (Pitman et al. 2006). Only when they hunt in groups are Harris's hawks capable of killing mammalian prey larger than themselves (Bednarz 1988). Small groups of lions do not kill buffalo, which are common prey for larger groups (Funston et al. 1998, Scheel & Packer 1991). Positive relationships between group size and prey mass have been described for many terrestrial mammalian carnivores (Gittleman 1989), including golden jackals (*Canis aureus*) (Lamprecht 1981), coyotes (*Canis latrans*) (Wells & Bekoff 1982), lions (Scheel & Packer 1991), spotted hyenas (Kruuk 1972), cheetahs (Caro 1994), wolves (Canis lupus) (MacNulty et al. 2014) and African wild dogs (Creel & Creel 2002).

African wild dogs (*Lycaon pictus*) are cooperative breeders that invariably move and hunt together in a highly coordinated manner to kill prey substantially larger than themselves (Fig. 1) (Creel and Creel 2002, Jordan et al. 2023). Wild dogs hunt by openly approaching prey and chasing them over long distances: successful chases are typically greater than 800 *m*, embedded in daily movements of 10-15 *km* to locate prey while avoiding dominant competitors, particularly lions (Creel and Creel 1995, Mills and Gorman 1997, Vanak et al. 2013, Hubel et al. 2016, Goodheart et al. 2022, Goodheart et al. 2024). Before hunting (usually at dawn and dusk), wild dogs engage in a rambunctious 'rally' that appears to coordinate the decision to begin moving. When prey are detected, the pack initiates a hunt with a stereotypical shoulder-to-shoulder walk directly at the prey, with heads lowered and ears flattened (Fig. 1). Some hunts are abandoned quickly, but escalated chases accelerate up to 60 km/h as prey begin to flee (Estes and Goddard 1967, Hubel et al. 2016, Creel et al. 2025b). Direct observation of 404 kills in 905 hunts by wild dogs in the Selous Game Reserve showed that larger packs had greater hunting success (kills per hunt), were more likely to kill multiple prey, had shorter chase distances, and killed larger prey (Creel and Creel 1995). Collectively, these effects caused the *per-capita* net energetic benefit of hunting to increase with increasing group size (Creel 1997).

For wild dogs in Selous, differences in prey selection by large and small packs were central to the benefits of cooperative hunting (Figs. 2 & 3). Impala (*Aepyceros melampus*), with a mean kill mass of 31.9 *kg*, were the most common prey for packs smaller than the median, but wildebeest (*Connochaetes taurinus*), with a mean kill mass of 92.7 *kg*, were the most common prey for packs larger than the median (Creel and Creel 1995). Differences in prey selection by large and small packs arose from differences in hunting behavior at every stage of the predation sequence (Creel and Creel 2002): small packs (< 9 adults) encountered, hunted and killed impala more often than large packs did, and large packs (≥ 9 adults) encountered, hunted and killed wildebeest more often than small packs did (Fig. 3). Large packs typically killed prey that were approximately three times larger, while also making shorter pursuits with a greater likelihood of success and of killing multiple prey. Together, these effects yielded an increase in the *per-capita* mass of food obtained per kilometer of hunting effort (Creel and Creel 1995).

Under the ecological conditions of the Selous Game Reserve in the 1990s, cooperative hunting favored life in larger groups, but ecological conditions are changing rapidly in most of the ecosystems that hold appreciable wild dog populations. In particular, excessive bushmeat hunting is causing herbivore populations to decline in most of sub-Saharan Africa (Lindsey et al. 2011, Lindsey et al. 2013, Ripple et al. 2015, Ripple et al. 2016, van Vliet et al. 2016). This decline of herbivores is causing parallel decline of large carnivores, including African wild dogs (Loveridge et al. 2020, Goodheart et al. 2021, Vinks et al. 2021, Becker et al. 2024, Creel et al. 2024, Reyes de Merkle et al. 2024, Creel et al. 2025a). Larger prey species are have declined more than smaller ones (Barnett 2000, Lindsey et al. 2013, Vinks et al. 2020), and in response some carnivore populations have shifted to smaller prey (or to livestock) (Woodroffe et al. 2005, Woodroffe et al. 2007, Creel et al. 2018, Vinks et al. 2020). Because the ability to kill large prey efficiently and effectively is an important benefit of hunting in larger groups, we hypothesized that prey depletion might alter the relationship between group size and hunting energetics, by shifting predation toward smaller prey that remain more abundant. We tested this hypothesis by combining data from long-term monitoring of large herbivore densities and distributions in two ecosystems, direct observation of kills made by radiocollared wild dog packs, and minute-by-minute data on wild dogs' movement and effort from high frequency triaxial accelerometers/magnetometers. The data came from 13 packs in areas with a broad range of prey densities, pack sizes and pack compositions.

Methods

Our data came from wild dog populations on study sites of ~8,000 km^2 in the Greater Kafue Ecosystem (GKE) and ~7,000 km^2 in the Luangwa Valley Ecosystem (LVE), which we have intensively monitored since 2011 and 2008 respectively. We have previously published detailed descriptions of the sites, their large herbivore populations (Schuette et al. 1028, Rosenblatt et al. 2019, Vinks et al. 2020), the density, demography and distribution of wild dogs and lions (Mweetwa et al. 2018, Vinks et al. 2021, Creel et al. 2024, Goodheart et al 2021, 2022, Reyes de Merkle et al. 2024,), and our methods for population monitoring, behavioral observation and accelerometry (Redcliffe et al. 2024, Creel et al. 2024, 2025s, 2025b), so our description of these methods here is concise.

Study Sites

Both study sites are bisected by a major river and the density of large herbivores is highest near this permanent water, including the primary prey of African wild dogs, which are puku (*Kobus vardonii*) and impala (*Aepyceros melampus*) in both ecosystems (Creel et al. 2025b). The densities of wild dogs, their prey and other large carnivores are all low in the GKE because of a long history of heavy bushmeat poaching (Vinks et al. 2020, Goodheart et al. 2021, Vinks et al. 2021, Becker et al. 2024, Goodheart et al. 2024, Creel et al. 2025a). The densities of wild dogs (GKE: 0.7 individuals/100 km^2, LVE: 4.0 individuals/100 km^2), their prey and their competitors are all higher in the LVE due to better protection (Rosenblatt et al. 2016, Mweetwa et al. 2018, Rosenblatt et al. 2019, Becker et al. 2024, Creel et al. 2024, Reyes de Merkle et al. 2024). Within the LVE, there is substantial spatial variation in wild dog density, survival and reproduction, which are all higher in well-protected areas with higher prey density, despite higher lion density (Reyes de Merkle et al. 2024). Wild dog density, survival and reproduction in the GKE are comparable to the least-protected portion of the LVE in the Lower Lupande Game Management Area, a buffer zone with less protection and lower prey density than the National Park itself (Watson et al. 2013, Watson et al. 2015, Goodheart et al. 2021, Reyes de Merkle et al. 2024).

Field Monitoring

For the structural equation model described below, we restricted data to areas in which all resident wild dog packs and lion prides were intensively monitored using VHF-GPS collars, and all individuals were individually recognized (Figs. 4 & S2). We radiocollared both species by darting with an air-powered DanInject rifle to deliver a 6:1 ratio of medetomidine and tiletamine–zolazepam, reversing the medetomidine with atipamezole after 45 – 60 min (see *Ethical Note* below for more details).

We used VHF and Iridium-GPS collars (Telonics MOD-335-3 and TGW-4277-4) to locate and observe wild dog packs while they hunted, usually around dawn and dusk, using methods described in detail by Creel & Creel (1995, 2002). We recorded the species of prey killed by wild dogs and recorded pack size by direct observation (Goodheart et al. 2021, Reyes de Merkle et al. 2024, Creel et al. 2025b). For the analysis of prey selection reported here, we analyzed 346 kills that were directly observed or located soon after the kill was made with no other carnivores present. These data came from all packs in the GKE and LVE study sites throughout the long-term study, and therefore sampled a slightly larger range of pack sizes than the data from accelerometry analyzed with structural equation modelling (see Results, Figs. 5 & 7), We estimated the mass of each prey type as described by Creel et al. (2025b), but our analysis (with the exception of Fig. 5b) does not rely on these estimates, which are provided primarily to assist readers unfamiliar with these species.

We mapped the intensity of use by lions (Figs. 4 & S2) using dynamic Brownian bridge movement models (dBBMMs) with a window of 35 locations and a margin of 7 locations fit to four GPS locations per day for a single lion in each pride, as described by Goodheart et al. (2022). To make temporally matched comparisons, we fit a dBBMM for each pride that overlapped with a sampled wild dog pack, in the dry season of the year in which accelerometer data were collected from wild dogs. We rasterized the utilization distribution for each pride using a1 km^2 grid and summed the rasters to create a single layer measuring the intensity space-use for all prides. We tested an alternative measure of lion space-use, with UD values weighted by the associated pride's size (range 1–14 individuals), again summing these to create a single layer measuring the intensity of lion space-use. The two methods yielded very similar inferences (Goodheart et al. 2024), and here we report results from the simpler, unweighted distribution.

We mapped prey density (Fig. 4) using data from distance sampling in 17 surveys over 2082 km of transects, which sampled an area of 1129.6 km^2, well-balanced between the GKE (1086 km) and LVE (996 km), as described by Rosenblatt et al. (2019), Vinks et al. (2020) and Creel et al. (2025b). Briefly, we established fixed transects (in 2011 in LVE and 2013 in GKE) and mapped them using GPS, spaced at a minimum of 5 km to prevent double counting, running perpendicular to permanent water to sample a range of distances to water, and sited to sample vegetation types representatively (Vinks et al. 2020, Rosenblatt et al. 2019). Transects included well-protected (National Parks) and less-protected (Game Management Areas) areas. Twice a year, once at the beginning of the dry season and once at the beginning of the wet season, we drove each transect at 10-15 km/h, with one individual driving, one navigating and recording data, and two observing from the roof. Whenever animals were detected we stopped and used range-finding binoculars to record the species, herd size (including singletons), bearing and distance. With these data, we fit Bayesian hierarchical distance sampling models to estimate environmental effects on the density of each herbivore species in each ecosystem, correcting for the probability of detection (Creel et al. 2025b). We analyzed data for puku and impala separately, but pooled data for five small antelopes (common duiker (*Sylvicapra grimmia*), grysbok (*Raphicerus sharpei*), oribi (*Ourebia ourebi*), bushbuck (*Tragelaphus scriptus),* and reedbuck (*Redunca arundinum*)) because their distributions were broadly similar at the scale of wild dog movements, and each species was too sparsely distributed to obtain precise estimates of effects on its density. These five species (hereafter 'small antelopes') are typically found alone or in small groups, broadly scattered, at much lower maximum local densities than impala or puku. Together, these seven species comprised 82% of wild dogs' diet in the two ecosystems (see *Results*). We fit negative binomial models of herd size, modeled the probability of detection (of herds) using hazard functions, and modeled herd density as a log–linear function of percent tree cover, distance to the nearest permanent river, distance to the nearest seasonal stream, and the frequency with which the location burned. We extracted values for these covariates from the Google Earth Engine Data Catalog at each herd's location using Google Earth Engine. We calculated the distance to rivers and streams to 1 m, using HydroSHEDs data. We determined percent tree cover using Copernicus proportional land cover satellite imagery with 100 m resolution. We calculated the local frequency of fires (the proportion of years between 2001 and 2023 in which an area burned) using MODIS imagery with 500 m resolution. These scales were sufficient to detect effects of prey density on wild dogs and lions (see *Results*). As described by Creel et al. (2025b) we combined species- and ecosystem-specific coefficients from the hierarchical distance sampling models with rasters for each predictor variable to map the expected density of each prey species. Because these values were estimated by distance sampling models, we allowed for estimation error in subsequent structural equation modelling, by treating prey density as a latent variable (see *Structural Equation Modelling*).

We determined protection status at each wild dog location (Fig. 4) using a raster of National Park and Game Management Area boundaries. Protection levels are considerably higher within National Parks than in adjacent Game Management Areas (Watson et al. 2013, Becker et al. 2024, Reyes de Merkle et al. 2024).

Movement and Energy Expenditure

We attached Daily Diary (DD) tags (Wilson et al. 2008) to Iridium-GPS radiocollars (TGW-4277-4, Telonics, Mesa, Arizona) fitted to 16 wild dogs in 13 packs to record orthogonal triaxial acceleration (-16 *g* to +16 *g* with 16 bit resolution) at 40 Hz and orthogonal triaxial magnetic field intensity at 7 Hz (Wilson et al. 2008). We collected the collars after 31 days, using a programmable release mechanism (Telonics CR-7B). Wild dog packs move and hunt in a highly cohesive manner (Creel and Creel 2002, Jordan et al. 2023), so we collared a single individual in each pack at any given time. Our sampling provided data from areas with the highest and lowest prey and lion densities within the two ecosystems, and a representative range of pack sizes and compositions ($\bar{X} = 13.7$ individuals $\pm$ $1.43\ S.E.$, range 5 – 25, $\bar{X} = 6.4$ adults $\pm$ $0.73\ S.E.$, range 1 – 11, $\bar{X} = 2.3$ yearlings $\pm$ $0.53\ S.E.$, range 0 – 8, $\bar{X} = 5.1$ pups $\pm$ $0.97\ S.E.$, range 0 – 13). We deployed nine DD collars in the LVE (in six packs) and seven in the GKE (in seven packs) in 2022 and 2023. In three packs, we collared two different individuals at different times, after a change in pack size and composition.

We used the DD tag data to determine each animal’s location at one-minute intervals using GPS-corrected dead reckoning, and thus determined the distance moved each minute (Bjørneraas et al. 2010, Bidder et al. 2015, Gunner et al. 2021). To obtain a measure of the energetic effort expended in each minute, we used DDMT software developed for the analysis of DD tag data to calculate vectorial dynamic body acceleration (VeDBA) from the accelerometer data at the original 40 Hz scale:

$$VeDBA = \sqrt{(A_{x_r} - A_{x_s})^2 + (A_{y_r} - A_{y_s})^2 + (A_{z_r} - A_{z_s})^2} \qquad Equation\ 1$$

where *A* is acceleration in orthogonal *x*, *y* and *z* axes, and *r* and *s* subscripts identify raw or smoothed values with a smoothing window of 2 *s* (Shepard et al. 2008, Qasem et al. 2012). We then smoothed these VeDBA values (‘effort’ or ‘energy expenditure’ hereafter) by taking the running mean over 2.5 seconds, and prior to analysis, we aggregated the smoothed values to the same one minute intervals used for movements.

Structural Equation Modelling

Finally, we used a structural equation model (SEM) to examine associations between local prey density and lion use, pack size, distance moved and energy expenditure. An SEM is well-suited to testing the relationship of between pack size and measures of hunting effort because there are multiple direct and indirect causal pathways among these variables, SEM can account for correlations between exogenous variables, and SEM allows the inclusion of latent variables (Grace 2008, Grace et al. 2010). We fit the model using Bayesian methods in R, using the package blavaan with its default distributions and priors for variables of each type (Merkle and Rosseel 2018).

The SEM's structure is shown in Figure 6. Because prey density at each location was estimated using distance sampling (Creel et al. 2025b), we treated it as a latent variable to allow for estimation error: this was the only latent variable. *A priori*, we began with a slightly more complex model than is shown in Figure 6, including direct effects of protection on local lion use, pack size on the number of pups present, and the number of pups on movement and energy expenditure. Among these effects, only the effect of pack size on the number of pups was strong: the other effects were not well supported and were dropped (Grace et al. 2010). These simplifications left the number of pups as an exogenous variable, so it was also dropped. These simplifications did not alter inferences about relationships that remained in the model. We standardized all variables by subtracting the mean and dividing by the standard deviation, to assist model convergence and to allow direct comparison of effect sizes. Prior to fitting the SEM we discarded 70,766 observations (from a total of 242,126) in areas where we could not quantify lion use. This filtering retained 171,360 locations at one minute intervals across all 24 hours, to incorporate both changes in behavior when active and/or changes in the duration of activity. At this time scale, the response variables of interest (hunting effort and movement) showed strong temporal autocorrelation, so to avoid pseudo-replication we selected a random subset of 40,000 observations prior to analysis. We used a Ljung-Box test to confirm that this sub-sampling removed autocorrelation for all combinations of lags from 1 to 10 (maximum autocorrelation = 0.006, $\chi^2 = 8.57$, $P = 0.57$). We also confirmed that different subsets produced very similar results and provided sufficient power to detect effects (see *Results*).

We tested for convergence of parameter estimates by confirming that trace plots for all parameters were well-mixed, all R-hat values were close to one (≥0.999 and ≤1.001), and all N_{eff} values were large (>1000) (Supplemental Table S2). We tested the model's fit by confirming that posterior estimates from the model matched the observed means for all variables (*i.e.,* posterior distributions of scaled variables were centered on zero), and by confirming that covariances from the model did not differ from covariances in the data (χ^2 = 72, P = 0.23, Supplemental Table S1). Regression of observed correlations between pairs of variables on correlations from the SEM further confirmed a good fit (b = 0.998 ± 0.0249 *S.E.,* R^2 = 0.995). Finally, we tested for prior sensitivity by altering priors from the blavaan defaults and confirming that coefficients showed little change and did not alter inferences.

Ethical Note

Because this was an observational field study, potential effects on the animals' welfare were mainly due to radiocollaring. When observing wild dogs from a vehicle, we avoided moving directly at them and remained at a distance that did not provoke reaction. We minimized the number of individuals (16) darted, anaesthetized and radiocollared by DD tagging only one wild dog in each pack and carefully selecting packs to provide data from a wide range of ecological conditions and pack sizes without redundancy. We darted and collared only apparently healthy and uninjured adults, at times and places with low risk. These procedures were performed by Zambian-registered veterinarians in collaboration with the Zambia Department of National Parks and Wildlife with MSU IACUC approval 2020-123, and we confirmed that radiocollaring did not affect survival (Creel et al. 2024). When collaring, we placed a priority on monitoring respiration and temperature, and that the animal was shaded, a custom sleeve protected the eyes, and the minor wound from the dart was treated with topical antibiotic. We used a Dan-Inject air rifle because it allowed low impact force but remained highly accurate. We used Pneu-Dart 5cc darts with 1" sleeved needles because these minimized weight, caused only a minor wound, and rarely bounced out. We used radiocollars with less than half the mass suggested as an ethical limit in widely-adopted guidelines from the American Society of Mammalogists.

Results

Pack Size and Prey Selection

For 346 observed kills in the LVE and GKE, pack size (number of adult hunters following Creel & Creel (1995)) had very little effect on the size of prey that were killed (χ^2 = 3.26, *df* = 3, *P* = 0.35). As shown in Figure 5, the likelihood of killing large antelopes did not increase with increasing pack size, as it did in Selous. Packs of all sizes relied heavily on kills of impala (LVE: 62.0%, GKE 27.8%) and puku (LVE:19.2%, GKE: 17.8%), with mean estimated kill mass of 31.9 *kg* for impala and 37.0 *kg* for puku. A set of small (estimated mean kill mass of 18 *kg)* antelopes that live in small, broadly scattered groups (common duiker, *Sylvicapra grimmia,* grysbok, *Raphicerus sharpei*, oribi, *Ourebia ourebi*, bushbuck, *Tragelaphus scriptus,* and reedbuck, *Redunca arundinum*) were frequently killed by both large and small packs, particularly in the GKE (25.8%). These species were killed less often (10.3%) in the LVE, where the densities of puku and impala are much higher than in the GKE (Rosenblatt et al. 2019, Vinks et al. 2020). The proportion of small antelopes in the diet increased as pack size rose to 6 or 7 adult hunters (offset by a decrease in the proportion impala), and then declined (offset by an increase in the proportion puku): overall, dependence on small prey was very similar for packs larger and smaller than the mean. Large prey such as wildebeest and hartebeest (*Alcelaphus buselaphus*) were rarely (6.3%) killed by packs of any size, and tended to be a smaller portion of kills by large packs (Fig. 5). There was no detectable change in mean prey mass across a range of adult pack sizes from 1 to 15 (Fig. 5b: *b* = -0.15 ± 0.021 *SE*, *t* = -0.72, *P* = 0.49), in contrast to prior results from Selous (Creel & Creel 2002), where mean prey mass tripled across a range of adult pack sizes from 3 to 20 (Fig. 5B).

Pack Size, Movement and Hunting Effort

Most of the relationships revealed by the SEM aligned well with prior research on relationships between African wild dogs, their prey and their dominant competitor the lion (Fig. 6, Supplementary Table S2). Prey density was positively related to the level of protection from poaching (*b* = 0.155 ± 0.005, posterior mean ± standard deviation, here and subsequently), and local lion density was greater in areas with high prey density (*b* = 0.435 ± 0.005). Wild dog packs were larger in areas with higher prey density (*b* = 0.098 ± 0.006) and smaller in areas with high usage by lions (*b* = -0.027 ± 0.006): combining the direct positive effect of prey density on pack size with the indirect negative pathway mediated by lion density, wild dog packs were slightly larger in areas with higher prey density (*b* = 0.086 ± 0.005). The effect of protection mediated by prey density was strongly positive for lion use (*b* = 0.068 ± 0.002) and weakly positive for wild dog pack size (*b* = 0.015 ± 0.001). As expected if prey depletion increases the energetic cost of hunting by requiring increased movement, prey density had negative direct relationships with distance moved per minute (*b* = -0.045 ± 0.006) and effort expended per minute (*b* = -0.053 ± 0.006). As expected if wild dog movements are affected by avoidance of lions, local lion use had a positive direct relationship with distance moved per minute (*b* = 0.019 ± 0.006) and effort expended per minute (*b* = 0.030 ± 0.006). Combining all direct and indirect pathways, the total effect of a decrease in prey density was to increase the distance moved (*b* = -0.032 ± 0.005) and effort expended per minute (*b* = -0.035 ± 0.005).

Unlike wild dogs hunting in an ecosystem with relatively abundant prey of all sizes (Creel and Creel 1995, Creel and Creel 2002), larger packs moved greater distances (*b* = 0.049 ± 0.005) and expended more effort (*b* = 0.055 ± 0.005), after accounting for the effects of prey density and lion usage. Mean pack size was smaller in Kafue (6.54 adults ± 0.30 *S.E.*) than in Luangwa (8.81 ± 0.59) or Selous (9.82 ± 0.80), but there was considerable overlap in the frequency distributions of pack size, and maximum pack sizes were similar (Kafue: 20 adults, Luangwa: 23, Selous: 24) (Fig. 7). Packs that were large enough to specialize on wildebeest in Selous (Figure 3) preyed almost entirely on impala, puku and small antelopes in Kafue and Luangwa (Fig. 5). In Selous, 47% of kills by packs of 9 or more adults were wildebeest (Table 5.2 in Creel & Creel 2002), but in Kafue and Luangwa only 2.2% of kills (*N* = 49) by packs of 9 or more adults were large antelopes (Fig. 5).

Collectively, these results reveal a chain of consequences for wild dogs hunting in areas with anthropogenic prey depletion (particularly of large prey). Larger packs do not kill larger prey (Fig. 5). In the absence of a switch to large prey, larger packs move more and expend more energy, after controlling for the effects of prey density, lion use and protection from human activities (Fig. 6). As would be expected if these consequences carry fitness costs, large packs are less common in prey depleted ecosystems (Fig. 7)

Discussion

Anthropogenic effects are rapidly altering ecological conditions in many ecosystems, and thus altering interactions between organisms, which in turn can alter the fitness effects of fundamental traits such as body size, morphology or behavior. Many protected areas in sub-Saharan Africa still hold large populations of the complete large carnivore guild and their large herbivore prey, but they are facing rapid change due to habitat loss and degradation, human-wildlife conflict and consequent persecution, and bushmeat poaching (Ripple et al. 2014, Ripple et al. 2016). In the long-term, climate change is likely to affect all of these threats. In the short term, commercial bushmeat poaching has emerged as a strong and immediate threat to large carnivores, partly due to direct mortality by snaring, but largely by reducing prey availability and altering the prey community's composition (because larger species have declined more than small ones) (Lindsey et al. 2011, Lindsey et al. 2013, Creel et al. 2018, Loveridge et al. 2020, Goodheart et al. 2021, Bauer et al. 2022, Becker et al. 2024, Reyes de Merkle et al. 2024, Creel et al. 2025a).

The densities of apex carnivores like the lion and spotted hyena correlate strongly with the density of prey, both within and between ecosystems (Hatton et al. 2015). In contrast, wild dog density has historically been low in areas with high prey density (Creel et al. 2023) due to strong interference competition from dominant competitors: wild dogs often lose their kills to spotted hyenas, and are often killed by lions (Fanshawe and Fitzgibbon 1993, Creel and Creel 1996, Mills and Gorman 1997, Swanson et al. 2014). When lion density declines due to prey depletion, wild dogs are not competitively released. They continue to avoid lions, survival and reproduction both decline, and their density becomes very low (*e.g.* <1 per 100 km^2 in the GKE) (Goodheart et al. 2021, Goodheart et al. 2022, Creel et al. 2023, Creel et al. 2024, Goodheart et al. 2024, Reyes de Merkle et al. 2024). These effects are linked to behavioral changes that would be expected with a decrease in prey availability: in areas depleted of prey, wild dogs move farther and expend more energy (Creel et al. 2025b). Beyond its energetic cost, increased movement in prey depleted areas exposes wild dogs to an increased risk of being snared themselves (Becker et al. 2024).

Here, a structural equation model revealed that this increase in movement and energy expenditure is partly driven by an unexpected change in the effect of group size on cooperative hunting. From prior research, we expected large packs to prey frequently on large species such as wildebeest, and to kill them efficiently (Creel and Creel 1995). Contrary to this expectation, large and small packs showed very similar patterns of prey selection. In the absence of prey switching, an increase in pack size was associated with an increase in movement and energy expenditure, unlike prior results. Under current ecological conditions, the most abundant prey in the GKE and LVE are intermediate-sized or small antelopes such as puku, impala and duiker (Schuette et al. 2018, Rosenblatt et al. 2019, Vinks et al. 2020). Larger prey such as wildebeest and hartebeest are less common (and wildebeest have historically not been common in the LVE). Collectively, the most parsimonious explanation of these patterns is that selective depletion of large prey (Lindsey et al. 2013) reduces the net benefit of cooperative hunting in large packs by constraining patterns of prey selection (Creel et al. 2018). If decisions that affect pack size (dispersal vs. philopatry) are not sufficiently flexible in response to ecological changes that alter the effects of pack size on fitness, prey depletion may put wild dogs in an ecological trap. If decisions that affect pack size are sufficiently flexible, the social and spatial organization of wild dogs may align with an extension of the resource dispersion hypothesis, with pack size determined by prey size and home range size determined by prey density (Macdonald 1983). Consistent with this hypothesis, the low density of wild dogs in the GKE (with strong prey depletion, particularly of large species: Creel et al. 2018, Vinks et al. 2020) is associated with relatively small pack sizes (Fig. 7) and large home ranges (Goodheart et al. 2021, Goodheart et al. 2024).

It has recently been suggested that wild dogs in Botswana might benefit from anthropogenic refuges or ‘human shields’, because lions avoid human-affected areas more than wild dogs do (Abrahms et al. 2025). Because Abrahms et al. (2025) did not consider data on prey distributions or the demographic consequences of using human-affected areas, they acknowledged that human-occupied areas could be either a refuge or an ecological trap for wild dogs. However, they did not consider studies of wild dogs in other ecosystems that have examined such data and found a trap. In both the Kafue and Luangwa Valley Ecosystems, areas that are more heavily affected by human activity (particularly illegal bushmeat hunting) have low densities of both lions and prey (Watson et al. 2013, Becker et al. 2024, Rosenblatt et al. 2019, Mweetwa et al. 2018, Vinks et al. 2020, 2021, Creel et al. 2025a). Wild dogs continue to avoid lions in these areas (Goodheart et al. 2022, 2024), and must increase their movement and energy expenditure to deal with the combination of anthropogenic prey depletion and lion avoidance (Creel et al. 2025b). In these areas, wild dogs have significantly lower survival, reproduction and population density than in adjacent areas that are better protected from human activities, as was also true for lions (Goodheart et al. 2021, Creel et al. 2024, Reyes de Merkle et al. 2024, (Creel et al. 2025a). The results presented here reveal an additional consequence of anthropogenic prey depletion for wild dogs: large pack sizes are beneficial in interactions with dominant competitors (Fanshawe & Fitzgibbon 1993, Creel & Creel 2002), but large packs face increased energetic costs of hunting, relative to small packs. As in Zambia, prey populations have declined due to heavy bushmeat poaching in the area suggested to offer human shields in Botswana (Rogan et al. 2017), with fitness costs noted for wild dogs (McNutt & Gusset 2012). Collectively, the data from Botswana, Zambia (and elsewhere, e.g. Kruger, Selous and Karongwe) are consistent with the conclusion that wild dogs are forced by their avoidance of lions to use areas with less-favorable foraging conditions, whether those conditions are created by humans or simply habitats with naturally lower prey density (Mills & Gorman 1997, Creel et al. 2001, 2024, Vanak et al. 2013, Dröge et al. 2017, Goodheart et al. 2024, Reyes de Merkle 2024). This conclusion is reinforced by continental and local distributions of wild dogs, which in the Anthropocene are mostly restricted to well-protected areas. For example, note the hard edge in wild dog locations in the inset of Figure 3: the obvious east-west line formed by the wild dogs' locations is the unfenced boundary of the National Park, south of which are villages encroaching into the less protected Game Management Area.

Because wild dogs maintain a tenuously positive energy budget, any environmental change that increases movement and energy expenditure is of concern (Creel 1997, Gorman et al. 1998, Goodheart et al. 2022, Creel et al. 2025b), but it seems likely that cooperative defense of pups, dens, territories and carcasses continue to favor larger groups (Creel et al. 2004). If so, decreases in pack size driven by prey depletion, like those seen in the GKE (Fig. 7) may carry fitness costs in other ways. For example, wild dogs can usually prevent kleptoparasitism by spotted hyenas if they outnumber the hyenas attempting to steal the carcass (Fanshawe & Fitzgibbon 1993, Creel & Creel 1996); particularly in open environments where hyenas can detect kills quickly, small packs are likely to be disadvantaged (Gorman et al. 1998, Creel et al. 2001). Given wild dogs' obligately cooperative social organization, a clear understanding of the ways that environmental change alters the relationship between group size and fitness may help to identify subtle but potentially important problems in their conservation.

In the Anthropocene, changes in many environmental conditions are large and rapid relative to the evolutionary history of wild dogs (or any species), but are nonetheless difficult to quantify (or even perceive) on the scale of most ecological and behavioral research. This creates a risk that shifting baselines will affect behavioral and ecological processes but go undetected. A study of predator-prey relations that began in the Kafue ecosystem today would obtain data that are profoundly affected by anthropogenic environmental change, but could easily be mistaken for baseline conditions. Long-term studies of behavioral and ecological processes (beyond monitoring of population size and trends) will be of increasing importance to detect effects like those we report here, and to understand their consequences for endangered species like the wild dog.

Code and Data Availability

An R script for data cleaning and analysis is provided in the supplementary material. Because the original data include detailed locations of an endangered species (wild dogs) and a threatened species that is subject to hunting (lions), they are not published but will be provided on reasonable request.

References

Abrahms, B., Rafiq, K., Nisi, A.C., Jordan, N.R., Wilson, A.M., Loveridge, A.J., Kotze, R., Sousa, L.L. and McNutt, J.W., 2025. Intraguild competition mediates human avoidance in an endangered African large carnivore. Proceedings of the Royal Society of London **292**: 20242835.

Banda, K., S. Creel, M. Sichande, T. Mweetwa, H. Mwape, J. Reyes de Merkle, L. Bwalya, T. Simpamba, R. McRobb, and M. Becker. 2023. Effects of de-snaring on the demography and population dynamics of African lions. Biological Conservation **286**:e110273.

Bauer, H., A. Dickman, G. Chapron, A. Oriol-Cotterill, S. K. Nicholson, C. Sillero-Zubiri, L. Hunter, P. Lindsey, and D. W. Macdonald. 2022. Threat analysis for more effective lion conservation. Oryx **56**:108-115.

Becker, M., S. Creel, M. Sichande, J. Reyes de Merkle, B. Goodheart, T. Mweetwa, H. Mwape, D. Smit, A. Kusler, K. Banda, B. Musalo, L. Bwalya, and R. McRobb. 2024. Wire-snare poaching and the large African carnivore guild: Impacts, knowledge gaps, and a method for collaboratively merging conservation science with field-based protection. Biological Conservation **289**:110376.

Bednarz, J. C. 1988. Cooperative hunting Harris' hawks (Parabuteo unicinctus). Science **239**:1525-1527.

Bidder, O. R., J. S. Walker, M. W. Jones, M. D. Holton, P. Urge, D. M. Scantlebury, N. J. Marks, E. A. Magowan, I. E. Maguire, and R. P. Wilson. 2015. Step by step: reconstruction of terrestrial animal movement paths by dead-reckoning. Movement Ecology **3**:23.

Bjørneraas, K., B. Van Moorter, C. M. Rolandson, and I. Herfindal. 2010. Screening Global Positioning System Location Data for Errors Using Animal Movement Characteristics. Journal of Wildlife Management **74**:1361-1366.

Boesch, C. 1994. Cooperative hunting in wild chimpanzees. Animal Behaviour **48**:653-667.

Bshary, R., and R. Noe. 1997. Red colobus and Diana monkeys provide mutual protection against predators. Animal Behaviour **54**:1461-1474.

Caro, T.M., 1994. Cheetahs of the Serengeti Plains: group living in an asocial species. University of Chicago Press, Chicago.

Caro, T. M., and D. A. Collins. 1987. Male Cheetah Social Organization and Territoriality. Ethology **74**:52-64.

Clutton-Brock, T. 2002. Breeding together: kin selection and mutualism in cooperative vertebrates. Science **296**:69.

Creel, S. 1997. Cooperative hunting and group size: assumptions and currencies. Animal Behaviour **54**:1319-1324.

Creel, S., M. S. Becker, J. R. de Merkle, and B. Goodheart. 2023. Hot or hungry? A tipping point in the effect of prey depletion on African wild dogs. Biological Conservation **282**:110043.

Creel, S., M. S. Becker, B. Goodheart, A. Kusler, K. Banda, K. Banda, M. Vinks, C. Sun, C. Dart, and S. Matsushima. 2025a. Changes in African lion demography and population growth with increased protection in a large, prey-depleted ecosystem. Conservation Science and Practice **7**:e13256.

Creel, S., and N. M. Creel. 1995. Communal hunting and pack size in African wild dogs, Lycaon pictus. Animal Behaviour **50**:1325-1339.

Creel, S., and N. M. Creel. 1996. Limitation of African Wild Dogs by Competition with Larger Carnivores. Conservation biology **10**:526-538.

Creel, S., and N. M. Creel. 2002. The African wild dog: behavior, ecology and conservation. Princeton University Press, Princeton.

Creel, S., W. Matandiko, P. Schuette, E. Rosenblatt, C. Sanguinetti, K. Banda, M. Vinks, and M. S. Becker. 2018. Changes in Zambian large carnivore diets over the past half century reveal the loss of large prey. Journal of Applied Ecology **55**:2908-2916.

Creel, S., M. G. L. Mills, and J. W. McNutt. 2004. Demography and population dynamics of African wild dogs in three critical populations. Pages 337-350 *in* D. W. Macdonald and C. Sillero-Zubiri, editors. Biology and Conservation of Wild Canids. Oxford University Press, Oxford.

Creel, S., J. Redcliffe, B. Goodheart, J. Reyes de Merkle, H. Mwape, S. Matsushima, C. Dart, K. Banda, B. Mayani, J. Njobvu, R. Kabungo, M. Mungolo, R. Kabwe, E. Kaseketi, W. Donald, A. Kaluka, C. Chifunte, H. Maimbo, L. Plankenhorn, D. Christianson, M. S. Becker, and R. P. Wilson. 2025b. Prey depletion, interspecific competition, and the energetics of hunting in endangered African wild dogs, Lycaon pictus. Proceedings of the National Academy of Sciences **122**:e2414772122.

Creel, S., J. Reyes de Merkle, B. Goodheart, T. Mweetwa, H. Mwape, T. Simpamba, and M. S. Becker. 2024. An integrated population model reveals source-sink dynamics for competitively subordinate African wild dogs linked to anthropogenic prey depletion. Journal of Animal Ecology **93**:417-427.

Creel, S. Spong, G. and N. Creel 2001. Interspecific competition and the population biology of extinction-prone carnivores, pp. 35-61 In: Carnivore Conservation Cambridge University Press (eds Gittleman, J. L., Funk, S. M., Macdonald, D. W. and R.K. Wayne)

Durant, S. M. 2000. Living with the enemy: avoidance of hyenas and lions by cheetahs in the Serengeti. Behavioral Ecology **11**:624-632.

Dröge, E., Creel, S., Becker, M.S. and M'soka, J., 2017. Spatial and temporal avoidance of risk within a large carnivore guild. Ecology and Evolution **7**:189-199.

Estes, R. D., and J. Goddard. 1967. Prey selection and hunting behavior of the African wild dog. The Journal of Wildlife Management:52-70.

Fanshawe, J. H., and C. D. Fitzgibbon. 1993. Factors influencing the hunting success of an African wild dog pack. Animal Behaviour **45**:479-490.

Fitzgibbon, C. D., and J. H. Fanshawe. 1989. The condition and age of Thomson's gazelles killed by cheetahs and wild dogs. Journal of Zoology **218**:99-107.

Funston, P.J., Mills, M.G.L., Biggs, H.C. and Richardson, P.R., 1998. Hunting by male lions: ecological influences and socioecological implications. Animal Behaviour **56**:1333-1345.

Gittleman, J. 1989. Carnivore group living: comparative trends. Pages 183 - 207 *in* J. Gittleman, editor. Carnivore Behavior, ecology and evolution. Springer, Boston.

Goodheart, B., S. Creel, M. S. Becker, M. Vinks, P. Schuette, K. Banda, C. Sanguinetti, E. Rosenblatt, C. Dart, and A. Kusler. 2021. Low apex carnivore density does not release a subordinate competitor when driven by prey depletion. Biological Conservation **261**:109273.

Goodheart, B., S. Creel, P. Schuette, E. Droge, Justine A. Becker, K. Banda, A. Kusler, S. Matsushima, K. Banda, R. Kabwe, W. Donald, J. Reyes de Merkle, A. Kaluka, C. Chifunte, and Matthew S. Becker. 2024. Spatial Risk Effects From Lions Compound Impacts of Prey Depletion on African Wild Dogs. Ecology and Evolution **14**:e70401.

Goodheart, B., S. Creel, M. Vinks, K. Banda, J. Merkle, A. Kusler, C. Dart, K. Banda, M. Becker, P. Indala, C. Simukonda, and A. Kaluku. 2022. African wild dog movements show contrasting responses to long and short term risk of encountering lions: analysis using dynamic Brownian bridge movement models. Movement Ecology **10**:10.1186/s40462-40022-00316-40467.Gorman, M. L., M. G. Mills, J. P. Raath, and J. R. Speakman. 1998. High hunting costs make African wild dogs vulnerable to kleptoparasitism by hyaenas. Nature **391**:479-481.

Götmark, F., Winkler, D. & Andersson, M. 1986. Flock-feeding on fish schools increases individual success in gulls. Nature **319**: 589–591.

Grace, J. B. 2008. Structural equation modeling for observational studies. The Journal of Wildlife Management **72**:14-22.

Grace, J. B., T. M. Anderson, H. Olff, and S. M. Scheiner. 2010. On the specification of structural equation models for ecological systems. Ecological monographs **80**:67-87.

Gunner, R. M., M. D. Holton, M. D. Scantlebury, O. L. Van Schalkwyk, H. M. English, H. J. Williams, P. Hopkins, F. Quintana, A. Gómez-Laich, and L. Börger. 2021. Dead-reckoning animal movements in R: a reappraisal using Gundog. Animal Biotelemetry **9**:1-37.

Hatton, I. A., K. S. McCann, J. M. Fryxell, T. J. Davies, M. Smerlak, A. R. E. Sinclair, and M. Loreau. 2015. The predator-prey power law: Biomass scaling across terrestrial and aquatic biomes. Science **349**:aac6284.

Holekamp, K.E., Smale, L., Berg, R. and Cooper, S.M., 1997. Hunting rates and hunting success in the spotted hyena (*Crocuta crocuta*). Journal of Zoology **242**: 1-15Hubel, T. Y., J. P. Myatt, N. R. Jordan, O. P. Dewhirst, J. W. McNutt, and A. M. Wilson. 2016. Energy cost and return for hunting in African wild dogs and cheetahs. Nature communications **7**:11034.

Jordan, N. R., K. A. Golabek, C. J. Marneweck, D. G. Marneweck, M. M. Mbizah, D. Ngatia, D. Rabaiotti, B. Tshimologo, and J. Watermeyer. 2023. Hunting Behavior and Social Ecology of African Wild Dogs. Pages 177-227 *in* M. Srinivasan and B. Würsig, editors. Social Strategies of Carnivorous Mammalian Predators: Hunting and Surviving as Families. Springer International Publishing, Cham.

Krebs, J.R., 1974. Colonial nesting and social feeding as strategies for exploiting food resources in the Great Blue Heron (*Ardea herodias*). Behaviour **71**:99-134.

Kruuk, H. 1972. The Spotted Hyena: a study of predation and social behavior. University of Chicago Press: Chicago.Lamprecht, J. 1978. The relationship between food competition and foraging group size in some larger carnivores: a hypothesis. Zeitschrift für Tierpsychologie **46**:337-343.

Lamprecht, J., 1981. The function of social hunting in larger terrestrial carnivores. Mammal Review **11**:169-179.

Lindsey, P. A., G. Balme, M. Becker, C. Begg, C. Bento, C. Bocchino, A. Dickman, R. W. Diggle, H. Eves, and P. Henschel. 2013. The bushmeat trade in African savannas: Impacts, drivers, and possible solutions. Biological Conservation **160**:80-96.

Lindsey, P. A., S. S. Romanach, C. J. Tambling, K. Chartier, and R. Groom. 2011. Ecological and financial impacts of illegal bushmeat trade in Zimbabwe. Oryx **45**:96-111.

Loveridge, A., L. Sousa, J. Seymour-Smith, J. Hunt, P. Coals, H. O'Donnell, P. Lindsey, R. Mandisodza-Chikerema, and D. Macdonald. 2020. Evaluating the spatial intensity and demographic impacts of wire-snare bush-meat poaching on large carnivores. Biological Conservation **244**:108504.

Macdonald, D. W. 1983. The ecology of carnivore social behaviour. Nature **301**:379-384.

MacNulty, D.R., Tallian, A., Stahler, D.R. and Smith, D.W., 2014. Influence of group size on the success of wolves hunting bison. PloS one **9**:e112884.

McNutt, J.W, and Gusset, M. 2012. Declining body size in an endangered large mammal, *Biological Journal of the Linnean Society* **105**: 8–12.

Major, P.F., 1978. Predator-prey interactions in two schooling fishes, *Caranx ignobilis* and *Stolephorus purpureus*. Animal Behaviour **26**:760-777.

Merkle, E. C., and Y. Rosseel. 2018. blavaan: Bayesian structural equation models via parameter expansion. Journal of statistical software **85**:1-30.

Mills, G.G.L., 1990. Kalahari Hyenas: Comparative Behavioral Ecology of Two Species. Unwin Hyemn Press, London.

Mills, M. G., and M. L. Gorman. 1997. Factors affecting the density and distribution of wild dogs in the Kruger National Park. Conservation biology **11**:1397-1406.

Montevecchi, W.A., 1979. Predator-prey interactions between ravens and kittiwakes. Zeitschrift für Tierpsychologie **49**:136-141.

Mweetwa, T., D. Christianson, M. Becker, S. Creel, E. Rosenblatt, J. Merkle, E. Droge, H. Mwape, J. M'soka, T. Simpamba, and J. Masonde. 2018. Quantifying demographic recovery in lions during a three-year moratorium on trophy hunting. PloS one **13(5): e0197030**.

Packer, C. and Ruttan, L., 1988. The evolution of cooperative hunting. The American Naturalist **132**:159-198.

Pitman, R.L., Ballance, L.T., Mesnick, S.I. and Chivers, S.J. (2001), Killer whalre predation on sperm whales: observations and implications. Marine Mammal Science **17**: 494-507.

Qasem, L., A. Cardew, A. Wilson, I. Griffiths, L. G. Halsey, E. L. Shepard, A. C. Gleiss, and R. Wilson. 2012. Tri-axial dynamic acceleration as a proxy for animal energy expenditure; should we be summing values or calculating the vector? PloS one **7**:e31187.

Redcliffe, J., S. Creel, B. Goodheart, J. Reyes de Merkle, S. S. Matsushima, M. Mungolo, R. Kabwe, E. Kaseketi, W. Donald, and A. Kaluka. 2024. Using triaxial accelerometry to detect hunts and kills by African wild dogs. Frontiers in Ecology and Evolution **12**:1465094.

Reyes de Merkle, J., S. Creel, M. S. Becker, B. Goodheart, T. Mweetwa, H. Mwape, E. Dröge, and T. Simpamba. 2024. Long-term data reveal fitness costs of anthropogenic prey depletion for a subordinate competitor, the African wild dog (Lycaon pictus). Ecology and Evolution **14**:e11402.

Ripple, W. J., K. Abernethy, M. G. Betts, G. Chapron, R. Dirzo, M. Galetti, T. Levi, P. A. Lindsey, D. W. Macdonald, and B. Machovina. 2016. Bushmeat hunting and extinction risk to the world's mammals. Royal Society Open Science **3**:160498.

Ripple, W. J., J. A. Estes, R. L. Beschta, C. C. Wilmers, E. G. Ritchie, M. Hebblewhite, J. Berger, B. Elmhagen, M. Letnic, and M. P. Nelson. 2014. Status and ecological effects of the world's largest carnivores. Science **343**:1241484.

Ripple, W. J., T. M. Newsome, C. Wolf, R. Dirzo, K. T. Everatt, M. Galetti, M. W. Hayward, G. I. Kerley, T. Levi, and P. A. Lindsey. 2015. Collapse of the world's largest herbivores. Science advances **1**:e1400103.

Rogan, M.S, P.A. Lindsey, C.J. Tambling, K.A. Golabek, M.J. Chase, K. Collins, J.W. McNutt. 2017. Illegal bushmeat hunters compete with predators and threaten wild herbivore populations in a global tourism hotspot. Biological Conservation **210**: 233-242.

Rood, J. P. 1986. Ecology and social evolution in the mongooses. Pages 131-152. *in* D. I. Rubenstein and R. Wrangham, W., editors. Ecological aspects of social evolution. Princeton Univeristy Press, Princeton, N.J.

Rosenblatt, E., S. Creel, M. S. Becker, J. Merkle, H. Mwape, P. Schuette, and T. Simpamba. 2016. Effects of a protection gradient on carnivore density and survival: an example with leopards in the Luangwa valley, Zambia. Ecology and Evolution **6**:3772-3785.

Rosenblatt, E., S. Creel, P. Schuette, M. S. Becker, D. Christianson, E. Dröge, T. Mweetwa, H. Mwape, J. Merkle, J. M'soka, J. Masonde, and T. Simpamba. 2019. Do protection gradients explain patterns in herbivore densities? An example with ungulates in Zambia's Luangwa Valley. PLOS ONE **14**:e0224438.

Schaller, G. B. 1972. The Serengeti lion: a study of predator-prey relations. University of Chicago Press, Chicago.

Scheel, D., and C. Packer. 1991. Group hunting behaviour of lions: a search for cooperation. Animal Behaviour **41**:697-709.

Schuette, P., M. Namukonde, M. Becker, F. Watson, S. Creel, C. Chifunte, W. Matandiko, P. Millhouse, E. Rosenblatt, and C. Sanguinetti. 2018. Boots on the ground: in defense of low-tech, inexpensive, and robust survey methods for Africa's under-funded protected areas. Biological Conservation.

Shepard, E. L., R. P. Wilson, L. G. Halsey, F. Quintana, A. G. Laich, A. C. Gleiss, N. Liebsch, A. E. Myers, and B. Norman. 2008. Derivation of body motion via appropriate smoothing of acceleration data. Aquatic Biology **4**:235-241.

Stander, P. E. 1992. Cooperative hunting in lions: the role of the individual. Behavioral Ecology and Sociobiology **29**:445-454.

Stander, P.E. and Albon, S.D., 1993, November. Hunting success of lions in a semi-arid environment. Symposia of the Zoological Society of *London* **65**: 127-143).

Swanson, A., T. Caro, H. DaviesGÇÉMostert, M. G. Mills, D. W. Macdonald, M. Borner, E. Masenga, and C. Packer. 2014. Cheetahs and wild dogs show contrasting patterns of suppression by lions. Journal of Animal Ecology **83**:1418-1427.

Vanak, A.T., Fortin, D., Thaker, M., Ogden, M., Owen, C., Greatwood, S. and Slotow, R., 2013. Moving to stay in place: behavioral mechanisms for coexistence of African large carnivores. Ecology **94**: 2619-2631.

van Vliet, N., D. Cornelis, H. Beck, P. Lindsey, R. Nasi, S. LeBel, J. Moreno, J. Fragoso, and F. Jori. 2016. Meat from the wild: extractive uses of wildlife and alternatives for sustainability. Pages 225-265 Current Trends in Wildlife Research. Springer.

Vinks, M. A., S. Creel, P. Schuette, M. S. Becker, E. Rosenblatt, C. Sanguinetti, K. Banda, B. Goodheart, K. Young-Overton, and X. Stevens. 2021. Response of lion demography and dynamics to the loss of preferred larger prey. Ecological Applications **31**:e02298.

Vinks, M. A., S. Creel, P. Schuette, E. Rosenblatt, W. Matandiko, C. Sanguinetti, K. Banda, B. Goodheart, M. Becker, and C. Chifunte. 2020. Testing the effects of anthropogenic pressures on a diverse African herbivore community. Ecosphere **11**:e03067.

Watson, F., M. S. Becker, R. McRobb, and B. Kanyembo. 2013. Spatial patterns of wire-snare poaching: Implications for community conservation in buffer zones around National Parks. Biological Conservation **168**:1-9.

Watson, F. G., M. S. Becker, J. Milanzi, and M. Nyirenda. 2015. Human encroachment into protected area networks in Zambia: Implications for large carnivore conservation. Regional Environmental Change **15**:415-429.

Wells, M.C. and Bekoff, M., 1982. Predation by wild coyotes: behavioral and ecological analyses. Journal of Mammalogy **63**: 118-127.

Wilson, R. P., E. L. C. Shepard, and N. Liebsch. 2008. Prying into the intimate details of animal lives: use of a daily diary on animals. Endangered Species Research **4**:123-137.

Woodroffe, R., P. Lindsey, S. Romañach, A. Stein, and S. M. K. ole Ranah. 2005. Livestock predation by endangered African wild dogs (Lycaon pictus) in northern Kenya. Biological Conservation **124**:225-234.

Woodroffe, R., P. A. Lindsey, S. S. Romanach, and S. M. o. Ranah. 2007. African wild dogs (Lycaon pictus) can subsist on small prey: implications for conservation. Journal of Mammalogy **88**:181-193.

Yip, E.C., Powers, K.S. and Avilés, L., 2008. Cooperative capture of large prey solves scaling challenge faced by spider societies. Proceedings of the National Academy of Sciences **105**: 11818-11822.

Figure 1. Among cooperatively hunting species, the size of hunting groups can affect all stages of the predation sequence (Figs. 2 & 3), but one of the most common benefits of cooperation is an increase in the mass of prey that can be killed as group size increases. (A) Wild dogs initiate a hunt with a synchronized, shoulder-to-shoulder walk toward prey with heads lowered and ears flattened, signaling the intention to attack. (B) A pack collectively subdues a puku that they have just captured. Three individuals at the back are redirecting to the pursuit of a second puku from the same herd; such behavior causes the likelihood of multiple kills from a single hunt to increase with an increasing number of hunters. (C) A pack that has used simultaneous attacks from multiple angles to separate a wildebeest calf from its herd. Once captured, some individuals restrain the prey while others attempt to kill it; injuries from unrestrained large prey are common. (D) Lion prides with fewer than 5 hunters (particularly males) rarely kill African buffalo (*Syncerus caffer*), which are common prey for large prides. Here, a male uses it's mass to restrain an adult female buffalo while a lioness asphyxiates it. (Photos: Ed Selfe, Matt Becker, Daan Smit, Egil Dröge).

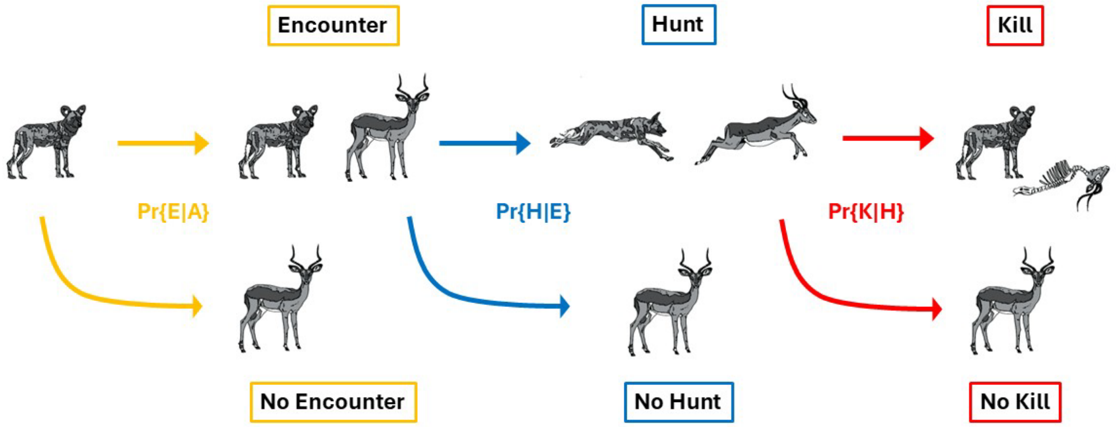


Figure 2. Prey selection by active hunters is determined by a sequence that begins with a decision on where to search, which affects the probability of encountering each type of prey, relative to its abundance. Next, a decision whether or not to hunt prey that have been encountered can reinforce or offset non-random patterns of encounter. Finally, hunting success, or the probability that a hunt will end with a kill, often differs among prey types. See Figure 3 for an example with data.

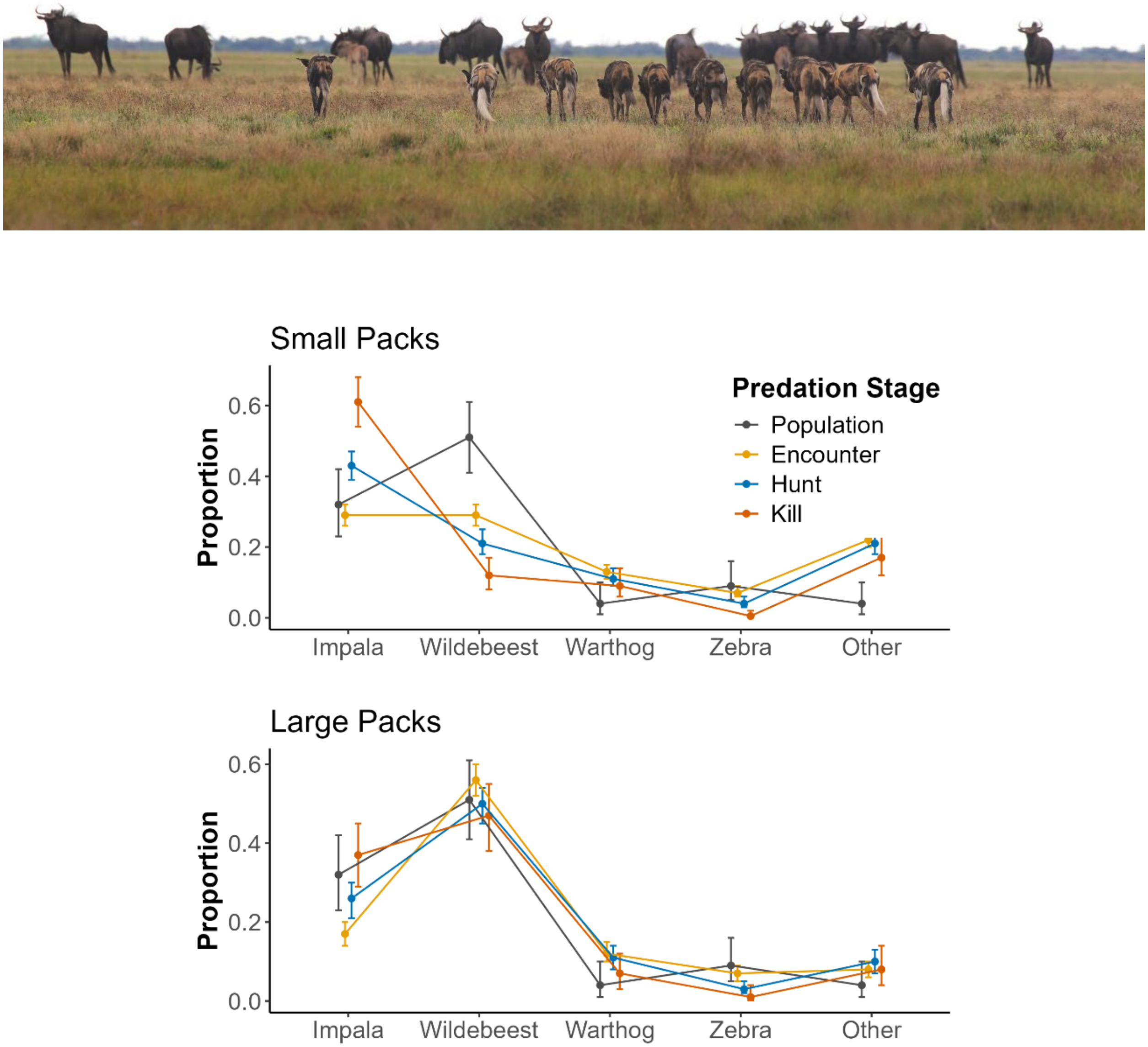


Figure 3 (*Upper*) A pack of 11 wild dogs initiates a hunt of wildebeest with an unconcealed approach. Their behavior suggests that they have selected two calves as focal points of a pursuit that will begin once the herd runs. (*Lower*) Patterns of prey selection by African wild dogs in Tanzania's Selous Game Reserve were affected by pack size at every stage of the predation sequence. Packs smaller than the median (< 9 adult hunters) killed impala more than three times as often as they killed wildebeest, and small packs encountered, hunted and killed impala significantly more often than large packs (≥ 9 adults) did. Wildebeest were the most common prey for large packs, and large packs encountered, hunted and killed wildebeest significantly more often than small packs did. Data from Table 5.2 in Creel & Creel (2002).

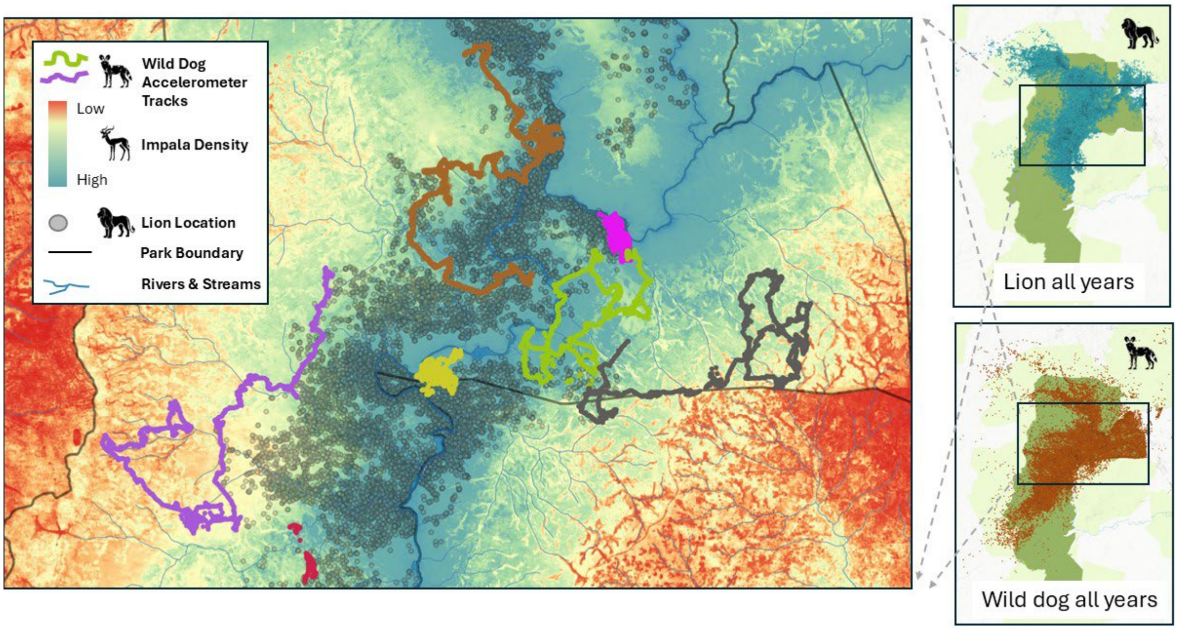


Figure 4. An example from Kafue National Park of dead-reckoned tracks of wild dog packs fitted with accelerometers in relation to prey density (shown here for impala), lion use, and protection (within National Parks or less-protected Game Management Areas). Lion use is shown here by transparent points (rather than a utilization distribution, shown in supplemental Fig. S2), so that the relationship to prey density can better be seen. Lions consistently use areas with high prey density, so that wild dogs face a trade-off between access to food and avoidance of dominant competitors. Here, we show lion locations from the dry season of 2022 (*N* = 27,683: in our analysis, accelerometer data were related to lion use during the season in which the accelerometer was deployed, and we restricted analysis to areas where all lion prides were GPS-collared in that season, discarding 70,766 observations (from a total of 242,126) in areas where we could not quantify lion use. Inset figures show lion and wild dog locations aggregated from 2013 to 2025: monitored groups were contiguous within the study area and it is unlikely that any lion groups that we did not monitor used areas included in the analysis.

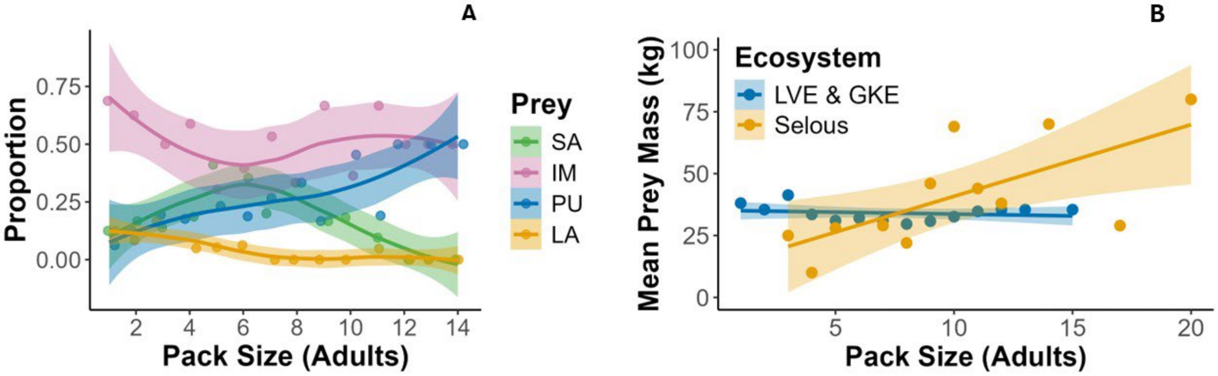


Figure 5. (*A*) The effect of pack size on prey selection by African wild dogs in Zambia's Luangwa Valley and Greater Kafue Ecosystems. Contrary to results from prior research, large packs rarely killed large prey (*e.g.*, wildebeest or hartebeest): the proportion of the diet comprised of large antelopes (LA) showed no tendency to increase as pack size increased, and large prey were a small fraction of the diet for packs of all sizes. Rather than increasing predation on large prey, larger packs reduced predation onsmall (*e.g.*, duiker and grysbok) antelopes (SA) and slightly increased predation on intermediate-sized puku (PU). Intermediate-sized impala (IM) were a large proportion of the diet for packs of all sizes. (B) Under current conditions in Luangwa and Kafue, mean prey mass did not change as pack size increased, while it increased significantly in Selous (tripling over the observed range of pack sizes). Data for Selous from Creel & Creel (1995).

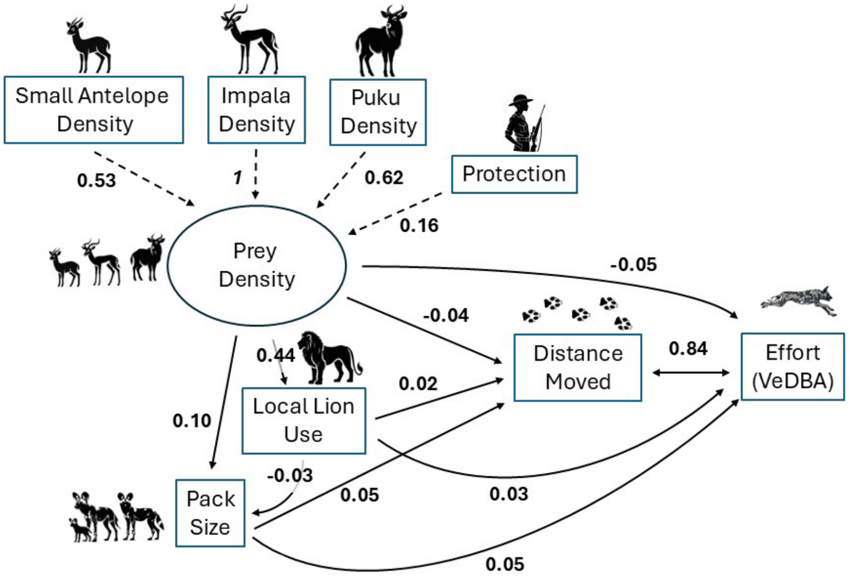


Figure 6. A structural equation model testing the effects of prey density and local lion use on pack size and the distance moved and effort expended by African wild dogs in Zambia's Luangwa Valley and Greater Kafue Ecosystems. Movement and effort increased significantly in areas where prey were depleted, and where local lion density was higher. Contrary to expectation from prior research, movement and hunting effort both increased significantly with increasing pack size. *Rectangle*: manifest variable. *Ellipse*: latent variable. *Solid arrow*: effect on manifest variable. *Dashed arrow*: effect on latent variable. *Two-headed arrow*: correlation between exogenous variables.

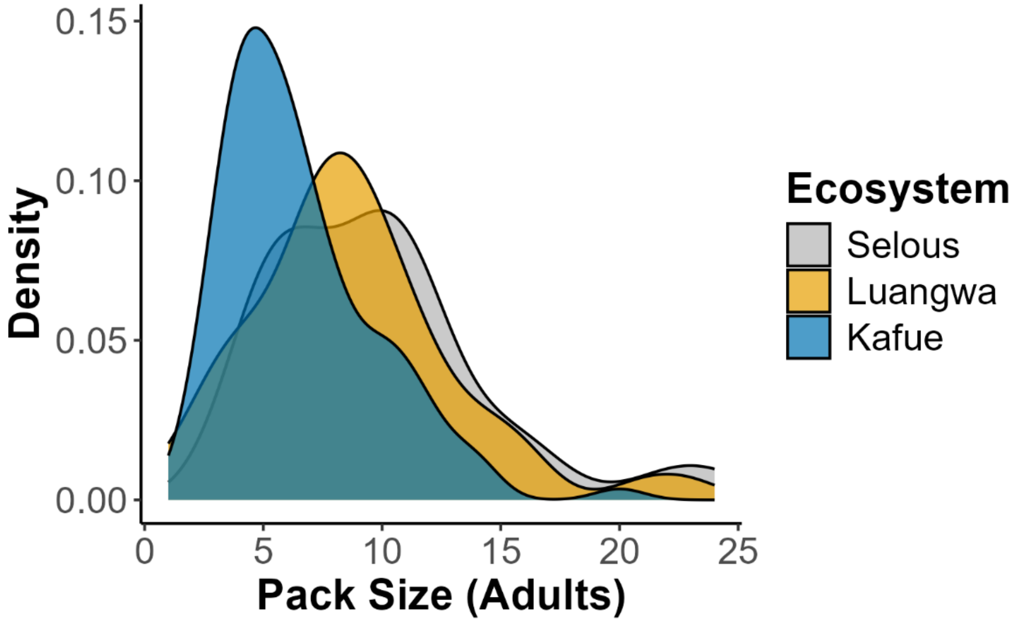
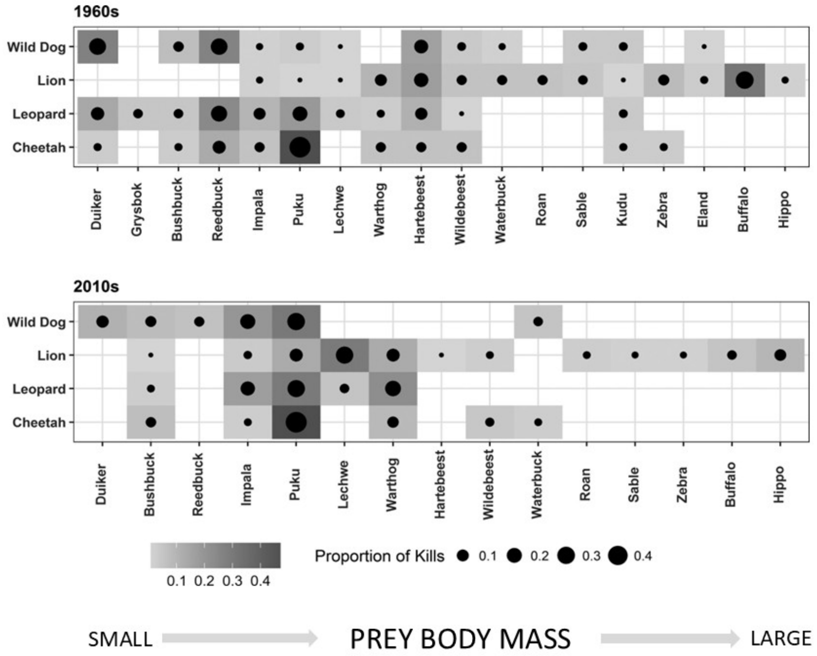
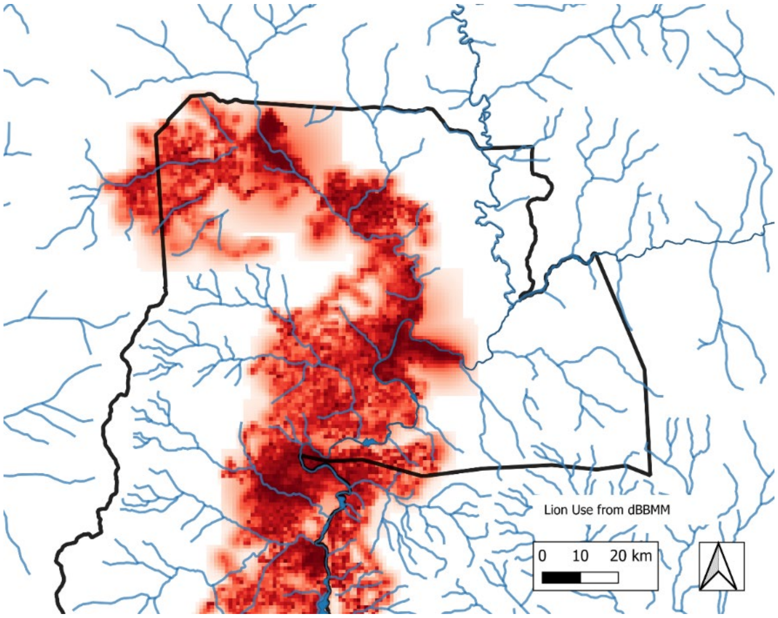


Figure 7. Frequency distributions for wild dog pack size in Luangwa, Kafue and Selous. Small packs were more common in the prey-depleted Kafue ecosystem, but an appreciable number of packs of nine or more adults (specialists on large antelopes in Selous) were found in all ecosystems.



Supplemental Figure S1. A comparison of the diets of large carnivores in the Kafue ecosystem during the 1960s and fifty years later in the 2010s revealed that large antelopes such as hartebeest, wildebeest, waterbuck, sable, kudu, roan and zebra have become significantly less common in the diets of both wild dogs and lions. Data from Creel et al. (2018).



Supplemental Figure S2. An example of variation in space use by lions, as quantified by a utilization distribution from a dynamic Brownian bridge movement model (dBBMM) fit to locations from Iridium-GPS collars. For analysis of effects on wild dog movement and energy expenditure, we determined a utilization distribution for each pride in each season, and summed them to determine population-level patterns of space use. We restricted our analysis to areas in which all prides were collared, with equal intensity of sampling for each pride. For prides with more than one radiocollar, these seasonal utilization distributions were always similar for both individuals, so we randomly selected one. See Goodheart et al. (2022, 2024) for more detail.

Supplemental Table S1. Correlations between pairs of variables in the original data were closely comparable to correlations from the structural equation model, indicating that the model was not missing important variables or paths Because variables were standardized, regression and correlation coefficients are the same.

Variable Pair	***Correlation within Data***	***Correlation from SEM***
Exogenous - Exogenous		
Distance Moved - Effort	0.856	0.838
Exogenous-Endogenous		
Effort – Lion Use	0.022	0.029
Effort – Pack Size	0.049	0.052
Distance Moved – Lion Use	0.000	0.019
Distance Moved– Pack Size	0.047	0.050
Endogenous-Endogenous		
Lion Use – Pack Size	0.011	-0.027

Supplementary Table S2. Direct, mediated and total (direct + mediated) relationships between prey density, lion use, protection and pack size on the distance moved and effort expended in hunting by African wild dogs, from the structural equation model of Figure 6.

Latent Variables:	Estimate	SD	Lower 95 CL	Upper 95 CI	R-hat
prey density=~					
impala density	1.000	---	---	---	---
small antelope density	0.525	0.004	0.516	0.533	0.999
puku density	0.624	0.004	0.617	0.632	0.999
protection	0.155	0.005	0.145	0.166	1.000
Direct Effects:					
lion use ~					
prey density	0.435	0.004	0.427	0.444	0.999
pack size ~					
prey density	0.098	0.005	0.087	0.109	1.000
lion use	-0.027	0.006	-0.038	-0.016	0.999
distance moved ~					
prey density	-0.045	0.006	-0.056	-0.034	1.001
lion use	0.019	0.006	0.008	0.030	1.002
pack size	0.049	0.005	0.039	0.059	0.999
effort (VeDBA) ~					
prey density	-0.053	0.006	-0.064	-0.043	1.001
lion use	0.030	0.006	0.019	0.041	1.001
pack size	0.055	0.005	0.045	0.065	1.000
Covariances:					
distance moved ~~					
effort (VeDBA)	0.838	0.007	0.825	0.851	0.999
Mediated (Indirect) Effects:					
small antelope-prey-lion	0.229	0.003	0.223	0.234	
puku-prey-lion	0.272	0.003	0.266	0.278	
impala-prey-lion	0.435	0.004	0.427	0.444	
protection-prey-lion	0.068	0.002	0.063	0.072	
small antelope – prey-pack size	0.051	0.003	0.046	0.057	
puku-prey-pack size	0.061	0.003	0.054	0.068	
impala-prey-pack size	0.098	0.005	0.087	0.108	

protection -prey- pack size	0.015	0.001	0.013	0.017
prey-lion-pack size	-0.012	0.002	-0.016	-0.007
prey-lion-distance moved	0.008	0.002	0.003	0.013
prey-lion-pack size- distance moved	-0.001	0.000	-0.000	0.000
prey-pack size- distance moved	0.005	0.001	0.004	0.006
prey-lion-effort	0.013	0.002	0.008	0.018
prey-lion-pack size- effort	-0.001	0.000	-0.000	0.000
prey-pack size- effort	0.005	0.001	0.004	0.006
Total (Direct + Indirect) Effects:				
protection – pack size	0.013	0.001	0.012	0.015
protection – lion use	0.068	0.002	0.063	0.072
prey – pack size	0.086	0.005	0.077	0.096
prey – distance moved	-0.032	0.005	-0.043	-0.022
prey – effort	-0.035	0.005	-0.045	-0.025