



Prey depletion, interspecific competition, and the energetics of hunting in endangered African wild dogs, *Lycaon pictus*

Scott Creel^{a,b,1} , James Redcliffe^c, Ben Goodheart^{a,b}, Johnathan Reyes de Merkle^{a,b}, Henry Mwape^b, Stephanie Matsushima^b , Chase Dart^b, Kachama Banda^b, Bridget Mayani^b, Johane Njobvu^b, Reuben Kabungo^b, Michelo Mungolo^b, Ruth Kabwe^{b,d}, Emmanuel Kaseketi^b, Will Donald^d, Adrian Kaluka^e, Clive Chifunte^f, Howard Maimbo^{b,f,g} , Luzy Plankenhorn^{b,g}, David Christianson^{b,g}, Matthew S. Becker^{a,b}, and Rory P. Wilson^c

Affiliations are included on p. 10.

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Large herbivores are in decline in much of the world, including sub-Saharan Africa, and true apex carnivores like the lion (*Panthera leo*) decline in parallel with their prey. As a consequence, competitively subordinate carnivores like the African wild dog (*Lycaon pictus*) are simultaneously experiencing a costly reduction in resources and a beneficial reduction in dominant competitors. The net effect is not intuitively obvious, but wild dogs' density, survival, and reproduction are all low in areas that are strongly affected by prey depletion. To assess whether these correlations are causal, we tested the hypothesized mechanism, using data from 13 wild dog packs in two ecosystems to relate the energetic costs and benefits of hunting to variation in prey density, while controlling for the effects of local lion density, pack size, the number of dependent pups, and the level of protection. All of these variables affected the energetic costs and benefits of hunting. In areas with low prey density, the magnitude of movements and vectorial dynamic body acceleration (a measure of energy expenditure) both increased, the mass of killed prey decreased, and the number of kills per day did not change detectably. Programs to reduce or reverse the decline of large herbivore populations should be an effective means of improving the status of endangered subordinate competitors like the wild dog, and should be a high priority. Our results demonstrate the utility of research that integrates data from biomonitoring with direct, long-term observation of endangered species, their competitors, and their resources.

conservation | competition | prey depletion | energetics | movement

Interspecific competition affects the distribution and abundance of most species (1, 2) and the limiting effects of competition within guilds of large carnivores are widely recognized (3–8). Within the African large carnivore guild, wild dogs (*Lycaon pictus*) are a highly endangered subordinate competitor with fewer than 1,500 breeding adults remaining in the wild (9). Although wild dogs are affected by many of the same processes that limit other large carnivores (9, 10), they are unusual because the highest densities that they ever attain are much lower than densities that are commonly attained by their dominant competitors (lions, *Panthera leo*, and spotted hyenas, *Crocuta crocuta*) (11). The densities of apex carnivores like the lion and spotted hyena show a strong positive correlation with the density of large herbivores, both within and between ecosystems (12–15). In contrast, wild dog density is usually low in areas with high prey density, due to strong interference competition from lions and spotted hyenas: Where dominant competitors are common, wild dogs often lose their kills to spotted hyenas and are often killed by lions (11, 16–27). More than 25 years ago, Creel and Creel (10) concluded that “wild dogs are rarely limited by prey availability.... the simple observation that spotted hyenas attain much higher densities, while relying on similar prey, makes this explanation unlikely... ecosystems with high prey densities do not maintain higher wild dog densities.” The most recent IUCN Red List assessment reiterates that dominant competitors “keep African Wild Dog numbers below the level that their prey base could support” (9).

The inference that wild dogs are not normally limited by prey availability had broad support under the ecological conditions of the past, but large herbivores are declining across much of sub-Saharan Africa (28–32). Declining populations of large herbivores are contributing to declines of apex carnivores like the lion (33–35), but for competitively subordinate carnivores like the wild dog, the expected effect of a simultaneous decrease in resources (prey) and dominant competitors (lions) is not obvious. Recent analyses show that when prey density falls below a tipping point, the costs of prey depletion exceed the benefits of competitive release for wild dogs: In prey-depleted areas, their survival, reproduction, and population density are all low, despite low densities of dominant competitors

Significance

Declines of endangered species are often correlated with simultaneous changes in several environmental conditions. Biomonitoring technologies can help to identify which correlations are causal, by testing the mechanism hypothesized to link a specific environmental change to population decline. The survival, reproduction, and population density of endangered African wild dogs are all low in areas where prey have been depleted by bushmeat poaching. Analysis coupling direct observation with data from high frequency accelerometers and magnetometers shows that the energetic costs of hunting increase and the benefits decrease when wild dogs hunt in prey-depleted areas. Prey depletion due to bushmeat poaching is widespread and likely to have similar effects on many carnivore populations.

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¹To whom correspondence may be addressed. Email: screel@montana.edu.

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(24–26, 36–39). Logically, resources must limit competitively subordinate carnivores at some point, because any predator's density must go to zero as prey density goes to zero: These recent results suggest that the binding constraint for wild dogs is now shifting from the density of dominant competitors to the density of prey, at least in some ecosystems. Because competition has strong effects on many species and resources of many types are being reduced by human activities, it is plausible to hypothesize that such fundamental changes may be common.

Inferences about the effect of prey depletion on wild dogs' density and demography would be strengthened by tests of a well-defined causal mechanism. Here, we tested the hypothesis that prey depletion alters the energetic costs and benefits of hunting. As would be expected from their invariably low density, wild dogs occupy large home ranges and make large daily movements (27, 40–46). They cooperatively hunt prey that are usually larger than themselves, using high-speed chases that typically exceed 500 m and occasionally cover several kilometers (27, 40, 45–50). Movement is one of the most energetically costly behaviors for most animals (51), and high-speed running is particularly costly for terrestrial mammals (52, 53), which makes the energetic costs of searching for prey over large areas and cursorial hunting substantial (18, 45, 49, 54). Wild dogs produce exceptionally large litters, so that the energetic costs of gestation and lactation are large relative to allometric expectation (55, 56). For all of these reasons, wild dogs maintain a tenuously positive energy budget (18, 57). Wild dogs expend ~3.09 MJ per hour of movement and hunting, obtain ~5.8 MJ per kilogram of food consumed (18, 58), and consume 2.0 to 2.5 Kg/individual/day (40). Thus, to offset the energetic cost of one extra hour of movement and hunting a wild dog would require 0.53 kg of food, which is 21.2 to 26.5% of typical daily intake (59). These observations motivate a hypothesis that the effects of prey depletion on wild dog demography and density (24, 25, 36, 37, 60) are mediated by changes to the landscape of energy (54, 61).

We tested this hypothesis by integrating data from high frequency triaxial accelerometers and magnetometers, GPS collars, direct behavioral observations assisted by VHF telemetry, and long-term monitoring of the densities and distributions of wild dogs, lions, and their prey. The data came from 13 packs in two ecosystems, in areas with a broad range of prey density, use by lions, and wild dog pack sizes and compositions. Recent advances in biologging are providing new tools to study behavior, movement, and energetics 62–65, and our results demonstrate the useful insights that can be gained by integrating these tools with direct behavioral observations and long-term ecological monitoring.

Methods

Study Sites, Wild Dog Populations, and Long-Term Monitoring. We collected data from two wild dog populations on study sites of ~8,000 km² in the Greater Kafue Ecosystem and ~7,000 km² in the Luangwa Valley Ecosystem that we have intensively monitored since 2013. Detailed descriptions of the study sites, their large herbivore populations, the density and demography of wild dogs on these sites, and our methods for monitoring have been published previously (25, 36, 59, 60, 66–68). Briefly, both sites are a mosaic of woodland and grassland, and both have pronounced annual wet and dry seasons. Both sites are bisected by a major river and its tributaries, and the density of large herbivores is consistently highest near this permanent water. This pattern includes the primary prey of African wild dogs, which are puku (*Kobus vardonii*) and impala (*Aepyceros melampus*) in both ecosystems (Results). The densities of wild dogs, their prey, and their dominant competitors the lion (*Panthera leo*) and spotted hyena (*Crocuta crocuta*) are all low in Kafue because of heavy poaching pressure (25, 37–39, 66, 68, 69). The Luangwa is better protected, and the densities of wild dogs (Kafue:

0.7 individuals/100 km², Luangwa: 4.0 individuals/100 km²), their prey, and their competitors are all higher in Luangwa than in Kafue (26, 36, 39, 67, 70–76). There is pronounced spatial variation within our Luangwa site in wild dog density, survival, and reproduction, which are all higher in well-protected areas with higher prey density, despite higher lion density in those areas (26, 36). Wild dog density, survival, and reproduction in Kafue are all similar to the least-protected portion of the Luangwa site in the Lower Lupande Game Management Area (GMA) (25, 26). GMAs are buffer zones with less protection and lower prey density than National Parks, in both ecosystems.

Accelerometer Data. We monitored all resident wild dog packs within these areas using a combination of VHF and satellite-GPS collars (MOD-335-3 and TGW-4277-4, Telonics, Mesa, AZ) on 1 to 2 adults in each pack to allow frequent direct observation. We radiocollared wild dogs after intramuscular injection of ~1.2 mg medetomidine and ~20 mg tiletamine-zolazepam, reversing the medetomidine by intramuscular injection of atipamezole after 45 min to 1 h. Anesthetics were injected by darting with an air-powered DanInject rifle, and all procedures were performed by an experienced and Zambian-registered veterinarian, in collaboration with the Zambia Department of National Parks and Wildlife, with MSU IACUC approval (2020–123). We confirmed that radiocollars did not detectably affect survival rates (36). Individual wild dogs were identified by variation in their coat patterns using a photographic ID database. Their sex was recorded by external genitalia. Most individuals were of known age, but age classes (pup, yearling, and adult) were also distinguished by size. We fitted 16 wild dogs in 13 packs with Daily Diary (DD) tags (65) attached to Iridium-GPS radiocollars (TGW-4277-4, Telonics, Mesa, AZ) 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. The DD system used two 750 mAh batteries with data written to a 16 GB micro-SD card, sealed in epoxy resin within a low-profile aluminum housing, with a total weight of 95 grams (Fig. 1A). Collars dropped off using a programmable release mechanism (Telonics CR-7B) after 31 d and were collected. Because wild dog packs move and hunt in a highly cohesive manner (40, 45, 48), we tagged a single individual in each sampled pack. We tagged packs that used areas spanning the highest and lowest prey densities within the two ecosystems (see *Prey Biomass Distributions* and *Lion Utilization Distributions*, below). Because lions preferentially use areas with high prey density (38, 59), these packs also moved across the full gradient of local lion density in the two ecosystems. The sampled packs also provided a broad and representative range of pack sizes and compositions [\bar{X} = 13.7 individuals (range: 5 to 25), \bar{X} = 6.4 adults (range: 1 to 11), \bar{X} = 2.3 yearlings (range: 0 to 8), \bar{X} = 5.1 pups (range: 0 to 13)]. We deployed DD collars in 2022 and 2023. Nine DD collars were deployed in Luangwa and seven in Kafue. In three packs, we collared two different individuals at different times, after a change in pack size and composition: twice in different years and once after an interval of 4 mo.

To measure the effort expended by wild dogs when hunting, we calculated vectorial dynamic body acceleration (VeDBA) from the 40-Hz accelerometer data as:

$$\text{VeDBA} = \sqrt{(A_{x_r} - A_{x_s})^2 + (A_{y_r} - A_{y_s})^2 + (A_{z_r} - A_{z_s})^2}, \quad [1]$$

where A is acceleration in orthogonal x , y , and z axis (Fig. 1), and r and s subscripts identify raw or smoothed values with a smoothing window of 2 s (77, 78). We then determined the running mean over 2.5 s of the VeDBA values defined by Eq. 1, to improve the signal-to-noise ratio (hereafter, VeDBA).

We also used these data to identify hunting efforts and kills (79). Briefly, the frequency distribution for VeDBA was highly bimodal for every individual, with most of the higher mode attributable to trotting, running and sprinting, each of which produce a distinct frequency and amplitude pattern in the triaxial acceleration data (Fig. 1B). Using DDMT software developed by the Swansea Laboratory for Animal Movement for analysis of data from DD tags (<http://wild-bytetechnologies.com/manual.pdf>), we identified a hunting effort when VeDBA was greater than 0.9 g. We selected 0.9 g because it consistently fell within the nadir between the two modes of the frequency distribution just described. We merged such events if they occurred within 10 s of each other. Of the identified events, we considered those with VeDBA values >0.9 g for >38 s to be hunting efforts. To identify kills, we examined the data following each identified hunt, looking for patterns that indicated feeding; we used accelerometer data (a

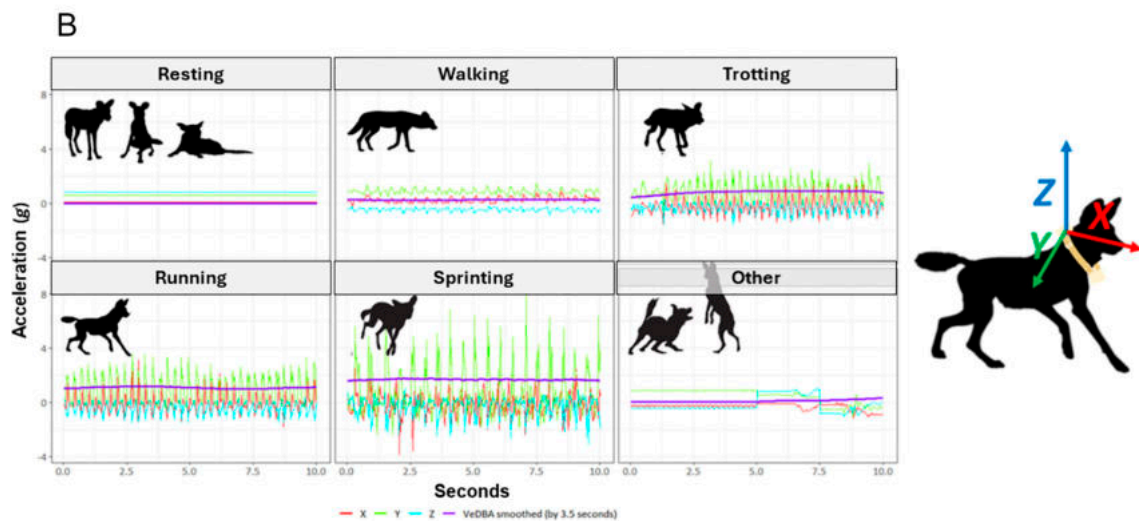


Fig. 1. (A) Daily diary tags with batteries and SD cards were deployed in a small, low-profile aluminum and epoxy housing, firmly attached to Iridium-GPS collars using hardware from the manufacturer (Telonics). The DD tag is at the top, above the black drop-off mechanism. (B) Continuous measurement of acceleration on three orthogonal axes at 40 Hz reveals distinct patterns of frequency and amplitude when wild dogs are in different behavioral states, allowing identification of time spent resting, walking, trotting/running, and sprinting, and by extension (*Methods*) hunts and kills.

change in pitch) showing that the head was lowered (to access a carcass) and that the animal was stationary but making brief, forceful movements with large components in the dorsoventral (heave) and longitudinal (surge) axes (to tug meat from a carcass or disarticulate it). Specifically, we identified kills as events within 375 s of a hunting effort, with periods >18 s with a pitch angle (mean over 5 s) $< -25^\circ$, and VeDBA (mean over 2 s) >0.02 g and VeDBA (mean over 5 s) <0.15 g, and acceleration in the heave axis (over 0.5 s) >0.7 g.

We developed these Boolean rules to identify hunting efforts and kills from DD data using first principles (79), by consideration of the patterns that would be produced by the hunting and feeding behavior of wild dogs (40, 43, 45, 46, 48, 80). We validated both rules by comparing the hunts and kills that they identified with data from direct observation of three DD-tagged packs in Kafue, using data from 47 d (79). Twenty-nine identified hunting efforts that overlapped with direct observation were all confirmed. Ten identified kills that overlapped with direct observation were all confirmed. One observed kill was not identified from the DD data because the collared animal did not feed until after the time window in our rules. Finally, we confirmed that temporal variation in VeDBA showed pronounced peaks around dawn and dusk that aligned well with observed periods of movement and hunting activity (Figs. 2 and 3).

We used GPS-corrected dead reckoning to determine each collared animal's location at 1-min intervals, and thus to determine the distance moved (81, 82). First, the GPS data were cleaned (81, 83) to remove GPS locations that were likely to have large errors, based on pronounced spikes in speed and turning angle. Second, the dead-reckoning algorithm constructed a path between GPS locations (at 30 min intervals) using normalized, calibrated magnetometer data to derive heading and VeDBA as a proxy for speed to derive distance (81, 83). We restricted dead-reckoned steps to time windows that were determined to be movements (with VeDBA >0.04 g and <1.5 g). To exclude acceleration traces that did not affect location (e.g., shaking, flinching, feeding, or social interactions) (84), we only included windows that met this movement criterion for >2 s. To account for drift in dead-reckoning we applied a compass offset and speed coefficient to each path segment so that its endpoint matched the next GPS location. This analysis was carried out in DDMT using raw 40 Hz acceleration data for all calculations, then aggregated and exported to provide a location and VeDBA value for each second. For the analyses presented here, these data were further aggregated to 1-min intervals using the aggregate function in R. Finally, we compared daily sums of 1-min movements to published estimates of daily movement using other (coarser-scaled) methods (*Results and Discussion*).

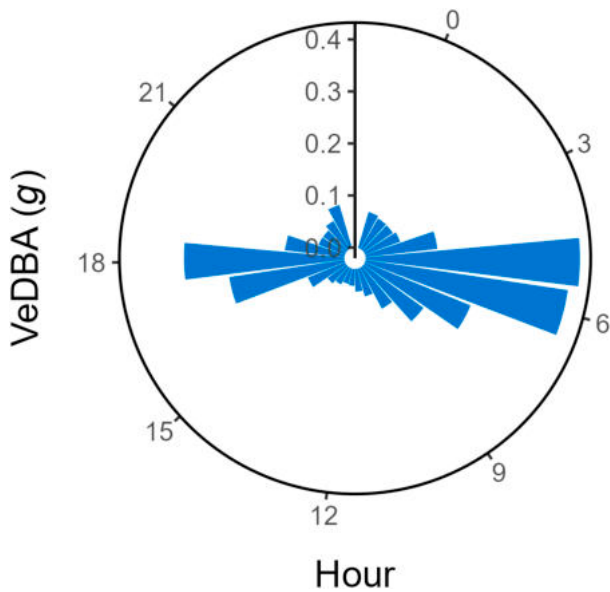


Fig. 2. VeDBA measured over 1 min showed a strongly crepuscular pattern, with pronounced peaks around dawn and dusk. Bars show mean VeDBA across all packs binned into 1-h intervals. This pattern aligns with temporal variation in hunting activity from direct observations, shown in Fig. 3.

These methods yielded estimates of hunting effort (VeDBA) and distance moved for 242,126 locations, and identified 1,428 hunting efforts and 423 kills. Prior to analysis, we restricted the data to 171,360 locations with data for all predictors: 70,766 observations fell in areas for which we could not accurately determine space use by lions (see *Lion Utilization Distributions* below).

Prey Biomass Distributions. We observed VHF-collared packs during hunting periods by following in a vehicle at distances of 20 to 400 m, recording 1,232 hunts and 740 kills between 2013 and 2023. As described above (*Accelerometer Data*), we used these observations to validate the Boolean rules that identified hunts and kills from accelerometer and magnetometer data. We also used these data to test for effects on the size of prey killed in areas with high and low prey density. To do this, we first had to identify the species that were relevant to estimation of prey density. As is typical of wild dogs (and other large carnivores), a small set of species formed most of the diet. Puku and impala comprised 63.3% of kills, and most (18.1%) of the remainder were five species of small antelopes (common duiker, *Sylvicapra grimmia*, grysbok, *Raphicerus sharpei*, oribi, *Ourebia ourebi*, bushbuck, *Tragelaphus scriptus*, and reedbuck, *Redunca arundinum*). 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 81.5% of observed kills (*Results*).

We mapped the expected density and distribution of these prey species by fitting Bayesian hierarchical distance sampling models to detections from repeated surveys of a fixed set of transects that sampled both study areas representatively with respect to vegetation type, and were stratified with respect to distance from water. We conducted surveys at the end of the wet season and the end of the dry season each year. Our methods for distance sampling have previously been described in detail, including demonstrations that the detection functions fit the data well (66, 67). Here, we analyzed detections of 2,967 herds of the seven prey species identified above (using herds as the sampling unit to satisfy the assumption that detections are independent), from 16 surveys over 1,982 km of transects that sampled an area of 1,089.6 km². The intensity of sampling was balanced between Kafue (986 km) and Luangwa (996 km), but higher population densities in Luangwa yielded more detections (2,124 vs. 843).

With these data, we fit Bayesian hierarchical distance sampling models (85) to estimate environmental effects on the density of each species in each ecosystem. We analyzed data for puku and impala separately, but pooled data for the five small antelopes because their distributions were broadly similar at the scale of wild dog movements and each species was too sparsely distributed to obtain independent estimates of effects on its density. R and JAGS code for

the hierarchical distance sampling model are provided at the GitHub link in the *Data, Materials, and Software Availability* statement (86). Briefly, we used a negative binomial model to describe herd size, modeled the probability of detection (of herds) as a hazard function of distance, 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, using java code provided at the GitHub link in the *Data, Materials, and Software Availability* statement (86). Distance to rivers and streams was calculated to 1 m from WWF HydroSHEDs data (rivers: order ≤ 5, streams: order = 6), percent tree cover came from Copernicus proportional land cover imagery at a resolution of 100 m, and the frequency of fires (the proportion of years between 2001 and 2023 in which an area burned) was determined from MODIS imagery with 500 m resolution. These scales were sufficient to detect effects on wild dogs’ movements and hunting (see *Results*: movement averaged 15.5 km/d and sometimes exceeded 1 km/min).

We selected the structure of the hierarchical distance sampling model by comparing its fit to models with alternative distributions and predictor variables (some recorded during the field observations and others extracted from the Google Earth Engine Data Catalog). We sought a simple model with predictors that were known to be relevant for these herbivores, with good explanatory power for all species in both ecosystems, using predictors from data that are readily available for all ecosystems. We combined species- and ecosystem-specific coefficients from the hierarchical distance sampling models with rasters for each predictor variable (again extracted from the Google Earth Engine Data Catalog) to map the expected density of each prey species. We converted these densities to biomass using estimates of mass from observed wild dog kills for each species, accounting for the sex and age-class killed (impala: 31.9 kg, puku: 37 kg, small antelopes: 18 kg). These maps of prey density or biomass (Fig. 4) are expectations based on

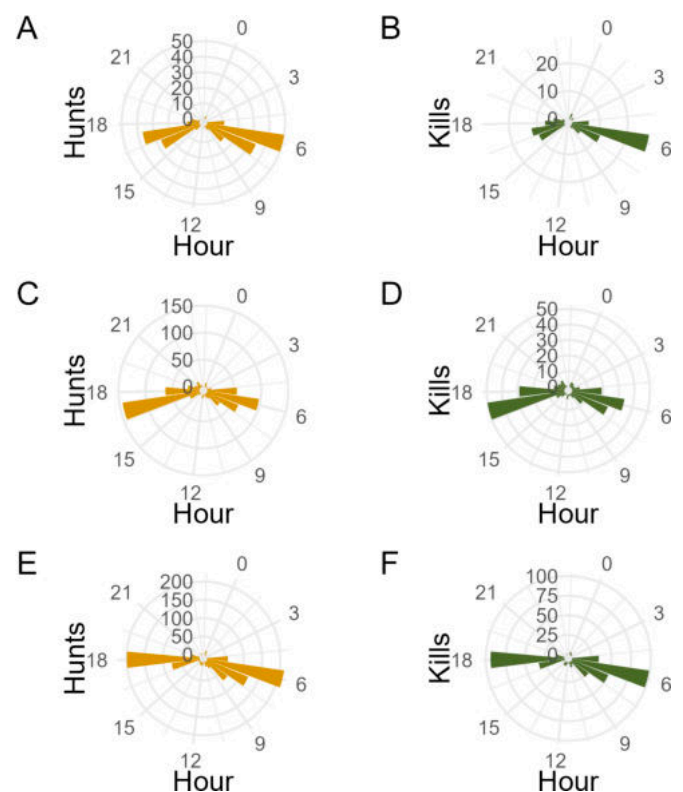


Fig. 3. Direct observations of VHF-collared wild dogs showed a strongly crepuscular pattern of hunting activity with pronounced peaks in both hunts (*Left*) and kills (*Right*) around dawn and dusk. (A and B) Greater Kafue Ecosystem. (C and D) Luangwa Valley Ecosystem. (E and F) Selous Game Reserve [from Creel and Creel (46)]. These patterns align with temporal variation in VeDBA shown in Fig. 2.

ecological conditions (vegetation, water, and fire), from data collected on transects that fell mainly in well-protected areas. Thus, they do not account for variation in prey density due to other causes, particularly protection from poaching. We addressed this issue by including the level of protection (National Park vs. Game Management Area) as a separate variable in subsequent analyses: Protection and prey density are considerably lower in GMAs (though there is variation within the two protection categories that this variable does not capture). As can be seen

in Fig. 4A, wild dog packs usually remained within National Park boundaries, sometimes moving directly along the boundary or turning sharply rather than entering the adjacent Game Management Area, but data from two DD tagged packs in the Luangwa site came mainly from the Lower Lupande GMA.

We deployed GPS-collars on five impala and four puku in Kafue, which provided eight locations per day for 1 y. We fit a 95% kernel utilization distribution for each animal using the adehabitatHR package, and used these distributions

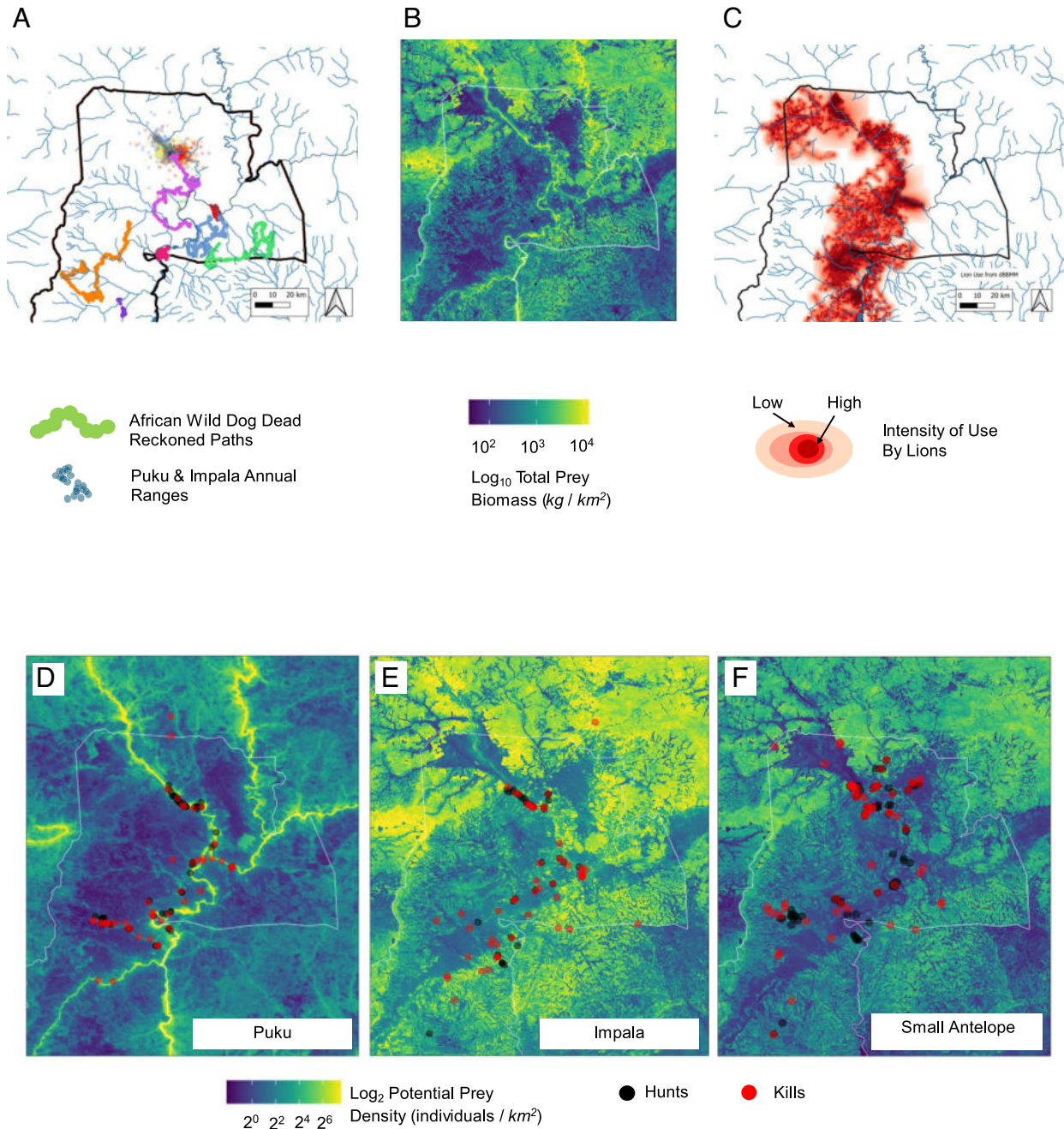


Fig. 4. Spatial variation in the expected biomass of common prey for African wild dogs in the Greater Kafue Ecosystem, and in the intensity of use by lions. (A) The movement paths (various colors) of wild dogs defined by dead reckoning of locations at 1-min intervals for 7 wild dog packs ($\bar{X} = 17$ d/pack). The annual home ranges (95% kernel UD) of 5 GPS-collared impala and 4 GPS-collared puku are also shown (various colors), showing that individual movements by prey over a year were small relative to movement by wild dogs over several days. Movements also show that wild dogs sometimes turned sharply or moved directly along the boundary of the National Park (black line) rather than entering the adjacent Game Management Area. (B) The combined biomass of puku, impala, and five species of less common small antelope (common duiker, bushbuck reedbuck, grysbok, oribi). These species comprise >80% of wild dogs' diet in the Kafue and Luangwa ecosystems and are listed above in decreasing order of importance. (C) Spatial variation in the intensity of use by lions, restricted to an area in which all lion prides were GPS collared. Lion use is shown for Kafue in 2022 but was determined separately for each year (and ecosystem). (D–F) Spatial variation in the densities of puku, impala, and small antelope, with the locations of directly observed unsuccessful hunts (black) and kills (red) of each species superimposed. The distributions of prey biomass, hunts, and kills coherently show that puku are concentrated near permanent rivers, impala are less concentrated, and small antelope are less concentrated still, at much lower maximum local densities.

simply to compare the scale of movement by individual prey relative to movement by individual wild dogs (Fig. 4A).

Lion Utilization Distributions. For each ecosystem in each year, we quantified spatial variation in the intensity of use by lions by fitting a dynamic Brownian bridge movement model to the locations of GPS-collared lions, using the move package in R (87). Using four locations per day for one lion from each pride, we fit dBMMs with a window of 35 locations and a margin of seven locations [following guidance from Kranstauber et al. (87)], to create a raster with 1 km² resolution from the resulting utilization distribution (59). For each site-year combination, we restricted this analysis to the area within which all resident lion prides were collared, to avoid low apparent use that was an artifact of inadequate sampling. Within this area, we summed the utilization distributions across prides to create a single distribution of the intensity of use by the lion population. To illustrate, Fig. 4C shows the resulting lion use utilization distribution for Kafue in 2022 from 27,683 locations.

Statistical Analysis. Using the methods described above, we obtained measurements of effort expended (VeDBA) and distance moved for wild dogs at known locations. For each location, we extracted values for expected prey biomass, lion utilization, and protection level (National Park vs. Game Management Area), and merged data on the number of adult hunters and the number of dependent pups to each observation. We then tested the effects of these variables on hunting effort and hunting success using the glmmTMB package, centering and scaling all continuous variables so that coefficients could be directly compared and to aid in convergence. We used gamma regressions with an inverse link to test for effects on hunting effort and distance moved per minute, including a lag one autoregression term to avoid the assumption that observations were independent (first confirming that the lag one autocorrelation was strong, and all other lags were weak.) We then used dplyr to aggregate the data from minutes to days, calculating total distance moved, the number of hunting efforts and kills, mean prey biomass and mean lion utilization for each day. We then used Poisson regressions with a log link to test for effects on the number of hunting efforts/day and kills/day. The data did not show detectable temporal autocorrelation at this time scale, so these models did not include an autoregression term. Finally, we used data from direct observation of wild dogs feeding at 730 kill sites in Kafue and Luangwa between 2013 and 2023 to fit a binomial regression with a logit link, testing whether the size of prey killed was related to local prey biomass. We confirmed goodness-of-fit for each model using the DHARMA package to examine QQ plots and to test for overdispersion, and the simulate function in base R to confirm that model-simulated values aligned well with the original data.

Results

Effort Expended. After accounting for temporal autocorrelation ($\hat{\beta} = -0.95 \pm 0.003, z = -297.0, P < 0.0001$), expended effort (VeDBA) increased in places with low prey density ($\hat{\beta} = -0.08 \pm 0.02, z = -3.90, P = 0.0001$), in places with heavy use by lions ($\hat{\beta} = 0.06 \pm 0.02, z = 2.60, P = 0.0095$) in GMAs relative to National Parks ($\hat{\beta} = -0.78 \pm 0.09, z = -80.4, P < 0.0001$), in packs with fewer adult hunters ($\hat{\beta} = -0.66 \pm 0.02, z = 32.4, P < 0.0001$) and in packs with more dependent pups ($\hat{\beta} = 0.36 \pm 0.002, z = 160.4, P < 0.0001$) (Figs. 4 and 5). Effort increased substantially at dawn and dusk when most hunting occurred (Figs. 2 and 3), and total daily effort was positively related to the number of hunting efforts/day (*OLS* $\hat{\beta} = 2.32 \pm 0.73, t = 3.186, P = 0.0019, r_{adj}^2 = 0.09$). As Fig. 5 shows, the effect of prey availability on expended effort was large: Within the range of prey biomass observed, VeDBA was two to three times greater in areas with low prey biomass.

Movement. Mean daily distance moved was 15.5 km \pm 0.6 SE, which is 17% greater than the largest value reported from other populations (13.2 km in Botswana's Moremi National Park) (43). Most effects on movement aligned with observed effects on energy expenditure. After accounting for temporal autocorrelation ($\hat{\beta} = -3.17 \pm 0.0037, z = -86.4, P < 0.0001$), distance moved per minute increased in places with low prey density ($\hat{\beta} = -0.29 \pm 0.07, z = -4.17, P < 0.0001$), in GMAs relative to National Parks ($\hat{\beta} = -0.06 \pm 0.012, z = -4.45, P < 0.0001$), in packs with fewer adult hunters ($\hat{\beta} = -0.66 \pm 0.02, z = -8.97, P < 0.0001$) and in packs with more dependent pups ($\hat{\beta} = 2.48 \pm 0.030, z = 8.39, P < 0.0001$). Distance moved per minute was not detectably related to the intensity of use by lions ($\hat{\beta} = 0.02 \pm 0.29, z = 0.06, P = 0.94$). The effects reported here used data restricted to the morning (4 to 8 am) and evening (5 to 7 pm) periods in which most movement and hunting occurs (Figs. 2 and 3). The inferences did not change using the same model fit to data from around the clock, but the effects were clearer when restricted to hunting periods, because the

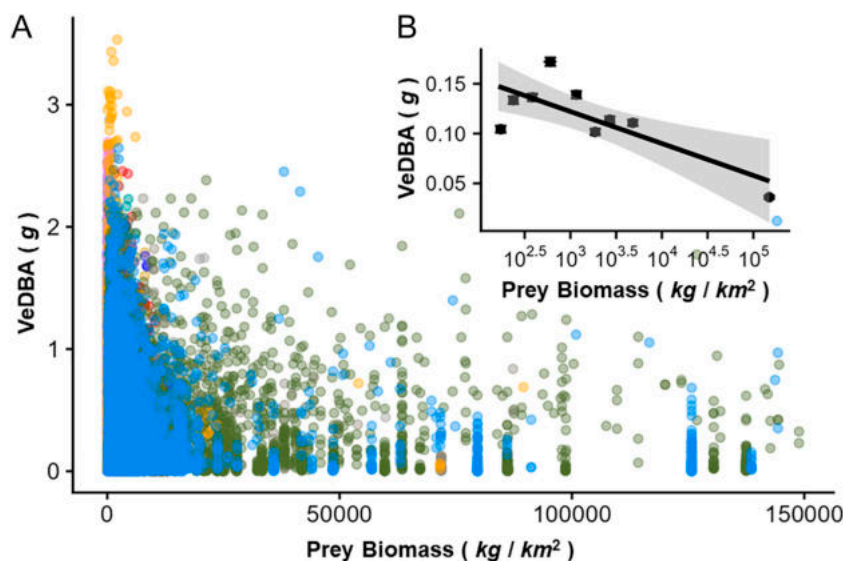


Fig. 5. (A) Hunting effort, measured by VeDBA, increased when wild dogs were in areas with lower predicted prey biomass, after controlling for autocorrelation and the effects of lion use, protection (National Park vs. Game Management Area), pack size, and the number of dependent pups. Colors identify data from different packs. (B) The same data binned into quantiles with error bars ± 1 SE and a logarithmic x axis to linearize the relationship, with the ordinary least squares regression and its 95% CI shown only for visual reference.

behavior of resting packs is affected little by pack size or ecological conditions.

Hunting Success and Kill Mass. The number of kills per day was lower in GMAs than within National Parks ($\hat{\beta} = 0.16 \pm 0.05$, $z = 2.86$, $P = 0.0042$) and increased with an increasing number of dependent pups ($\hat{\beta} = 0.23 \pm 0.07$, $z = 3.07$, $P = 0.0021$) but was not detectably affected by the number of adult hunters ($\hat{\beta} = -0.078 \pm 0.074$, $z = -1.06$, $P = 0.29$), the intensity of use by lions ($\hat{\beta} = 0.014 \pm 0.062$, $z = 0.23$, $P = 0.81$), or by prey biomass ($\hat{\beta} = -0.05 \pm 0.07$, $z = -0.75$, $P = 0.45$) (Fig. 6).

The mean mass of prey killed (Luangwa: 30.7 kg, Kafue: 26.6 kg) was comparable to but smaller than values from most other ecosystems. The most common prey were impala (Luangwa: 62.0%, Kafue: 27.8%) and puku (Luangwa: 19.2%, Kafue: 17.8%), but small antelopes (grysbok, duiker, oribi, bushbuck, and reedbuck) were also common prey, particularly in the Kafue (25.8%), where they were collectively killed more often than puku and almost as often as impala. Small antelopes were less commonly (10.3%) killed in Luangwa, where the densities of puku and impala are much higher (37, 66, 67). Using 542 directly observed kills (from 2013 to 2023) of these species with known locations, logistic regression showed that the likelihood of killing small antelopes (18.0 kg) rather than puku (37.0 kg) or impala (31.9 kg) was significantly higher in areas with low prey biomass ($\hat{\beta} = 0.095 \pm 0.037$, $z = 2.558$, $P = 0.0105$) (Figs. 4 and 7). The likelihood of shifting predation from preferred prey to small antelopes increased by 30% in areas with low prey density, an effect large enough to be biologically meaningful (Fig. 7). The remainder of kills were species that were either killed too rarely to assess spatial patterns of predation, too uncommon to accurately determine their distribution, or both. These included greater kudu (*Tragelaphus strepsiceros*, 3 kills), porcupine (*Hystrix cristata*, 1), scrub hare (*Lepus saxatilis*, 7), blue wildebeest (*Connochaetes taurinus*, 1), waterbuck (*Kobus ellipsiprymnus*, 7), warthog (*Phacochoerus africanus*, 10), hartebeest (*Alcelaphus buselaphus*, 28), red lechwe (*Kobus lechwe*, 1), and sable antelope

(*Hippotragus niger*, 5). Kills of the larger species in this set were juveniles with a body mass similar to adult puku or impala, so the range of body mass for these kills was comparable to those included in our analysis.

Discussion

Prey populations, particularly the populations of larger-bodied prey, have been depleted by poaching in much of the Kafue ecosystem and in the Game Management Areas adjacent to Luangwa National Park (66–69, 75, 76). While prey depletion is unambiguously expected to cause apex carnivores like the lion to decline (13–15, 33), its expected effect on wild dogs is not clear from theory alone. Wild dogs are strongly limited by the density of dominant competitors like the lion, and their population density has historically had a negative relationship to the density of competitors, rather than a simple positive relationship to the density of prey (37). Recent data from Kafue and Luangwa show that wild dogs' density, survival, and reproduction are all low in the areas where prey density is lowest, even though the density of lions is also low in such areas (25, 26, 36).

Our results show a coherent pattern of increased energetic costs and decreased energetic benefits of hunting in areas with low prey biomass. Wild dogs cover greater distances when hunting in prey depleted areas and are more likely to kill small prey. VeDBA, which correlates well with energy expenditure (64, 78), increases when hunting in prey depleted areas. These results suggest that the effects of prey depletion on wild dog demography and dynamics are caused at least in part by effects on the energetics of hunting.

We detected no effect of prey density on the number of kills per day, suggesting that wild dogs adjust their hunting effort to meet their immediate needs. This point has seen considerable attention in prior discussions of cooperative hunting, leading to consensus that data on both costs and benefits are needed to determine whether sociality is favored by its effects on hunting (40, 45, 58, 88). While the number of kills was not related to prey density (at a daily time scale) within the broad range of conditions that we sampled, the mean number of kills/day (3.44 ± 0.19) was larger

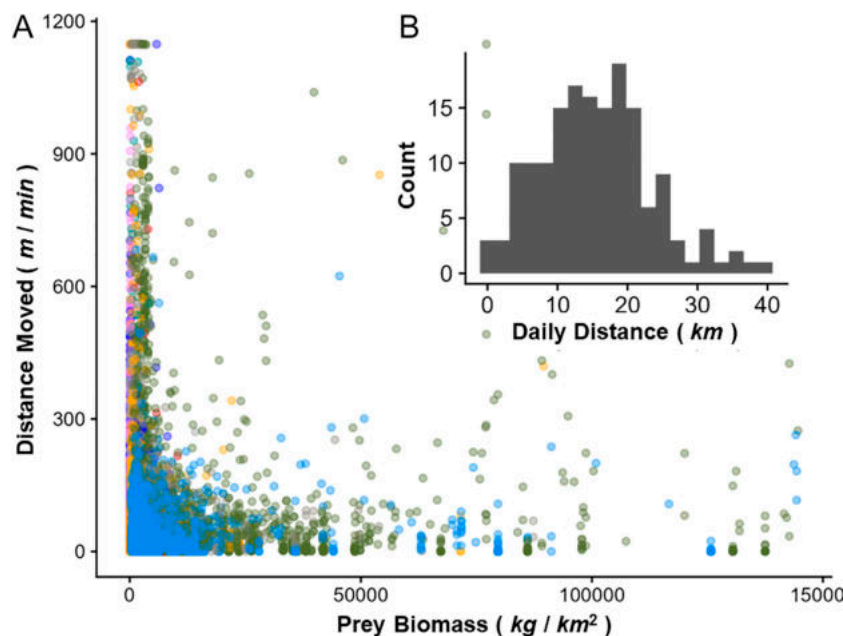


Fig. 6. (A) The distance moved per minute increased when wild dogs were in areas with lower prey biomass, after controlling for autocorrelation and the effects of lion use, protection (National Park vs. Game Management Area), pack size, and the number of dependent pups. Colors identify data from different packs. (B) Mean daily movement determined from locations at 1-min intervals was $15.5 \text{ km} \pm 0.6 \text{ SE}$.

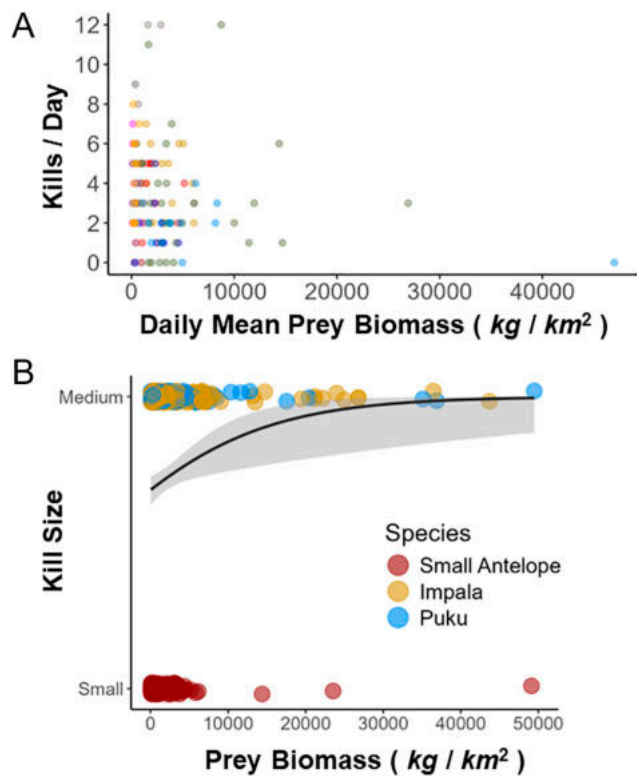


Fig. 7. (A) The number of inferred kills per day was not detectably related to the biomass of prey along the path traveled that day. Colors identify data from different packs. (B) The probability of killing small antelopes (rather than puku or impala) increased in areas with low prey biomass. In areas with high prey biomass, almost all kills were puku and impala.

than has been reported for other populations. Estes and Goddard (48) reported 2 kills/d (for one pack of eight adults sampled for 10 d) in Tanzania's Ngorongoro Crater. Fuller and Kat (42) reported "a mean of at least 3 animals/day" (for one pack of 17 to 43 including pups, sampled for 55 d) in Aitong, Kenya. In both these studies, Thomson's gazelle were the most common prey, but wildebeest contributed substantially to the mass consumed. Creel and Creel (46) reported 1.8 kills/day (for 11 packs with a median of 10 adults sampled for 310 d) in Tanzania's Selous Game Reserve, where impala were the most common prey, but wildebeest were most important in terms of mass consumed. Data from accelerometers deployed on one pack in Botswana's Moremi National Park allow a daily kill rate of 2.3 animals/day to be inferred from values reported for other variables: In this population, impala were both the most common prey and the most important with respect to mass consumed (47).

These comparisons suggest that a decrease in the size of prey might require an increase in the number of kills per day, which is likely to cause an increase in movement and energy expenditure. It has long been noted that wild dogs opportunistically kill small prey, even though they typically kill prey that are ~120% of their own mass (89). Estes and Goddard (48) noted that "independent kills of concealed small prey" were common for wild dogs moving in search of larger prey (usually wildebeest) in Ngorongoro. Without observing a hunt, "the observer would suddenly notice that a dog was carrying part of a gazelle fawn or a young hare that must simply have been grabbed." Our observations of wild dogs hunting in Liuwa Plains National Park, where visibility is excellent, show the same pattern: 51 (20.1%) of 254 wild dog kills were springhares or oribi fawns, with a quick pursuit by one or few dogs lasting only a few seconds and the prey killed almost instantly upon capture. In Tanzania's Serengeti National Park,

Fanshawe and Fitzgibbon (27) observed that captures of Thomson's gazelle fawns lasted less than 20 s with a success rate near 100%. Using scat analysis, Woodroffe et al. (90) estimated that dikdiks (*Madoqua kiriki*), with a mean mass of 3.5 kg, comprised 70% of wild dogs' diet in Kenya's Laikipia Plateau, a site where cattle were common, wild dogs' typical prey were depleted, and dikdiks attained an unusually high density. While wild dogs frequently make opportunistic kills of small animals and might even subsist on such prey (90), it is unlikely that a decrease in prey mass is without cost: Wild dogs depend heavily on prey larger than themselves if such prey are available. Our results show that increased movement and energy expenditure accompany a decrease in the mass of killed prey when hunting in prey-depleted areas.

Comparison of movement between populations remains confounded by differences in the resolution of the available data. Mean daily distance moved was 15.5 km \pm 0.6, which is similar to but larger than values from other populations. Daily distance moved was 12.3 km in Selous (40). In Moremi, it was 13.2 (43), and in Aitong, it was 'at least 10 km' (42). The straight-line distance between locations separated by 1 d was 5.6 km in Laikipia (41). In Moremi, the daily distance based on 4 locations/day (44) was 8.5 km, considerably less than the estimate of 13.2 km from ref. 43 using fine-scaled data from accelerometers in the same population.

The effects of prey depletion on movement and the mass of prey killed can both be converted to units of energy with existing equations (58). If the assumptions of these conversions are valid (58), wild dogs expend ~3,042 kJ/h during hunting periods, and gain ~7,304 kJ/kg of prey (impala) killed. The regression coefficient we estimated for the effect of prey biomass (in kg/km²) on movement (in m/min) equates to a reduction of 118.8 m/d for an increase of one impala/km². A reduction of 118.8 m is 0.77% of the mean daily distance moved (15.5 km). An increase of one impala/km² is 2.59% of the mean impala density (36.7 individuals/km²) for the locations analyzed here. Thus, a 1% increase in impala density predicts a 0.30% decrease in energy expenditure due to movement. Due to excessive bushmeat poaching, the densities of impala (and other species) in prey-depleted areas of our study sites are several times lower than have previously been reported for ecosystems with comparable vegetation and rainfall, using the same methods (39, 66). Even a modest recovery to 50% above current prey densities in depleted areas would be expected to yield a substantial 15% decrease in wild dogs' energy expenditure (or 2,738 kJ/d). The energy that wild dogs obtain should also increase, but this effect is smaller. As prey density doubled from 10,000 to 20,000 kg/km², the mean mass of prey was estimated to increase by 10% (from 31.2 to 34.5 kg), and the number of kills per day did not change detectably. Taken together, the effects of prey density on the energetic costs and benefits of hunting establish a causal mechanism linking prey depletion to low survival, reproduction and population density (25, 26, 36). Increases in prey density that are feasible with increased protection (39) could substantially improve the energetic costs and benefits of hunting for wild dogs.

The distance moved per minute was not detectably related to the intensity of use by lions, even though VeDBA was greater in locations that were heavily used by lions. This was the only effect that did not directly align with the hypothesis that movement is the primary determinant of variation in VeDBA for wild dogs. This result also does not align with prior results showing that wild dogs moved slowly in areas that were heavily used by lions in the long term (59), perhaps to allow careful assessment of short-term risk before moving into an area with high long-term risks (91). The same study also found that wild dogs moved more quickly

when they were close to lions in the short term, perhaps to avoid a risk that had already been assessed and found to be high (59). It is logical to expect that such short-term responses are more common in areas that are heavily used by lions in the long term. If that is true, then unmeasured short-term responses may have interfered with our ability to detect responses to the long-term use of an area by lions, because we did not have meaningful data to assess variation in wild dogs' proximity to lions on the scale of minutes. We also did not have data to quantitatively describe space use by spotted hyenas, but opportunistic sightings show that they are most common in areas that are also heavily used by lions (60). In Kafue, spotted hyenas are rarely observed (69) and came to only one wild dog kill.

The effect of protection (NP vs. GMA) on distance moved per minute aligned with the effect of protection on VeDBA, with both measures increasing in less protected GMAs. This increase in movement does not align with prior results using coarser data, showing that movement decreased in GMAs (92). This discrepancy might arise because the prior analysis did not include data on prey density, which would cause omitted variable bias. Alternatively, effects on movement can be affected by the scale on which they are measured, so a difference in the linearity of short-term (1-min) movements could potentially explain why displacement over longer (6 h) periods decreased, even though distance moved per minute increased. Finally, most of the packs in this study rarely moved into GMAs (and never into the portions most affected by humans), so our understanding of differences in movement between National Parks and GMAs remains somewhat limited.

The movements of prey over an entire year were very small relative to the movements of wild dogs over a few days (Fig. 4A), so individual prey animals occupied a relatively fixed location for wild dogs making decisions about where to hunt. Areas with high and low prey density are probably relatively static for these decisions. This might explain why wild dogs encounter their preferred prey in a nonrandom manner. In the Selous Game Reserve, packs larger than the median preferentially killed wildebeest, and packs smaller than the median preferentially killed impala (46). In parallel, large packs encountered wildebeest more frequently than small packs did, and small packs encountered impala more frequently than large packs did (46). The movements of predators and prey are often treated as a shell game, with each player responding to the movements of its opponent (63, 93), but it is important to recognize that the speed and scale of movements can differ by orders of magnitude.

Wild dogs are astonishingly fast in full pursuit of prey, and their top speed has seen considerable attention. From dead reckoning of wild dogs' speed over a minute, 1,148 m/min was the upper limit (99.8th percentile). Direct observations in Selous suggested a top speed of at least 1,020 m/min (46), but opportunities to match wild dogs running at top speed while observing them from a vehicle are not common. Estes and Goddard (48) noted that "a wild dog can perhaps exceed 35 mph (938 m/min) and can sustain a pace of about 30 mph (805 m/min) for several miles." Using accelerometers, Hubel et al. (47) reported a maximum speed of 19 m/s or 1,140 m/min, closely matching our result using similar methods.

The highly crepuscular pattern of activity that we observed has frequently been reported, with minor variation in the timing of peaks around dawn and dusk, and always with some activity on moonlit nights (27, 40, 42, 45, 48). For wild dogs in Moremi, Cozzi et al (94) found that 26% of activity was nocturnal, an unusual pattern.

The effects of pack size that we detected confirm that cooperative hunting favors living in groups, in large part by decreasing

the costs of hunting (40, 45, 46). An increase in the number of adult hunters (from 1 to 11) was associated with lower energy expenditure and less distance moved, but did not detectably affect the number of kills per day. We did not consider yearlings to be hunters because they sometimes assist with hunts but sometimes interfere, and the number of yearlings is not consistently related to hunting effort or its outcome (46). Prior research has also shown that neither hunting effort nor success are affected by the sex ratio of the hunters, probably because males are only 3 to 7% larger than females (46). We considered the number of adults to be the number of hunters and confirmed several benefits of hunting in larger groups. It has been suggested that differences in the paths taken by different individuals during a hunt indicate a lack of cooperation (47). We disagree with this interpretation, partly because of the measured effects of group size on hunting effort and hunting success, and partly because of the complex coordination of behavior during hunts, including the initiation of chases, catching prey, and killing them (45, 46, 48). Many species live in groups but forage independently (95), but wild dogs virtually never move or hunt alone. The enthusiastic social rally that precedes periods of activity is one of the most distinctive features of wild dogs' behavior, and its most obvious function is to coordinate the movement and hunting that almost invariably follows (45). Even when hunting small animals in areas affected by prey depletion, wild dogs always hunted in highly cohesive and coordinated groups, in both ecosystems. Large prey species have been reduced by poaching more than smaller prey (69), and wild dogs rarely killed large animals in this study. This is a marked contrast with wild dog predation in the Selous Game Reserve in the 1990s, where wildebeest were abundant. There, wildebeest were the most common prey for packs with 10 or more hunters, due to selection at all stages of the predation sequence (encounters, hunts and kills) (46). By reducing the ability of large packs to switch to large prey, it is likely that prey depletion reduces the optimal pack size for hunting.

The effects of the number of pups that we detected were also consistent with prior research showing that reproduction is energetically costly for wild dogs (55). An increase in the number of dependent pups (from 0 to 13) was associated with increased hunting effort as measured by VeDBA, increased distance moved, and more kills per day.

Conclusions

Human activities are altering environmental conditions in virtually all ecosystems, and it is widely recognized that these changes are causing the decline of many species. Less obviously, changes in environmental conditions may cause a fundamental change in the critical factor that limits a species. Recent studies suggest that the depletion of large herbivore prey is causing such a shift for African wild dogs, so that they are now limited from the bottom up by prey availability, for which there was little evidence in the past (25, 26, 36, 37). Our results reinforce this inference, by showing that the energetic costs of hunting increase and benefits decrease in areas affected by prey depletion. Our results demonstrate the utility of research that integrates tools for biomonitoring with direct observation and long-term monitoring of endangered species, their competitors, and their resources. By confirming the mechanisms hypothesized to link prey depletion to effects on wild dogs' density and demography, these results strengthen the inference that the relationship is causal. This confirmation is important because many ecological conditions are changing simultaneously in most ecosystems, so that declines of endangered species might be correlated with processes that are not causally related. Programs

to reduce or reverse the widespread decline of large herbivore populations are a direct means of improving the status of endangered wild dog populations, and should be a high priority. Areas depleted of prey also have higher rates of snaring for wild dogs themselves (39), and increased movement due to prey depletion is likely to increase wild dogs' rate of encounter with snares, compounding the effects of prey depletion.

Data, Materials, and Software Availability. Some study data are available for download on GitHub (https://github.com/scott-creel/wild_dog_hunting/tree/main) (86). R, Java, and JAGS scripts for data processing and analysis have been deposited there. The data were collected with permission from the Zambia Department of National Parks and Wildlife, who retain the right to share the data. Direct requests for access are required, but access will be granted upon reasonable request (Email: matt@zambiacarnivores.org).

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Author affiliations: ^aDepartment of Ecology, Montana State University, Bozeman, MT 59717; ^bZambian Carnivore Programme, Mfuwe, Eastern Province, Zambia; ^cSwansea Lab for Animal Movement, Biosciences, College of Science, Swansea University, Swansea, Wales SA2 8PP, United Kingdom; ^dMusekese Conservation, Kafue National Park, Lusaka Province, Zambia; ^eZambia Department of National Parks, Chilanga, Lusaka Province, Zambia; ^fZambia Department of National Parks and Wildlife, Mumbwa, Central Province, Zambia; and ^gDepartment of Ecosystem Science and Management University of Wyoming, Laramie, WY 82072

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