

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

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

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

25 Introduction

26 Interspecific competition affects the distribution and abundance of most species (1, 2) and the limiting
27 effects of competition within guilds of large carnivores are widely recognized (3-8). Within the African large
28 carnivore guild, wild dogs (*Lycaon pictus*) are a highly endangered subordinate competitor with fewer than
29 1500 breeding adults remaining in the wild (9). Although wild dogs are affected by many of the same
30 processes that limit other large carnivores (9, 10), they are unusual because the highest densities that they
31 ever attain are much lower than densities that are commonly attained by their dominant competitors (lions,
32 *Panthera leo*, and spotted hyenas, *Crocuta crocuta*) (11). The densities of apex carnivores like the lion and
33 spotted hyena show a strong positive correlation with the density of large herbivores, both within and
34 between ecosystems (12-15). In contrast, wild dog density is usually low in areas with high prey density, due
35 to strong interference competition from lions and spotted hyenas: where dominant competitors are common,
36 wild dogs often lose their kills to spotted hyenas and are often killed by lions (11, 16-27). More than 25 years
37 ago, Creel & Creel (10) concluded that “wild dogs are rarely limited by prey availability... the simple
38 observation that spotted hyenas attain much higher densities, while relying on similar prey, makes this
39 explanation unlikely... ecosystems with high prey densities do not maintain higher wild dog densities”. The
40 most recent IUCN Red List assessment reiterates that dominant competitors “keep African Wild Dog
41 numbers below the level that their prey base could support” (9).

42 The inference that wild dogs are not normally limited by prey availability had broad support under the
43 ecological conditions of the past, but large herbivores are declining across much of sub-Saharan Africa (28-
44 32). Declining populations of large herbivores are contributing to declines of apex carnivores like the lion (33-
45 35), but for competitively subordinate carnivores like the wild dog, the expected effect of a simultaneous
46 decrease in resources (prey) and dominant competitors (lions) is not obvious. Recent analyses show that
47 when prey density falls below a tipping point, the costs of prey depletion exceed the benefits of competitive
48 release for wild dogs: in prey-depleted areas, their survival, reproduction and population density are all low,
49 despite low densities of dominant competitors (24-26, 36-39). Logically, resources must limit competitively
50 subordinate carnivores at some point, because any predator’s density must go to zero as prey density goes to
51 zero, and these recent results suggest that the binding constraint for wild dogs is shifting from the density of

52 dominant competitors to the density of prey, at least in some ecosystems. Because competition has strong
53 effects on many species and resources of many types are being reduced by human activities, it is plausible to
54 hypothesize that such fundamental changes may be common.

55 Inferences about the effect of prey depletion on wild dogs' density and demography would be
56 strengthened by tests of a well-defined causal mechanism. Here, we tested the hypothesis that prey
57 depletion alters the energetic costs and benefits of hunting. As would be expected from their invariably low
58 density, wild dogs occupy large home ranges and make large daily movements (27, 40-46). They
59 cooperatively hunt prey that are usually larger than themselves, using high-speed chases that typically
60 exceed 500 m and occasionally cover several kilometers (27, 40, 45-50). Movement is one of the most
61 energetically costly behaviors for most animals (51), and high-speed running is particularly costly for
62 terrestrial mammals (52, 53), which makes the energetic costs of searching for prey over large areas and
63 cursorial hunting substantial (18, 45, 49, 54). Wild dogs produce exceptionally large litters, so that the
64 energetic costs of gestation and lactation are large relative to allometric expectation (55, 56). For all of these
65 reasons, wild dogs maintain a tenuously positive energy budget (18, 57). Wild dogs expend ~3.09 MJ per hour
66 of movement and hunting, obtain ~5.8 MJ per kilogram of food consumed (18, 58), and consume 2.0 - 2.5
67 kilograms/individual/day (40). Thus, to offset the energetic cost of one extra hour of movement and hunting a
68 wild dog would require 0.53 kg of food, which is 21.2 – 26.5% of typical daily intake (59). These observations
69 motivate a hypothesis that the effects of prey depletion on wild dog demography and density (24, 25, 36, 37,
70 60) are mediated by changes to the landscape of energy (54, 61, 62).

71 We tested this hypothesis by integrating data from high frequency triaxial accelerometers and
72 magnetometers, GPS collars, direct behavioral observations assisted by VHF telemetry, and long-term
73 monitoring of the densities and distributions of wild dogs, lions and their prey. The data came from 13 packs
74 in two ecosystems, in areas with a broad range of prey density, use by lions, and wild dog pack sizes and
75 compositions. Recent advances in biologging are providing new tools to study behavior, movement and
76 energetics (63-65), and our results demonstrate the useful insights that can be gained by integrating these
77 tools with direct behavioral observations and long-term ecological monitoring.

78 **Methods**

79 *Study Sites, Wild Dog Populations and Long-Term Monitoring*

80 We collected data from two wild dog populations on study sites of ~8,000 km² in the Greater Kafue
81 Ecosystem and ~7,000 km² in the Luangwa Valley Ecosystem that we have intensively monitored since 2013.
82 Detailed descriptions of the study sites, their large herbivore populations, the density and demography of wild
83 dogs on these sites, and our methods for monitoring have been published previously (25, 36, 59, 60, 66-68).
84 Briefly, both sites are a mosaic of woodland and grassland, and both have pronounced annual wet and dry
85 seasons. Both sites are bisected by a major river and its tributaries, and the density of large herbivores is
86 consistently highest near this permanent water. This pattern includes the primary prey of African wild dogs,
87 which are puku (*Kobus vardonii*) and impala (*Aepyceros melampus*) in both ecosystems (see *Results*). The
88 densities of wild dogs, their prey and their dominant competitors the lion (*Panthera leo*) and spotted hyena
89 (*Crocuta Crocuta*) are all low in Kafue because of heavy poaching pressure (25, 37-39, 66, 68, 69). The
90 Luangwa is better protected, and the densities of wild dogs (Kafue: 0.7 individuals/100 km², Luangwa: 4.0
91 individuals/100 km²), their prey and their competitors are all higher in Luangwa than in Kafue (26, 36, 39, 67,
92 70-76). There is pronounced spatial variation within our Luangwa site in wild dog density, survival and
93 reproduction, which are all higher in well-protected areas with higher prey density, despite higher lion density
94 in those areas (26, 36). Wild dog density, survival and reproduction in Kafue are all similar to the least-
95 protected portion of the Luangwa site in the Lower Lupande Game Management Area (GMA) (25, 26). GMAs
96 are buffer zones with less protection and lower prey density than National Parks, in both ecosystems.

97 *Accelerometer Data*

98 We monitored all resident wild dog packs within these areas using a combination of VHF and satellite-GPS
99 collars (MOD-335-3 and TGW-4277-4, Telonics, Mesa, Arizona) on 1–2 adults in each pack to allow frequent
100 direct observation. We radiocollared wild dogs after intramuscular injection of ~1.2 mg medetomidine and
101 ~20 mg tiletamine–zolazepam, reversing the medetomidine by intramuscular injection of atipamezole after
102 45 min to 1 h. Anaesthetics were injected by darting with an air-powered DanInject rifle, and all procedures
103 were performed by an experienced and Zambian-registered veterinarian, in collaboration with the Zambia
104 Department of National Parks and Wildlife, with MSU IACUC approval (2020-123). We confirmed that
105 radiocollars did not detectably affect survival rates (36). Individual wild dogs were identified by variation in

106 their coat patterns using a photographic ID database. Their sex was recorded by external genitalia. Most
 107 individuals were of known age, but age classes (pup, yearling and adult) were also distinguished by size. We
 108 fitted 16 wild dogs in 13 packs with Daily Diary (DD) tags (65) attached to Iridium-GPS radiocollars (TGW-
 109 4277-4, Telonics, Mesa, Arizona) to record orthogonal triaxial acceleration (-16 g to +16 g with 16 bit
 110 resolution) at 40 Hz and orthogonal triaxial magnetic field intensity at 7 Hz. The DD system used two 750 mAh
 111 batteries with data written to a 16 GB micro-SD card, sealed in epoxy resin within a low-profile aluminum
 112 housing, with a total weight of 95 grams (Figure 1A). Collars dropped off using a programmable release
 113 mechanism (Telonics CR-7B) after 31 days and were collected. Because wild dog packs move and hunt in a
 114 highly cohesive manner (40, 45, 48), we collared a single individual in each sampled pack. We tagged packs
 115 that used areas spanning the highest and lowest prey densities within the two ecosystems (see *Prey Biomass*
 116 *Distributions* and *Lion Utilization Distributions*, below). Because lions preferentially use areas with high prey
 117 density (38, 59), these packs also moved across the full gradient of local lion density in the two ecosystems.
 118 The sampled packs also provided a broad and representative range of pack sizes and compositions ($\bar{X} = 13.7$
 119 individuals [range: 5 – 25], $\bar{X} = 6.4$ adults [range: 1 – 11], $\bar{X} = 2.3$ yearlings [range: 0 – 8], $\bar{X} = 5.1$ pups [range:
 120 0 – 13]). We deployed DD collars in 2022 and 2023. Nine DD collars were deployed in Luangwa and seven in
 121 Kafue. In three packs, we collared two different individuals at different times, after a change in pack size and
 122 composition: twice in different years and once after an interval of four months.

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

$$125 \quad VeDBA = \sqrt{(A_{x_r} - A_{x_s})^2 + (A_{y_r} - A_{y_s})^2 + (A_{z_r} - A_{z_s})^2} \quad \text{Equation 1}$$

126 where A is acceleration in orthogonal x , y and z axes (Figure 1), and r and s subscripts identify raw or
 127 smoothed values with a smoothing window of 2 s (77, 78). We then determined the running mean over 2.5
 128 seconds of the VeDBA values defined by Equation 1, to improve the signal-to-noise ratio (hereafter, VeDBA).
 129 We also used these data to identify hunting efforts and kills (79). Briefly, the frequency distribution for VeDBA
 130 was highly bimodal for every individual, with most of the higher mode attributable to trotting, running and
 131 sprinting, each of which produce a distinct frequency and amplitude pattern in the triaxial acceleration data

132 (Figure 1B). Using DDMT software developed by the Swansea Laboratory for Animal Movement for analysis of
133 data from DD tags (<http://wildbytetechologies.com/manual.pdf>), we identified a hunting effort when VeDBA
134 was greater than 0.9 g. We selected 0.9 g because it consistently fell within the nadir between the two modes
135 of the frequency distribution just described. We merged such events if they occurred within 10 s of each
136 other. Of the identified events, we considered those with VeDBA values > 0.9 g for >38 seconds to be hunting
137 efforts. To identify kills, we examined the data following each identified hunt, looking for patterns that
138 indicated feeding; we used accelerometer data (a change in pitch) showing that the head was lowered (to
139 access a carcass) and that the animal was stationary but making brief, forceful movements with large
140 components in the dorsoventral (heave) and longitudinal (surge) axes (to tug meat from a carcass or
141 disarticulate it). Specifically, we identified kills as events within 375 s of a hunting effort, with periods > 18 s
142 with a pitch angle (mean over 5 s) < -25°, and VeDBA (mean over 2 s) >0.02 g and VeDBA (mean over 5 s) <0.15
143 g, and acceleration in the heave axis (over 0.5 s) > 0.7 g.

144 We developed these Boolean rules to identify hunting efforts and kills from DD data using first
145 principles (79), by consideration of the patterns that would be produced by the hunting and feeding behavior
146 of wild dogs (40, 43, 45, 46, 48, 81). We validated both rules by comparing the hunts and kills that they
147 identified with data from direct observation of three DD-tagged packs in Kafue, using data from 47 days (79).
148 Twenty-nine identified hunting efforts that overlapped with direct observation were all confirmed. Ten
149 identified kills that overlapped with direct observation were all confirmed. One observed kill was not
150 identified from the DD data because the collared animal did not feed until after the time window in our rules.
151 Finally, we confirmed that temporal variation in VeDBA showed pronounced peaks around dawn and dusk
152 that aligned well with observed periods of movement and hunting activity (Figures 2 & 3).

153 We used GPS-corrected dead reckoning to determine each collared animal's location at one-minute
154 intervals, and thus to determine the distance moved (82, 83). First, the GPS data were cleaned (82, 84) to
155 remove GPS locations that were likely to have large errors, based on pronounced spikes in speed and turning
156 angle. Second, the dead-reckoning algorithm constructed a path between GPS locations (at 30 minute
157 intervals) using normalized, calibrated magnetometer data to derive heading and VeDBA as a proxy for speed
158 to derive distance (82, 84). We restricted dead-reckoned steps to time windows that were determined to be

159 movements (with $V_{eDBA} > 0.04 g$ and $< 1.5 g$). To exclude acceleration traces that did not affect location (e.g.
160 shaking, flinching, feeding, or social interactions) (85), we only included windows that met this movement
161 criterion for $> 2 s$. To account for drift in dead-reckoning we applied a compass offset and speed coefficient to
162 each path segment so that its endpoint matched the next GPS location. This analysis was carried out in
163 DDMT using raw 40 Hz acceleration data for all calculations, then aggregated and exported to provide a
164 location and V_{eDBA} value for each second. For the analyses presented here, these data were further
165 aggregated to one-minute intervals using the aggregate function in R. Finally, we compared daily sums of
166 one-minute movements to published estimates of daily movement using other (coarser-scaled) methods
167 (see *Results* and *Discussion*).

168 These methods yielded estimates of hunting effort (V_{eDBA}) and distance moved for 242,126
169 locations, and identified 1428 hunting efforts and 423 kills. Prior to analysis, we restricted the data to 171,360
170 locations with data for all predictors: 70,766 observations fell in areas for which we could not accurately
171 determine space use by lions (see *Lion Utilization Distributions* below).

172 *Prey Biomass Distributions*

173 We observed VHF-collared packs during hunting periods by following in a vehicle at distances of 20 – 400 m,
174 recording 1,232 hunts and 740 kills between 2013 and 2023. As described above (*Accelerometer Data*), we
175 used these observations to validate the Boolean rules that identified hunts and kills from accelerometer and
176 magnetometer data. We also used these data to test for effects on the size of prey killed in areas with high
177 and low prey density. To do this, we first had to identify the species that were relevant to estimation of prey
178 density. As is typical of wild dogs (and other large carnivores), a small set of species formed most of the diet.
179 Puku and impala comprised 63.3% of kills, and most (18.1%) of the remainder were five species of small
180 antelopes (common duiker, *Sylvicapra grimmia*, grysbok, *Raphicerus sharpei*, oribi, *Ourebia ourebi*,
181 bushbuck, *Tragelaphus scriptus*, and reedbuck, *Redunca arundinum*). These five species (hereafter ‘small
182 antelopes’) are typically found alone or in small groups, broadly scattered, at much lower maximum local
183 densities than impala or puku. Together, these seven species comprised 81.5% of observed kills (see
184 *Results*).

185 We mapped the expected density and distribution of these prey species by fitting Bayesian
186 hierarchical distance sampling models to detections from repeated surveys of a fixed set of transects that
187 sampled both study areas representatively with respect to vegetation type and were stratified with respect to
188 distance from water. We conducted surveys at the end of the wet season and the end of the dry season each
189 year. Our methods for distance sampling have previously been described in detail, including demonstrations
190 that the detection functions fit the data well (66, 67). Here, we analyzed detections of 2,967 herds of the
191 seven prey species identified above (using herds as the sampling unit to satisfy the assumption that
192 detections are independent), from 16 surveys over 1982 km of transects that sampled an area of 1089.6 km².
193 The intensity of sampling was balanced between Kafue (986 km) and Luangwa (996 km), but higher
194 population densities in Luangwa yielded more detections (2124 vs 843).

195 With these data, we fit Bayesian hierarchical distance sampling models (86) to estimate
196 environmental effects on the density of each species in each ecosystem. We analyzed data for puku and
197 impala separately, but pooled data for the five small antelopes because their distributions were broadly
198 similar at the scale of wild dog movements and each species was too sparsely distributed to obtain
199 independent estimates of effects on its density. R and JAGS code for the hierarchical distance sampling
200 model are provided in the supplemental material. Briefly, we used a negative binomial model to describe
201 herd size, modeled the probability of detection (of herds) as a hazard function of distance, and modeled herd
202 density as a log-linear function of percent tree cover, distance to the nearest permanent river, distance to the
203 nearest seasonal stream, and the frequency with which the location burned. We extracted values for these
204 covariates from the Google Earth Engine Data Catalog at each herd's location using Google Earth Engine,
205 using java code provided in the supplemental material. Distance to rivers and streams were calculated to 1 m
206 from WWF HydroSHEDs data (rivers: order \leq 5, streams: order = 6), percent tree cover came from Copernicus
207 proportional land cover imagery at a resolution of 100 m, and the frequency of fires (the proportion of years
208 between 2001 and 2023 in which an area burned) was determined from MODIS imagery with 500m resolution.
209 These scales were sufficient to detect effects on wild dogs' movements and hunting (see *Results*: movement
210 averaged 15.5 km/day and sometimes exceeded 1 km/min).

211 We selected the structure of the hierarchical distance sampling model by comparing its fit to models
212 with alternative distributions and predictor variables (some recorded during the field observations and others
213 extracted from the Google Earth Engine Data Catalog). We sought a simple model with predictors that were
214 known to be relevant for these herbivores, with good explanatory power for all species in both ecosystems,
215 using predictors from data that are readily available for all ecosystems. We combined species- and
216 ecosystem-specific coefficients from the hierarchical distance sampling models with rasters for each
217 predictor variable (again extracted from the Google Earth Engine Data Catalog) to map the expected density
218 of each prey species. We converted these densities to biomass using estimates of mass from observed wild
219 dog kills for each species, accounting for the sex and age-class killed (impala: 31.9 kg, puku: 37 kg, small
220 antelopes: 18 kg). These maps of prey density or biomass (Figure 4) are expectations based on ecological
221 conditions (vegetation, water and fire), from data collected on transects that fell mainly in well-protected
222 areas. Thus, they do not account for variation in prey density due to other causes, particularly protection
223 from poaching. We addressed this issue by including the level of protection (National Park vs. Game
224 Management Area) as a separate variable in subsequent analyses: protection and prey density are
225 considerably lower in GMAs (though there is variation within the two protection categories that this variable
226 does not capture). As can be seen in Figure 4A, wild dog packs usually remained within National Park
227 boundaries, sometimes moving directly along the boundary or turning sharply rather than entering the
228 adjacent Game Management Area, but data from two DD tagged packs in the Luangwa site came mainly from
229 the Lower Lupande GMA.

230 We deployed GPS-collars on five impala and four puku in Kafue, which provided eight locations per
231 day for one year. We fit a 95% kernel utilization distribution for each animal using the adehabitatHR package,
232 and used these distributions simply to compare the scale of movement by individual prey relative to
233 movement by individual wild dogs (Fig. 4A).

234 *Lion Utilization Distributions*

235 For each ecosystem in each year, we quantified spatial variation in the intensity of use by lions by fitting a
236 dynamic Brownian bridge movement model (86) to the locations of GPS-collared lions, using the move
237 package in R (88). Using four locations per day for one lion from each pride, we fit dBMMs with a window of

238 35 locations and a margin of 7 locations (following guidance from Kranstauber et al. (88)), to create a raster
239 with 1 km² resolution from the resulting utilization distribution (59). For each site-year combination, we
240 restricted this analysis to the area within which all resident lion prides were collared, to avoid low apparent
241 use that was an artefact of inadequate sampling. Within this area, we summed the utilization distributions
242 across prides to create a single distribution of the intensity of use by the lion population. To illustrate, Fig 4C
243 shows the resulting lion use utilization distribution for Kafue in 2022 from 27,683 locations.

244 *Statistical Analysis*

245 Using the methods described above, we obtained measurements of effort expended (VeDBA) and distance
246 moved for wild dogs at known locations. For each location, we extracted values for expected prey biomass,
247 lion utilization and protection level (National Park vs. Game Management Area), and merged data on the
248 number of adult hunters and the number of dependent pups to each observation. We then tested the effects
249 of these variables on hunting effort and hunting success using the glmmTMB package, centering and scaling
250 all continuous variables so that coefficients could be directly compared and to aid in convergence. We used
251 gamma regressions with an inverse link to test for effects on hunting effort and distance moved per minute,
252 including a lag one autoregression term to avoid the assumption that observations were independent (first
253 confirming that the lag one autocorrelation was strong, and all other lags were weak.) We then used dplyr to
254 aggregate the data from minutes to days, calculating total distance moved, the number of hunting efforts and
255 kills, mean prey biomass and mean lion utilization for each day. We then used Poisson regressions with a log
256 link to test for effects on the number of hunting efforts/day and kills/day. The data did not show detectable
257 temporal autocorrelation at this time scale, so these models did not include an autoregression term. Finally,
258 we used data from direct observation of wild dogs feeding at 730 kill sites in Kafue and Luangwa between
259 2013 and 2023 to fit a binomial regression with a logit link, testing whether the size of prey killed was related
260 to local prey biomass. We confirmed goodness-of-fit for each model using the DHARMA package to examine
261 QQ plots and to test for overdispersion, and the simulate function in base R to confirm that model-simulated
262 values aligned well with the original data.

263 **Results**

264 *Effort Expended*

265 After accounting for temporal autocorrelation ($\hat{\beta} = -0.95 \pm 0.003, z = -297.0, P < 0.0001$), expended effort
 266 (VeDBA) increased in places with low prey density ($\hat{\beta} = -0.08 \pm 0.02, z = -3.90, P = 0.0001$), in places with
 267 heavy use by lions ($\hat{\beta} = 0.06 \pm 0.02, z = 2.60, P = 0.0095$), in GMAs relative to National Parks ($\hat{\beta} = -0.78 \pm$
 268 $0.09, z = -80.4, P < 0.0001$), in packs with fewer adult hunters ($\hat{\beta} = -0.66 \pm 0.02, z = 32.4, P < 0.0001$) and
 269 in packs with more dependent pups ($\hat{\beta} = 0.36 \pm 0.002, z = 160.4, P < 0.0001$) (Figures 4 & 5). Effort
 270 increased substantially at dawn and dusk when most hunting occurred (Figures 2 & 3), and total daily effort
 271 was positively related to the number of hunting efforts/day (*OLS* $\hat{\beta} = 2.32 \pm 0.73, t = 3.1860.4, P =$
 272 $0.0019, r_{adj}^2 = 0.09$). As Figure 5 shows, the effect of prey availability on expended effort was large: within the
 273 range of prey biomass observed, VeDBA was two to three times greater in areas with low prey biomass.

274 *Movement*

275 Mean daily distance moved was 15.5 kilometers ($\pm 0.6 SE.$), which is 17% greater than the largest value
 276 reported from other populations (13.2 km in Botswana's Moremi National Park) (43). Most effects on
 277 movement aligned with observed effects on energy expenditure. After accounting for temporal
 278 autocorrelation ($\hat{\beta} = -3.17 \pm 0.0037, z = -86.4, P < 0.0001$), distance moved per minute increased in
 279 places with low prey density ($\hat{\beta} = -0.29 \pm 0.07, z = -4.17, P < 0.0001$), in GMAs relative to National Parks
 280 ($\hat{\beta} = -0.06 \pm 0.012, z = -4.45, P < 0.0001$), in packs with fewer adult hunters ($\hat{\beta} = -0.66 \pm 0.02, z =$
 281 $-8.97, P < 0.0001$) and in packs with more dependent pups ($\hat{\beta} = 2.48 \pm 0.030, z = 8.39, P < 0.0001$).
 282 Minutely distance moved was not detectably related to the intensity of use by lions ($\hat{\beta} = 0.02 \pm 0.29, z =$
 283 $0.06, P = 0.94$). The effects reported here used data restricted to the morning (4–8 am) and evening (5–7
 284 pm) periods in which most movement and hunting occurs (Figures 2 & 3). The inferences did not change
 285 using the same model fit to data from around the clock, but the effects were clearer when restricted to
 286 hunting periods, because the behavior of resting packs is affected little by pack size or ecological conditions.

287 *Hunting Success and Kill Mass*

288 The number of kills per day was lower in GMAs than within National Parks ($\hat{\beta} = 0.16 \pm 0.05, z = 2.86, P =$
 289 0.0042) and increased with an increasing number of dependent pups ($\hat{\beta} = 0.23 \pm 0.07, z = 3.07, P = 0.0021$)
 290 but was not detectably affected by the number of adult hunters ($\hat{\beta} = -0.078 \pm 0.074, z = -1.06, P = 0.29$),

291 the intensity of use by lions ($\hat{\beta} = 0.014 \pm 0.062, z = 0.23, P = 0.81$), or by prey biomass ($\hat{\beta} = -0.05 \pm$
292 $0.07, z = -0.75, P = 0.45$) (Figure 6).

293 The mean mass of prey killed (Luangwa: 30.7 kg, Kafue: 26.6 kg) was comparable to but smaller than
294 values from most other ecosystems. The most common prey were impala (Luangwa: 62.0%, Kafue: 27.8%)
295 and puku (Luangwa: 19.2%, Kafue: 17.8%), but small antelopes (grysbok, duiker, oribi, bushbuck and
296 reedbuck) were also common prey, particularly in the Kafue (25.8%), where they were collectively killed more
297 often than puku and almost as often as impala. Small antelopes were less commonly (10.3%) killed in
298 Luangwa, where the densities of puku and impala are much higher (37, 66, 67). Using 542 directly observed
299 kills (from 2013 – 2023) of these species with known locations, logistic regression showed that the likelihood
300 of killing small antelopes (18.0 kg) rather than puku (37.0 kg) or impala (31.9 kg) was significantly higher in
301 areas with low prey biomass ($\hat{\beta} = 0.095 \pm 0.037, z = 2.558, P = 0.0105$) (Figures 4 & 7). The likelihood of
302 shifting predation from preferred prey to small antelopes increased by 30% in areas with low prey density, an
303 effect large enough to be biologically meaningful (Figure 7). The remainder of kills were species that were
304 either killed too rarely to assess spatial patterns of predation, too uncommon to accurately determine their
305 distribution, or both. These included greater kudu (*Tragelaphus strepsiceros*, 3 kills), porcupine (*Hystrix*
306 *cristata*, 1), scrub hare (*Lepus saxatilis*, 7), blue wildebeest (*Connochaetes taurinus*, 1) waterbuck (*Kobus*
307 *ellipsiprymnus*, 7), warthog (*Phacochoerus africanus*, 10), hartebeest (*Alcelaphus buselaphus*, 28), red
308 lechwe (*Kobus lechwe*, 1) and sable antelope (*Hippotragus niger*, 5). Kills of the larger species in this set were
309 juveniles with a body mass similar to adult puku or impala, so the range of body mass for these kills was
310 comparable to those included in our analysis.

311 Discussion

312 Prey populations, particularly the populations of larger-bodied prey, have been depleted by poaching in much
313 of the Kafue ecosystem and in the Game Management Areas adjacent to Luangwa National Park (66-69, 75,
314 76). While prey depletion is unambiguously expected to cause apex carnivores like the lion to decline (13-15,
315 33), its expected effect on wild dogs is not clear from theory alone. Wild dogs are strongly limited by the

316 density of dominant competitors like the lion, and their population density has historically had a negative
317 relationship to the density of competitors, rather than a simple positive relationship to the density of prey
318 (37). Recent data from Kafue and Luangwa show that wild dogs' density, survival and reproduction are all low
319 in the areas where prey density is lowest, even though the density of lions is also low in such areas (25, 26,
320 36).

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

326 We detected no effect of prey density on the number of kills per day, suggesting that wild dogs adjust
327 their hunting effort to meet their immediate needs. This point has seen considerable attention in prior
328 discussions of cooperative hunting, leading to consensus that data on both costs and benefits are needed to
329 determine whether sociality is favored by its effects on hunting (40, 45, 58, 89). While the number of kills was
330 not related to prey density (at a daily time scale) within the broad range of conditions that we sampled, the
331 mean number of kills/day (3.44 ± 0.19) was larger than has been reported for other populations. Estes &
332 Goddard (48) reported 2 kills/day (for one pack of 8 adults sampled for 10 days) in Tanzania's Ngorongoro
333 Crater. Fuller & Kat (42) reported "a mean of at least 3 animals/day" (for one pack of 17-43 including pups,
334 sampled for 55 days) in Aitong, Kenya. In both these studies, Thomson's gazelle were the most common prey,
335 but wildebeest contributed substantially to the mass consumed. Creel & Creel (46) reported 1.8 kills/day (for
336 11 packs with a median of 10 adults sampled for 310 days) in Tanzania's Selous Game Reserve, where impala
337 were the most common prey, but wildebeest were most important in terms of mass consumed. Data from
338 accelerometers deployed on one pack in Botswana's Moremi National Park allow a daily kill rate of 2.3
339 animals/day to be inferred from values reported for other variables: in this population, impala were both the
340 most common prey and the most important with respect to mass consumed (47).

341 These comparisons suggest that a decrease in the size of prey might require an increase in the
342 number of kills per day, which is likely to cause an increase in movement and energy expenditure. It has long

343 been noted that wild dogs opportunistically kill small prey, even though they typically kill prey that are ~120%
344 of their own mass (90). Estes & Goddard (48) noted that “independent kills of concealed small prey” were
345 common for wild dogs moving in search of larger prey (usually wildebeest) in Ngorongoro. Without observing
346 a hunt, “the observer would suddenly notice that a dog was carrying part of a gazelle fawn or a young hare
347 that must simply have been grabbed”. Our unpublished observations of wild dogs hunting in Liuwa Plains
348 National Park, where visibility is excellent, show the same pattern: 51 (20.1%) of 254 wild dog kills were
349 springhares or oribi fawns, with a quick pursuit by one or few dogs lasting only a few seconds and the prey
350 killed almost instantly upon capture. In Tanzania’s Serengeti National Park, Fanshawe & Fitzgibbon (27)
351 observed that captures of Thomson’s gazelle fawns lasted less than 20 seconds with a success rate near
352 100%. Using scat analysis, Woodroffe et al. (91) estimated that dikdiks (*Madoqua kirki*), with a mean mass of
353 3.5 kg, comprised 70% of wild dogs’ diet in Kenya’s Laikipia Plateau, a site where cattle were common, wild
354 dogs’ typical prey were depleted, and dikdiks attained an unusually high density. While wild dogs frequently
355 make opportunistic kills of small animals and might even subsist on such prey (91), it is unlikely that a
356 decrease in prey mass is without cost: wild dogs depend heavily on prey larger than themselves if such prey
357 are available. Our results show that increased movement and energy expenditure accompany a decrease in
358 the mass of killed prey when hunting in prey-depleted areas.

359 Comparison of movement between populations remains confounded by differences in the resolution
360 of the available data. Mean daily distance moved was $15.5 \text{ km} \pm 0.6$, which is similar to but larger than
361 values from other populations. Daily distance moved was 12.3 km in Selous (40). In Moremi it was 13.2 (43),
362 and in Aitong it was ‘at least 10 km’ (42). The straight-line distance between locations separated by one day
363 was 5.6 km in Laikipia (41). In Moremi, the daily distance based on 4 locations/day (44) was 8.5 km,
364 considerably less than the estimate of 13.2 km from Hubel et al. (43) using fine-scaled data from
365 accelerometers in the same population.

366 The effects of prey depletion on movement and the mass of prey killed can both be converted to units
367 of energy with existing equations (58). If the assumptions of these conversions are valid (58), wild dogs
368 expend $\sim 3042 \text{ kJ/h}$ during hunting periods, and gain $\sim 7304 \text{ kJ/kg}$ of prey (impala) killed. The regression
369 coefficient we estimated for the effect of prey biomass (in kg/km^2) on movement (in m/min) equates to a

370 reduction of 118.8 *m/day* for an increase of one impala/*km*². A reduction of 118.8 *m* is 0.77% of the mean
371 daily distance moved (15.5 *km*). An increase of one impala/*km*² is 2.59% of the mean impala density (36.7
372 individuals/*km*²) for the locations analyzed here. Thus, a 1% increase in impala density predicts a 0.30%
373 decrease in energy expenditure due to movement. Due to excessive bushmeat poaching, the densities of
374 impala (and other species) in prey-depleted areas of our study sites are several times lower than have
375 previously been reported for ecosystems with comparable vegetation and rainfall, using the same methods
376 (39, 66). Even a modest recovery to 50% above current prey densities in depleted areas would be expected to
377 yield a substantial 15% decrease in wild dogs' energy expenditure (or 2738 *kJ/d*). The energy that wild dogs
378 obtain should also increase, but this effect is smaller. As prey density doubled from 10,000 to 20,000 *kg/km*²,
379 the mean mass of prey was estimated to increase by 10% (from 31.2 to 34.5 *kg*), and the number of kills per
380 day did not change detectably. Taken together, the effects of prey density on the energetic costs and benefits
381 of hunting establish a causal mechanism linking prey depletion to low survival, reproduction and population
382 density (25,26,36). Increases in prey density that are feasible with increased protection (39) could
383 substantially improve the energetic costs and benefits of hunting for wild dogs.

384 The distance moved per minute was not detectably related to the intensity of use by lions, even
385 though VeDBA was greater in locations that were heavily used by lions. This was the only effect that did not
386 directly align with the hypothesis that movement is the primary determinant of variation in VeDBA for wild
387 dogs. This result also does not align with prior results showing that wild dogs moved slowly in areas that were
388 heavily used by lions in the long term (59), perhaps to allow careful assessment of short-term risk before
389 moving into an area with high long-term risks (92). The same study also found that wild dogs moved more
390 quickly when they were close to lions in the short term, perhaps to avoid a risk that had already been
391 assessed and found to be high (59). It is logical to expect that such short-term responses are more common
392 in areas that are heavily used by lions in the long term. If that is true, then unmeasured short-term responses
393 may have interfered with our ability to detect responses to the long-term use of an area by lions, because we
394 did not have meaningful data to assess variation in wild dogs' proximity to lions on the scale of minutes. We
395 also did not have data to quantitatively describe space use by spotted hyenas, but opportunistic sightings

396 show that they are most common in areas that are also heavily used by lions (60). In Kafue, spotted hyenas
397 are rarely observed (69) and came to only one wild dog kill.

398 The effect of protection (NP vs. GMA) on distance moved per minute aligned with the effect of
399 protection on VeDBA, with both measures increasing in less protected GMAs. This increase in movement
400 does not align with prior results using coarser data, showing that movement decreased in GMAs (93). This
401 discrepancy might arise because the prior analysis did not include data on prey density, which would cause
402 omitted variable bias. Alternatively, effects on movement can be affected by the scale on which they are
403 measured, so a difference in the linearity of short term (one minute) movements could potentially explain
404 why displacement over longer (6 hour) periods decreased, even though distance moved per minute
405 increased. Finally, most of the packs in this study rarely moved into GMAs (and never into the portions most
406 affected by humans), so our understanding of differences in movement between National Parks and GMAs
407 remains somewhat limited.

408 The movements of prey over an entire year were very small relative to the movements of wild dogs
409 over a few days (Figure 4A), so individual prey animals occupied a relatively fixed location for wild dogs
410 making decisions about where to hunt. Areas with high prey and low prey density are probably relatively
411 static for these decisions. This might explain why wild dogs encounter their preferred prey in a non-random
412 manner. In the Selous Game Reserve, packs larger than the median preferentially killed wildebeest, and
413 packs smaller than the median preferentially killed impala (46). In parallel, large packs encountered
414 wildebeest more frequently than small packs did, and small packs encountered impala more frequently than
415 large packs did (46). The movements of predators and prey are often treated as a shell game, with each
416 player responding to the movements of its opponent (63, 94), but it is important to recognize that the speed
417 and scale of movements can differ by orders of magnitude.

418 Wild dogs are astonishingly fast in full pursuit of prey, and their top speed has seen considerable
419 attention. From dead reckoning of wild dogs' speed over a minute, 1148 m/min was the upper limit (99.8th
420 percentile). Direct observations in Selous suggested a top speed of at least 1020 m/min (46), but
421 opportunities to match wild dogs running at top speed while observing them from a vehicle are not common.
422 Estes & Goddard (48) noted that "a wild dog can perhaps exceed 35 mph (938 m/min) and can sustain a pace

423 of about 30 mph (805 m/min) for several miles.” Using accelerometers, Hubel et al. (47) reported a
424 maximum speed of 19 m/s or 1140 m/min, closely matching our result using similar methods.

425 The highly crepuscular pattern of activity that we observed has frequently been reported, with minor
426 variation in the timing of peaks around dawn and dusk, and always with some activity on moonlit nights (27,
427 40-42, 45, 48, 94). For wild dogs in Moremi, Cozzi et al (96) found that 26% of activity was nocturnal, an
428 unusual pattern.

429 The effects of pack size that we detected confirm that cooperative hunting favors living in groups, in
430 large part by decreasing the costs of hunting (40, 45, 46). An increase in the number of adult hunters (from 1
431 to 11) was associated with lower energy expenditure and less distance moved, but did not detectably affect
432 the number of kills per day. We did not consider yearlings to be hunters because they sometimes assist with
433 hunts but sometimes interfere, and the number of yearlings is not consistently related to hunting effort or its
434 outcome (46). Prior research has also shown that neither hunting effort nor success are affected by the sex
435 ratio of the hunters, probably because males are only 3-7% larger than females (46). We considered the
436 number of adults to be the number of hunters and confirmed several benefits of hunting in larger groups. It
437 has been suggested that differences in the paths taken by different individuals during a hunt indicates a lack
438 of cooperation (47). We disagree with this interpretation, partly because of the measured effects of group
439 size on hunting effort and hunting success, and partly because of the complex coordination of behavior
440 during hunts, including the initiation of chases, catching prey and killing them (45, 46, 48). Many species live
441 in groups but forage independently (96), but wild dogs virtually never move or hunt alone. The enthusiastic
442 social rally that precedes periods of activity is one of the most distinctive features of wild dogs' behavior, and
443 its most obvious function is to coordinate the movement and hunting that almost invariably follows (45).
444 Even when hunting small animals in areas affected by prey depletion, wild dogs always hunted in highly
445 cohesive and coordinated groups, in both ecosystems. Large prey species have been reduced by poaching
446 more than smaller prey (69), and wild dogs rarely killed large animals in this study. This is a marked contrast
447 with wild dog predation in the Selous Game Reserve in the 1990s, where wildebeest were abundant. There,
448 wildebeest were the most common prey for packs with 10 or more hunters, due to selection at all stages of

449 the predation sequence (encounters, hunts and kills) (46). By reducing the ability of large packs to switch to
450 large prey, it is likely that prey depletion reduces the optimal pack size for hunting.

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

455 **Conclusions**

456 Human activities are altering environmental conditions in virtually all ecosystems, and it is widely recognized
457 that these changes are causing the decline of many species. Less obviously, changes in environmental
458 conditions may cause a fundamental change in the critical factor that limits a species. Recent studies
459 suggest that the depletion of large herbivore prey is causing such a shift for African wild dogs, so that they are
460 now limited from the bottom up by prey availability, for which there was little evidence in the past (25, 26, 36,
461 37). Our results reinforce this inference, by showing that the energetic costs of hunting increase and benefits
462 decrease in areas affected by prey depletion. Our results demonstrate the utility of research that integrates
463 new tools for biomonitoring with direct observation and long-term monitoring of endangered species, their
464 competitors and their resources. By confirming the mechanisms hypothesized to link prey depletion to
465 effects on wild dogs' density and demography, these results strengthen the inference that the relationship is
466 causal. This confirmation is important because many ecological conditions are changing simultaneously in
467 most ecosystems, so that declines of endangered species might be correlated with processes that are not
468 causally related. Programs to reduce or reverse the widespread decline of large herbivore populations are a
469 direct means of improving the status of endangered wild dog populations, and should be a high priority.
470 Areas depleted of prey also have higher rates of snaring for wild dogs themselves (39), and increased
471 movement due to prey depletion is likely to increase wild dogs' rate of encounter with snares, compounding
472 the effects of prey depletion.

473 **Code and Data Availability**

474 R, Java and JAGS scripts for data processing and analysis are publicly available at [https://github.com/scott-
475 creel/wild_dog_hunting/tree/main](https://github.com/scott-creel/wild_dog_hunting/tree/main). Data are available from the authors upon reasonable request.

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References

1. G. Hardin, The competitive exclusion principle. *Science* **131**, 1292-1297 (1960).
2. S. A. Levin, Community equilibria and stability, and an extension of the competitive exclusion principle. *The American Naturalist* **104**, 413-423 (1970).
3. F. Palomares, T. M. Caro, Interspecific killing among mammalian carnivores. *The American Naturalist* **153**, 492-508 (1999).
4. S. Creel, G. Spong, N. Creel, "Interspecific competition & population biology of extinction-prone carnivores" in *Carnivore Conservation*, J. L. Gittleman, S. M. Funk, D. W. Macdonald, R. K. Wayne, Eds. (Cambridge, 2001), pp. 35-61.
5. T. Caro, C. Stoner, The potential for interspecific competition among African carnivores. *Biological Conservation* **110**, 67-75 (2003).
6. K. U. Karanth *et al.*, Spatio-temporal interactions facilitate large carnivore sympatry across a resource gradient. *Proceedings of the Royal Society B: Biological Sciences* **284**, 20161860 (2017).
7. J. Hunter, T. Caro, Interspecific competition and predation in American carnivore families. *Ethology Ecology & Evolution* **20**, 295-324 (2008).
8. K. J. Sivy, C. B. Pozzanghera, K. E. Colson, M. A. Mumma, L. R. Prugh, Apex predators and the facilitation of resource partitioning among mesopredators. *Oikos* **127**, 607-621 (2018).
9. R. Woodroffe, C. Sillero Zubiri (2020) *Lycaon pictus* (amended version of 2012 assessment). The IUCN Red List of Threatened Species 2020. e.T12436A166502262. in pe.T12436A166502262.
10. S. Creel, N. M. Creel, Six ecological factors that may limit African wild dogs, *Lycaon pictus*. *Animal Conservation* **1**, 1-9 (1998).
11. S. Creel, N. M. Creel, Limitation of African Wild Dogs by Competition with Larger Carnivores. *Conservation Biology* **10**, 526-538 (1996).
12. K. G. V. Orsdol, J. P. Hanby, J. D. Bygott, Ecological correlates of lion social organization (*Panthera leo*). *Journal of Zoology* **206**, 97-112 (1985).
13. I. A. Hatton *et al.*, The predator-prey power law: Biomass scaling across terrestrial and aquatic biomes. *Science* **349**, aac6284 (2015).
14. M. W. Hayward, J. O'Brien, G. I. Kerley, Carrying capacity of large African predators: predictions and tests. *Biological Conservation* **139**, 219-229 (2007).
15. C. Packer *et al.*, Ecological change, group territoriality, and population dynamics in Serengeti lions. *Science* **307**, 390-393 (2005).
16. M. G. Mills, M. L. Gorman, Factors affecting the density and distribution of wild dogs in the Kruger National Park. *Conservation Biology* **11**, 1397-1406 (1997).
17. S. Creel, Four factors modifying the effect of competition on carnivore population dynamics as illustrated by African wild dogs. *Conservation Biology* **15**, 271-274 (2001).
18. M. L. Gorman, M. G. Mills, J. P. Raath, J. R. Speakman, High hunting costs make African wild dogs vulnerable to kleptoparasitism by hyaenas. *Nature* **391**, 479-481 (1998).
19. M. G. L. Mills, H. C. Biggs (1993) Prey apportionment and related ecological relationships between large carnivores in Kruger National Park. in *Mammals as predators* (Clarendon Press, London), pp 253-268.
20. A. Swanson *et al.*, Cheetahs and wild dogs show contrasting patterns of suppression by lions. *Journal of Animal Ecology* **83**, 1418-1427 (2014).
21. R. J. Groom, K. Lannas, C. R. Jackson, The impact of lions on the demography and ecology of endangered African wild dogs. *Animal Conservation* **20**, 382-390 (2017).
22. C. R. Jackson *et al.*, Heading for the hills: risk avoidance drives den site selection in African wild dogs. *PLoS One* **9**, e99686 (2014).
23. A. B. Davies *et al.*, Spatial heterogeneity facilitates carnivore coexistence. *Ecology* **102**, e03319 (2021).
24. D. G. Marneweck, D. J. Druce, J. P. Cromsigt, E. Le Roux, M. J. Somers, The relative role of intrinsic and extrinsic drivers in regulating population change and survival of African wild dogs (*Lycaon pictus*). *Mammalian Biology* **102**, 1215-1229 (2022).

25. B. Goodheart *et al.*, Low apex carnivore density does not release a subordinate competitor when driven by prey depletion. *Biological Conservation* **261**, 109273 (2021).
26. J. Reyes de Merkle *et al.*, 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 (2024).
27. J. H. Fanshawe, C. D. Fitzgibbon, Factors influencing the hunting success of an African wild dog pack. *Animal Behaviour* **45**, 479-490 (1993).
28. W. J. Ripple *et al.*, Bushmeat hunting and extinction risk to the world's mammals. *Royal Society Open Science* **3**, 160498 (2016).
29. W. J. Ripple *et al.*, Collapse of the world's largest herbivores. *Science advances* **1**, e1400103 (2015).
30. D. Western, S. Russell, I. Cuthill, The status of wildlife in protected areas compared to non-protected areas of Kenya. *PloS one* **4**, e6140 (2009).
31. D. T. Bolger, W. D. Newmark, T. A. Morrison, D. F. Doak, The need for integrative approaches to understand and conserve migratory ungulates. *Ecology Letters* **11**, 63-77 (2008).
32. P. A. Lindsey *et al.*, The bushmeat trade in African savannas: Impacts, drivers, and possible solutions. *Biological Conservation* **160**, 80-96 (2013).
33. H. Bauer *et al.*, Threat analysis for more effective lion conservation. *Oryx* **56**, 108-115 (2022).
34. J. Riggio *et al.*, The size of savannah Africa: a lion's (*Panthera leo*) view. *Biodiversity and Conservation* **22**, 17-35 (2013).
35. P. A. Lindsey *et al.*, More than \$1 billion needed annually to secure Africa's protected areas with lions. *Proceedings of the National Academy of Sciences* **115**, E10788-E10796 (2018).
36. S. Creel *et al.*, 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 (2024).
37. S. Creel, M. S. Becker, J. R. de Merkle, B. Goodheart, Hot or hungry? A tipping point in the effect of prey depletion on African wild dogs. *Biological Conservation* **282**, 110043 (2023).
38. M. A. Vinks *et al.*, Response of lion demography and dynamics to the loss of preferred larger prey. *Ecological Applications* **31**, e02298 (2021).
39. M. Becker *et al.*, 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* **287**, in press (2023).
40. S. Creel, N. M. Creel, Communal hunting and pack size in African wild dogs, *Lycaon pictus*. *Animal Behaviour* **50**, 1325-1339 (1995).
41. R. Woodroffe, Ranging behaviour of African wild dog packs in a human-dominated landscape. *Journal of Zoology* **283**, 88-97 (2011).
42. T. K. Fuller, P. W. Kat, Movements, activity, and prey relationships of African wild dogs (*Lycaon pictus*) near Aitong, southwestern Kenya. *African Journal of Ecology* **28**, 330-350 (1990).
43. T. Y. Hubel *et al.*, Energy cost and return for hunting in African wild dogs and cheetahs. *Nature communications* **7**, 11034 (2016).
44. M. A. Pomilia, J. W. McNutt, N. R. Jordan, Ecological predictors of African wild dog ranging patterns in northern Botswana. *Journal of Mammalogy* **96**, 1214-1223 (2015).
45. N. R. Jordan *et al.*, "Hunting behavior and social ecology of African wild dogs" in *Social Strategies of Carnivorous Mammalian Predators: Hunting and Surviving as Families*, M. Srinivasan, B. Würsig, Eds. (Springer International Publishing, Cham, 2023), 10.1007/978-3-031-29803-5_6, pp. 177-227.
46. S. Creel, N. M. Creel, *The African wild dog: Behavior, Ecology and Conservation* (Princeton University Press, Princeton, 2002).
47. T. Y. Hubel *et al.*, Additive opportunistic capture explains group hunting benefits in African wild dogs. *Nature communications* **7**, 11033 (2016).
48. R. D. Estes, J. Goddard, Prey selection and hunting behavior of the African wild dog. *The Journal of wildlife management*, 52-70 (1967).
49. S. Creel, "Cooperative Hunting and Sociality in African Wild Dogs, *Lycaon pictus*" in *Model Systems in Behavioral Ecology: Integrating Conceptual, Theoretical, and Empirical Approaches*, D. Lee Alan, Ed. (Princeton University Press, 2002), doi:10.1515/9780691207247-025, pp. 466-490.

50. S. Creel, N. M. Creel, A. Creel, B. Creel, Hunting on a hot day: effects of temperature on interactions between African wild dogs and their prey. *Ecology* **97**, 2910-2916 (2016).
51. R. M. Alexander, *Principles of Animal Locomotion* (Princeton University Press, Princeton, N.J., 2013).
52. C. R. Taylor, K. Schmidt-Nielsen, J. L. Raab, Scaling of energetic cost of running to body size in mammals. *American Journal of Physiology--Legacy Content* **219**, 1104-1107 (1970).
53. C. R. Taylor, N. C. Heglund, G. M. O. Maloiy, Energetics and mechanics of terrestrial locomotion. I. Metabolic energy consumption as a function of speed and body size in birds and mammals. *Journal of Experimental Biology* **97**, 1-21 (1982).
54. R. P. Wilson *et al.*, Luck in food finding affects individual performance and population trajectories. *Current Biology* **28**, 3871-3877. e3875 (2018).
55. S. R. Creel, N. M. Creel, Energetics, reproductive suppression and obligate communal breeding in carnivores. *Behavioral Ecology and Sociobiology* **28**, 263-270 (1991).
56. S. Creel, N. M. Creel, M. G. L. Mills, S. L. Monfort, Rank and reproduction in cooperatively breeding African wild dogs: Behavioral and endocrine correlates. *Behavioral Ecology* **8**, 298-306 (1997).
57. J. R. Speakman, M. L. Gorman, M. G. Mills, J. P. Raath, Wild dogs and kleptoparasitism: some misunderstandings. *African Journal of Ecology* **54**, 125-127 (2015).
58. S. Creel, Cooperative hunting and group size: assumptions and currencies. *Animal Behaviour* **54**, 1319-1324 (1997).
59. B. Goodheart *et al.*, 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 (2022).
60. B. Goodheart *et al.*, Spatial risk effects from lions compound impacts of prey depletion on African wild dogs. *Ecology and Evolution* **14**: e70401.
61. A. J. Gallagher, S. Creel, R. P. Wilson, S. J. Cooke, Energy landscapes and the landscape of fear. *Trends in ecology & evolution* **32**, 88-96 (2017).
62. R. P. Wilson *et al.*, Moving towards acceleration for estimates of activity-specific metabolic rate in free-living animals: the case of the cormorant. *Journal of Animal Ecology* **75**, 1081-1090 (2006).
63. H. M. English, L. Börger, A. Kane, S. Ciuti, Advances in biologging can identify nuanced energetic costs and gains in predators. *Movement Ecology* **12**, 7 (2024).
64. R. P. Wilson *et al.*, Estimates for energy expenditure in free-living animals using acceleration proxies: A reappraisal. *Journal of Animal Ecology* **89**, 161-172 (2020).
65. R. P. Wilson, E. Shepard, N. Liebsch, Prying into the intimate details of animal lives: use of a daily diary on animals. *Endangered species research* **4**, 123-137 (2008).
66. M. A. Vinks *et al.*, Testing the effects of anthropogenic pressures on a diverse African herbivore community. *Ecosphere* **11**, e03067 (2020).
67. E. Rosenblatt *et al.*, Do protection gradients explain patterns in herbivore densities? An example with ungulates in Zambia's Luangwa Valley. *PLOS ONE* **14**, e0224438 (2019).
68. P. Schuette *et al.*, Boots on the ground: in defense of low-tech, inexpensive, and robust survey methods for Africa's under-funded protected areas. *Biological Conservation* (2018).
69. S. Creel *et al.*, Changes in Zambian large carnivore diets over the past half century reveal the loss of large prey. *Journal of Applied Ecology* **55**, 2908-2916 (2018).
70. T. Mweetwa *et al.*, Quantifying demographic recovery in lions during a three-year moratorium on trophy hunting. *PloS one* **13(5)**: e0197030 (2018).
71. E. Rosenblatt *et al.*, Detecting declines of apex carnivores and evaluating their causes: An example with Zambian lions. *Biological Conservation* **180**, 176-186 (2014).
72. E. Rosenblatt *et al.*, 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 (2016).
73. K. Banda *et al.*, Effects of de-snaring on the demography and population dynamics of African lions. *Biological Conservation* **286**, e110273 (2023).
74. M. Becker *et al.*, Evaluating wire-snare poaching trends and the impacts of by-catch on elephants and large carnivores. *Biological Conservation* **158**, 26-36 (2013).

75. F. Watson, M. S. Becker, R. McRobb, B. Kanyembo, Spatial patterns of wire-snare poaching: Implications for community conservation in buffer zones around National Parks. *Biological Conservation* **168**, 1-9 (2013).
76. F. G. Watson, M. S. Becker, J. Milanzi, M. Nyirenda, Human encroachment into protected area networks in Zambia: Implications for large carnivore conservation. *Regional Environmental Change* **15**, 415-429 (2015).
77. E. L. Shepard *et al.*, Derivation of body motion via appropriate smoothing of acceleration data. *Aquatic Biology* **4**, 235-241 (2008).
78. L. Qasem *et al.*, Tri-axial dynamic acceleration as a proxy for animal energy expenditure; should we be summing values or calculating the vector? *PLoS one* **7**, e31187 (2012).
79. J. Redcliffe *et al.*, Using triaxial accelerometry to detect hunts and kills by African wild dogs. *Frontiers in Ecology and Evolution Volume* **12**, doi 10.3389 (2024).
80. R. Wilson *et al.*, Give the machine a hand: A Boolean time-based decision-tree template for rapidly finding animal behaviours in multisensor data. *Methods in Ecology and Evolution* **9**, 2206 (2018).
81. L. H. Frame, J. R. Malcolm, G. W. Frame, H. Van Lawick, Social organization of African wild dogs (*Lycaon pictus*) on the Serengeti plains, Tanzania 1967–1978 1. *Zeitschrift für Tierpsychologie* **50**, 225-249 (1979).
82. R. M. Gunner *et al.*, Dead-reckoning animal movements in R: a reappraisal using Gundog. *Animal Biotelemetry* **9**, 1-37 (2021).
83. O. R. Bidder *et al.*, Step by step: reconstruction of terrestrial animal movement paths by dead-reckoning. *Movement Ecology* **3**, 23 (2015).
84. K. Bjørneraas, B. Van Moorter, C. M. Rolandson, I. Herfindal, Screening Global Positioning System Location Data for Errors Using Animal Movement Characteristics. *The Journal of Wildlife Management* **74**, 1361-1366 (2010).
85. R. M. Gunner *et al.*, Decision rules for determining terrestrial movement and the consequences for filtering high-resolution global positioning system tracks: a case study using the African lion (*Panthera leo*). *Journal of The Royal Society Interface* **19**, 20210692 (2022).
86. M. Kery, J. A. Royle, *Applied Hierarchical Modeling in Ecology: Analysis of distribution, abundance and species richness in R and BUGS: Volume 1: Prelude and Static Models* (Academic Press, 2015).
87. B. Kranstauber, R. Kays, S. D. LaPoint, M. Wikelski, K. Safi, A dynamic Brownian bridge movement model to estimate utilization distributions for heterogeneous animal movement. *Journal of Animal Ecology* **81**, 738-746 (2012).
88. B. Kranstauber, M. Smolla, A. Scharf (2020) Package 'move': visualizing and analyzing animal track data. (CRAN, Gland).
89. C. Packer, T. Caro, Foraging costs in social carnivores. *Animal Behaviour* **54**, 1317-1318 (1997).
90. M. W. Hayward, J. O'Brien, M. Hofmeyr, G. I. Kerley, Prey preferences of the African wild dog *Lycaon pictus* (Canidae: Carnivora): ecological requirements for conservation. *Journal of Mammalogy* **87**, 1122-1131 (2006).
901. R. Woodroffe, P. A. Lindsey, S. S. Romanach, S. M. o. Ranah, African wild dogs (*Lycaon pictus*) can subsist on small prey: implications for conservation. *Journal of Mammalogy* **88**, 181-193 (2007).
92. E. Dröge *et al.*, Response of wildebeest (*Connochaetes taurinus*) movements to spatial variation in long term risks from a complete predator guild. *Biological Conservation* **233**, 139-151 (2019).
93. S. Creel *et al.*, Carnivores, competition and genetic connectivity in the Anthropocene. *Scientific Reports* **9**, 16339 (2019).
94. W. A. Mitchell, S. L. Lima, Predator-prey shell games: large-scale movement and its implications for decision-making by prey. *Oikos* **99**, 249-259 (2002).
95. M. Mills (1993) Prey apportionment and related ecological relationships between large carnivores in Kruger National Park. in *Symposium of the Zoological Society of London*, pp 253-268.
96. Cozzi, G., Broekhuis, F., McNutt, J. W., Turnbull, L. A., Macdonald, D. W., & Schmid, B. Fear of the dark or dinner by moonlight? Reduced temporal partitioning among Africa's large carnivores. *Ecology*, **93**, 2590-2599 (2012).

97. P. M. Waser, M. S. Waser, *Ichneumia alhicauda* and the evolution of viverrid gregariousness. *Zeitschrift für Tierpsychologie* **68**, 137-151 (198

Figure Legends

Figure 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 (see *Methods*) hunts and kills.

Figure 2. Vectorial dynamic body acceleration (VeDBA) measured over one minute showed a strongly crepuscular pattern, with pronounced peaks around dawn and dusk. Bars shown mean VeDBA across all packs binned into one-hour intervals. This pattern aligns with temporal variation in hunting activity from direct observations, shown in Figure 3.

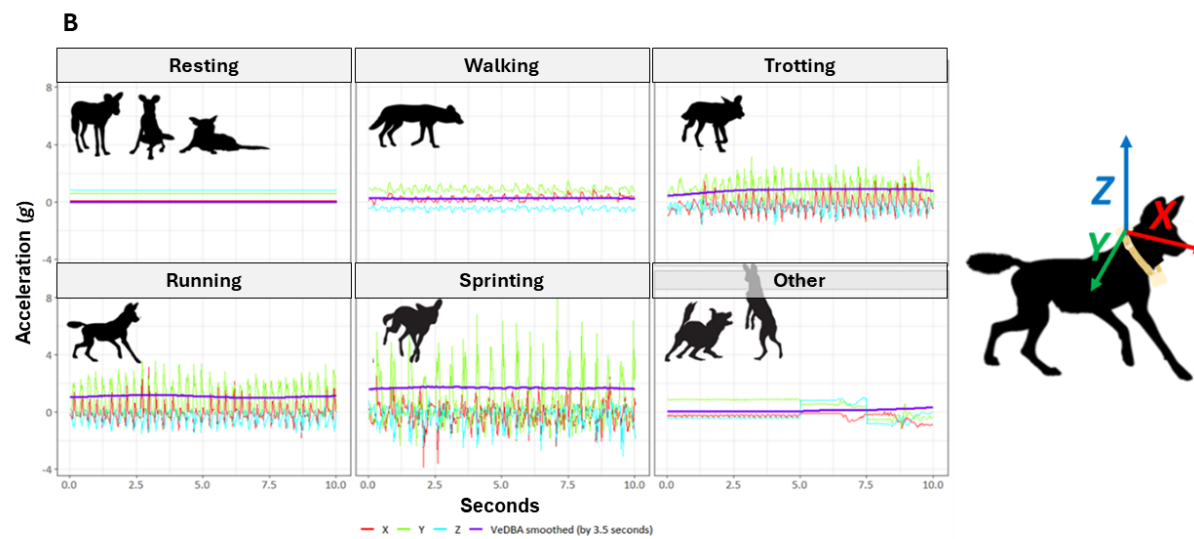
Figure 3. Direct observations of VHF-collared wild dogs showed a strongly crepuscular pattern of hunting activity with pronounced peaks in both hunts (left) and kills (right) around dawn and dusk. (A - B) Greater Kafue Ecosystem. (C - D) Luangwa Valley Ecosystem. (E - F) Selous Game Reserve (from Creel & Creel 2002). These patterns align with temporal variation in VeDBA shown in Figure 2.

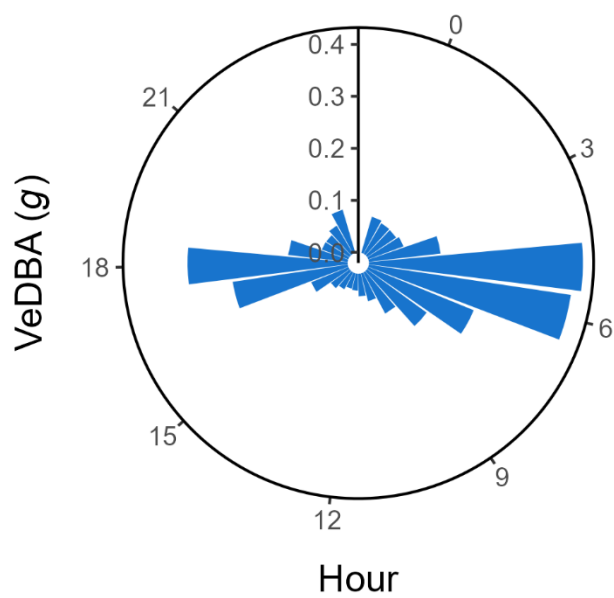
Figure 4. Spatial variation in the expected biomass of common prey for African wild dogs in the Greater Kafue Ecosystem, and in the intensity of use by lions. (A) The movement paths (various colors) of wild dogs defined by dead reckoning of locations at one minute intervals for 7 wild dog packs (\bar{X} = 17 days/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, E, 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.

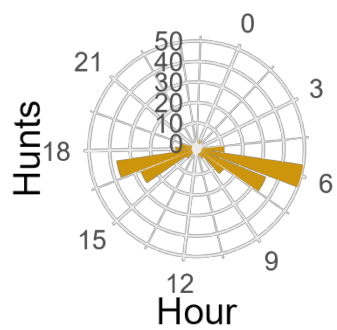
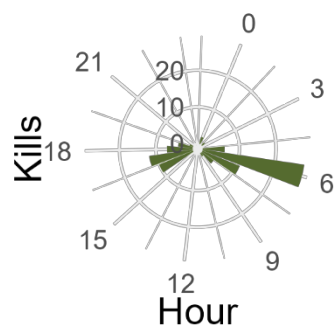
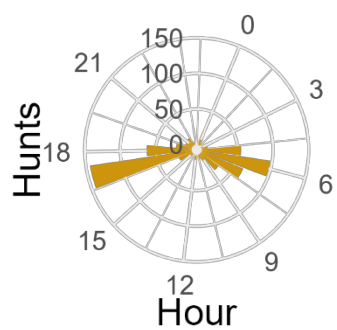
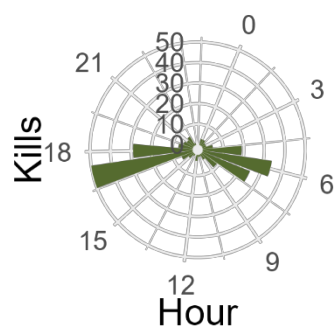
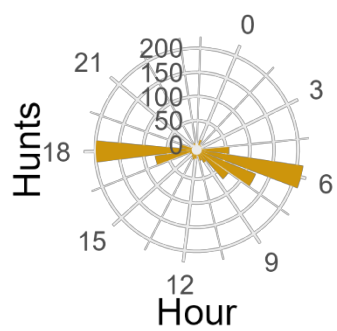
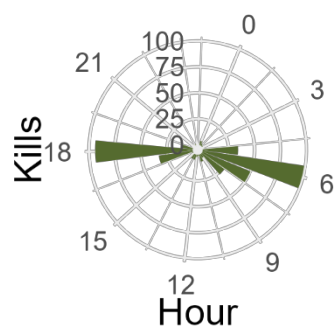
Figure 5. (A) Hunting effort, measured by vectorial dynamic body acceleration (VeDBA), increased when wild dogs were in areas with lower predicted prey biomass, after controlling for autocorrelation and the effects of lion use, protection (National Park vs. Game Management Area), pack size and the number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

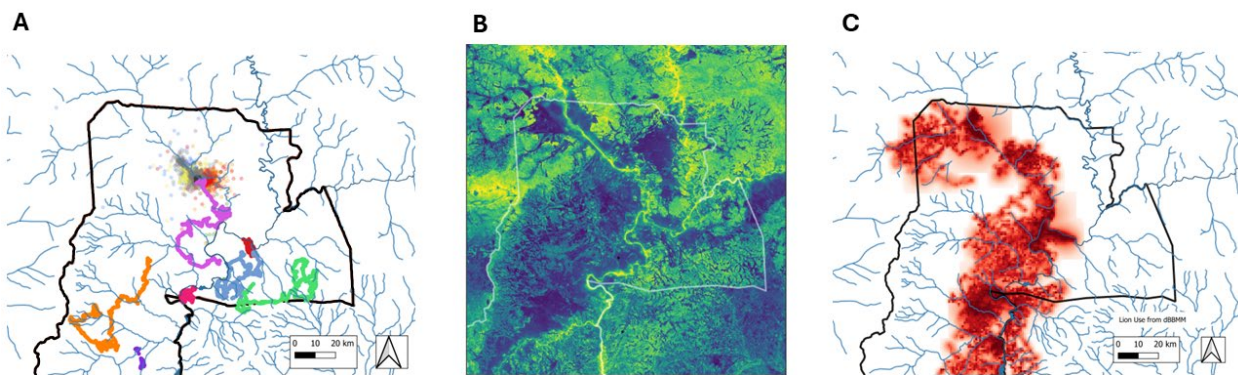
Figure 6. (A) The distance moved per minute increased when wild dogs were in areas with lower prey biomass, after controlling for autocorrelation and the effects of lion use, protection (National Park vs. Game Management Area), pack size and the number of dependent pups. Colors identify data from different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



Figure 7. (A) The number of inferred kills per day was not detectably related to the biomass of prey along the path travelled 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.




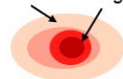


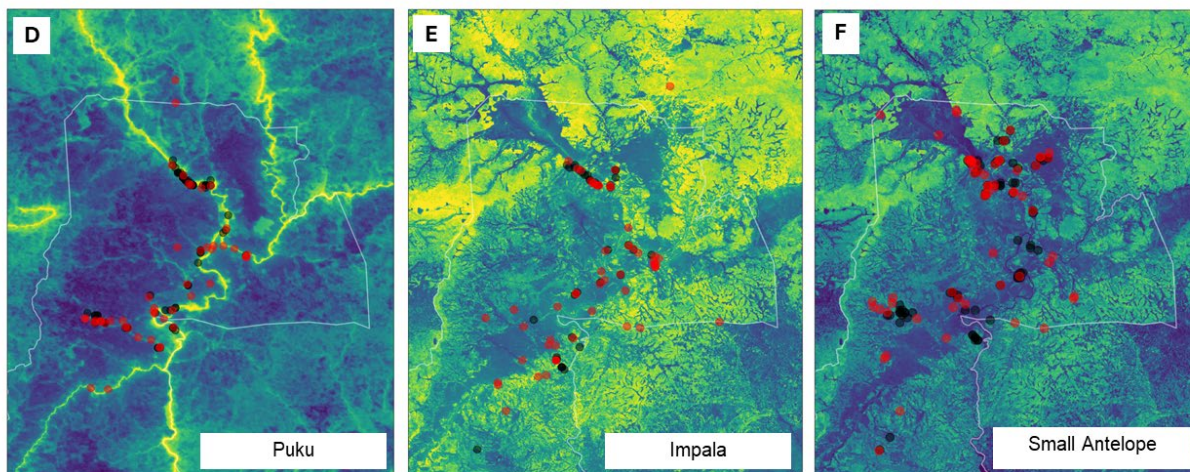
A**B****C****D****E****F**






 African Wild Dog Dead Reckoned Paths
 Puku & Impala Annual Ranges


 10^2 10^3 10^4
 Log₁₀ Total Prey Biomass (kg / km²)

Low High
 Intensity of Use By Lions




 2^0 2^2 2^4 2^6 Log₂ Potential Prey Density (individuals / km²)

 Hunts  Kills

