Appendix 2

Achilles' Heel of Sociality Revealed by Energetic Poverty Trap in Cursorial Hunters

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ABSTRACT: This study empirically tests two foundation ecological theories: (1) pack hunting is a driver for the evolution of sociality; and (2) species have a finite energy potential, whereby increased maintenance costs result in decreased reproductive effort. Using activity and prey data from 22 packs of African wild dogs (*Lycaon pictus*), we parameterized a model detailing the energetic cost/benefit of cooperative hunting. Larger pack size increased foraging time, prey size, and capture probability while reducing chase distance, resulting in a rapidly increasing net rate of energy intake up to a pack size of five, which peaked at 10 individuals and then declined. With a streamlined body plan necessary for hypercursoriality limiting stomach capacity in smaller packs, it was demonstrated that the group hunting benefit will rather accrue to widely foraging predators than to "sit-and-wait" ones. Reproductive effort, measured by the number of pups born, revealed smaller litters with decreasing pack size, validated finite energy theory, and highlighted a "poverty trap" where smaller groups have lower foraging gains, smaller litters, and increased vulnerability to extirpation. Consequently, these results demonstrated a mechanistic example of pervasive selection for maximal body size (Cope's rule), leading to a macroevolutionary ratchet,

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where sociality linked to hypercursoriality is betrayed by an Achilles' heel.

Hunting as a pack, seemingly a conspicuous expression of cooperation in some group-living animals, formerly was uncritically accepted as a factor favoring the evolution of sociality. An obvious prediction of this interpretation would be a positive relationship between group size and foraging returns, but the evidence has proven to be equivocal (Kleiman and Eisenberg 1973; Kruuk 1975, 1986; Nudds 1978; Lamprecht 1981; Macdonald 1983; Bekoff et al. 1984; Packer 1986; Packer and Ruttan 1988; Caro 1989, 1994; Gittleman 1989; Caro and FitzGibbon 1992; Creel and Macdonald 1995; Holekamp et al. 2000; Creel 2001; Creel and Creel 2002; Macdonald et al. 2004). This has prompted an ongoing controversy, at the core of which lies the challenge of measuring costs as well as benefits accrued by cooperative hunting (Creel 1997; Packer and Caro 1997). Earlier studies focused almost exclusively on gross benefits, expressed as per capita food intake, whereas the relevant measure is the per capita net rate of energy intake (Stephens and Krebs 1986; Giraldeau and Caraco 2000). This currency accounts for individual variation in hunting effort but is difficult to measure under natural conditions.

For the proposition that cooperative hunting has favored the evolution of sociality to be supported, it must be demonstrated to provide a net benefit, ultimately measured in terms of individual fitness. This would define an optimal group size below and above which that benefit would deteriorate. The energetic payoff to hunting in a pack is thus likely to affect a life-history trade-off in the proportional energetic allocation between maintenance and reproductive effort (Boggs 1992), since reproduction is energetically costly in carnivores (Gittleman and Oftedal 1987; Oftedal and Gittleman 1989; Creel and Creel 1991). If the finite energy available to animals is partitioned between maintenance and reproductive effort, then members

of groups smaller than the optimum, which thus experience higher maintenance costs, are expected to have less energy to invest in reproduction (Bekoff et al. 1981, 1984; Gittleman 1986, 1993; Moehlman 1986; Creel and Macdonald 1995; Geffen et al. 1996; Moehlman and Hofer 1997; Macdonald et al. 2004). In canids, probably the best-studied taxonomic group in this regard, it was deduced that lower female prenatal food availability resulted in smaller litter sizes (Geffen et al. 1996). However, there has been no empirical demonstration of such an energetic life-history trade-off.

African wild dogs (*Lycaon pictus*) are an ideal species to assess the role of cooperative hunting in the evolution of sociality and to evaluate whether constraints on hunting as a pack result in a reproductive life-history trade-off. Wild dogs can be deemed eusocial (Sherman et al. 1994), living in packs that usually contain an alpha breeding pair with reproductively suppressed helpers. When embarking on a hunt, depending on pack size, a pup guard is sometimes left behind at the den (Courchamp et al. 2002). Wild dogs are hypercursorial hunters (defined as having specialized morphological and physiological adaptations to running) that mainly predate on "least-fit" ungulates and rarely scavenge (Hayward et al. 2006). They share food equitably among pack members and seemingly benefit from foraging in packs (Fanshawe and FitzGibbon 1993; Fuller and Kat 1993; Creel and Creel 1995, 2002; Carbone et al. 1997, 2005; Creel 1997, 2001). For wild dogs, hunting is energetically extremely costly (Gorman et al. 1998), and they have the highest known energetic costs of gestation among all group-living carnivores (Creel and Creel 1991). We thus predict (1) a relationship between optimal pack size and the per capita net rate of energy intake and (2) a reproductive life-history trade-off (i.e., smaller litters) if small packs are energetically compromised. To test these two predictions, we compiled an extensive data set for one wild dog population, which was used to parameterize a model for a detailed energetic cost/benefit analysis of cooperative hunting in this species.

Methods

Pack Composition and Size

Wild dogs were observed by one of us (G. S. A. Rasmussen) between April 1994 and December 2002 in an area totaling 5,500 km^2 in and around Hwange National Park, northwestern Zimbabwe. The habitat is characterized by deciduous tree savanna (45%), miombo woodland on Kalahari sand (40%), and dry early deciduous savanna woodland (15%), with annual rainfall averaging 500–610 mm (Rasmussen 1999). Data were collected during the two distinct periods of a wild dog's year, namely the denning (D) sea-

son (when pups are too small to follow on hunts, with foraging wild dogs having to return to the den) and the nomadic (N) phase (when pups follow on hunts). Data were collected from 22 radio-collared packs, with a study duration of 29.5 ± 20.1 months (mean ± SD) per pack. A pack was defined as a potential breeding unit containing at least one adult of each sex. Three age classes were distinguished: pups (<1 year; P), yearlings (1 year; Y), and adults (≥2 years; A). During a given observation session, once a pack had been located, it was monitored nonstop from a distance of ≥50 m for as long as practically feasible (up to 28 days). Activity, continually monitored visually or from motion sensors incorporated in the radio collars, was recorded at 5-min scan intervals. By using triangulation or visual observation and a GPS unit, location fixes were taken from the radio-collared animal whenever a change in activity mode (resting, walking, or chasing) or direction occurred. Only activity and location data were recorded using radiotelemetry.

For the purpose of the model, a year started with the birth of the pups, with model parameters being equated to the number of adults and yearlings (n_{AY}) during the denning season and to the number of adults, yearlings, and pups (n_{AYP}) during the nomadic phase. For activities involving hunting, the number of yearling and adult wild dogs active in prey procurement (i.e., foraging group size) was used (n_H). To model the data relative to the number of adults and yearlings, relationships between n_{AY}, n_{AYP}, and n_H were ascertained. To test for a relationship between pack size and number of pups born (i.e., litter size), the mean pack size for the year before the pups were born was determined either from direct observations or, if unobserved at that time, by taking the mean n_{AY} at the beginning and end of the year. Maternal parity was noted, and pups were counted as soon as possible after emergence from the den and the week postparturition noted. To determine whether pup mortality could influence reliability of the natality data, pup mortality was recorded between the time the pups were first seen and when the pack became nomadic (weeks observed). In case of subordinate reproduction resulting in multiple litters in a pack, each litter was treated separately to assess individual reproductive output contingent on females' variation in energetic condition during gestation.

Energetic Expenditure

A hunt period (HP) was defined as the active period from rest to rest during which wild dogs sought to procure prey. Wild dogs were observed hunting in the morning and evening and during moonlight. An HP was considered successful when it resulted in at least one kill. Number of HPs per day (n_{HP}) was defined as the sum of all HPs

recorded during the 24-h period between 0000 and 2359 hours. When a moonlight HP encompassed two study days, the HP was allocated to the day in which the greater proportion of the activity had fallen. To evaluate energetic expenditure (kJ/h), the length of a hunt in both time (min) and distance (km) was recorded for each HP. Hunt period time (HPT) was calculated as the time from the moment a pack left its resting site to the start of the first subsequent resting period of more than 30 min. Hunt period distance (HPD) was defined as the sum of all interfix distances during an HP.

An HP constituted of two types of activity: chasing and walking. A chase was defined as a high-speed pursuit of prey. Chases were detected visually, by sound, or by radiotelemetry, with the outcome of observed chases being classified as either success or failure. Chase distance for an HP (CD) was defined as the sum of all interfix distances during a chase and is inevitably an underestimate of the actual distance. Outcomes that were judged, retrospectively, as testing prey (defined as approaching prey with intent but without actually hunting it) were excluded from the analysis. Walking distance (WD) was defined as the distance traveled during an HP when not chasing (WD = HPD − CD).

Energy expenditure (E) was categorized according to activity modes, namely resting (E_r) and hunting (E_h), with the latter comprising walking (E_w) and chasing (E_c). Daily energetic expenditure (DEE) was then calculated from these parameters as the daily resting energetic expenditure (DEE$_r$) plus the daily hunting (walking and chasing) energetic expenditure (DEE$_h$ = DEE$_w$ + DEE$_c$).

Daily resting energetic expenditure (DEE$_r$). Energy expenditure while resting was calculated at E_r = 217.5 kJ/h (Gorman et al. 1998). To assess the time spent resting every day, we multiplied HPT by n_{HP}. The result was subtracted from 24 h to give daily resting allocation. The DEE$_r$ is thus given by the following equation:

$$DEE_r = E_r \times \left(24 - \frac{HPT}{60} \times n_{HP}\right). \tag{1}$$

Daily hunting energetic expenditure (DEE$_h$). The E_h from a pack of 21 adults and yearlings (n_{AY} = 21) was determined to be 10,830 kJ for 3.45 h of hunting (Gorman et al. 1998). This equates to E_h = 3,140 kJ/h. This was deemed the baseline figure for the maximum pack size in our study population (n_{AY} = 15) and corresponded to the sum of energy spent for both walking (E_w) and chasing (E_c). To determine a baseline E_w and E_c (for n_{AY} = 15) per hour, E_w was calculated using the average weight of a wild dog (m_d), its walking speed (v_w), and the following equation (Taylor et al. 1982):

$$E_w =$$
$$m_d \times (10.7 \times m_d^{-0.316} \times v_w + 6.03 \times m_d^{-0.303}) \times 3.6. \tag{2}$$

From this, E_c was determined as follows:

$$E_c = E_h - E_w. \tag{3}$$

This enabled baseline hunt period (for n_{AY} = 15) walking and chasing energetic expenditures (HPE$_w$ and HPE$_c$) to be calculated for both the denning and nomadic periods as follows:

$$HPE_w = \frac{HPT}{60} \times E_w, \tag{4}$$

$$HPE_c = \frac{HPT}{60} \times E_c. \tag{5}$$

Because CD was inversely related to n_H, respective energetic multipliers (C and W) were derived as a function of pack size to cater to the fact that smaller packs expended more energy chasing and less walking, with the baseline for both C and W set at 1.0 for n_{AY} = 15.

Because CDs obtained were interfix distances and thus made no allowance for any zigzagging that may have occurred during a chase or for short testing chases, a conservative additional factor Z was applied to the resultant E_c. This is further justified by the fact that, as a result of the high speed of chases, it was not possible to obtain as many fixes as would accurately reflect the actual distance chased. The DEE$_w$ and DEE$_c$ were thus calculated as follows (for n_{AY} = 2–15):

$$DEE_w = HPE_w \times W \times n_{HP}, \tag{6}$$

$$DEE_c = HPE_c \times C \times n_{HP} \times Z. \tag{7}$$

Consequently, total DEE was obtained by summing equations (1), (6), and (7). Because HPE differed between the denning and nomadic periods (^{D}DEE and ^{N}DEE), the annual mean daily energetic expenditure (^{A}DEE) was given by the following equation (^DD is the pack size–dependent number of days denning):

$$^ADEE = \frac{^DDEE \times {^DD} + {^NDEE} \times (364 - {^DD})}{364}. \tag{8}$$

Energetic Gain

During each HP, kills were recorded according to species, sex, and age class. When the dogs were not visible, if they were in the same position yet active over two consecutive scan samples, radiotelemetry was used as an alert to a kill, which was then visually investigated. Only verified kills were included in the analysis. Microscopic examination of cross sections and scale patterns of hair extracted from wild dog feces was used to confirm that visual observation provided a reliable indicator of smaller prey. Commensurate prey mass was obtained from Skinner and Smithers (1990), the Hwange Ungulate Project, and the Natural History Museum Zimbabwe (table A1 in the online edition of the *American Naturalist*). To equate the total available carcass energetic value (CEV; kJ) of prey relative to their body mass (McClintock 1986), a best-approximation formula was derived to determine mass-related available energetic value (EV; kJ/kg) for different prey masses, and this was multiplied by prey mass. Estimation of EV was based on carcass components (Drew 1991). Accordingly, using EVs based on flesh, viscera, bone, and skin ratios for impala (*Aepyceros melampus*; 31.9 kg at 7,304 kJ/kg) and wildebeest (*Connochaetes taurinus*; 92.7 kg at 6,419 kJ/kg; Creel and Creel 2002), data points were extrapolated to determine values for the range of prey masses in our study area. Because wild dog jaws are insufficiently strong to crack the bones of larger prey, a CEV equation was derived on the basis that EV would reach a lower asymptote (L). On the basis of a ratio of bone to body mass of 0.12 for larger ungulates (Drew 1991) and calculations for impala and wildebeest (Creel and Creel 2002), this asymptote was derived at 5,644 kJ/kg (fig. A1 in the online edition of the *American Naturalist*). Conversely, complete digestion of smaller prey is evidenced by wild dog feces containing only the prey's hair and keratinous portions of the hoofs. Consequently, on the basis of a 4% higher intake being available (since all bones are consumed) in prey smaller than impala, the upper asymptote (U) was derived at 7,337 kJ/kg (fig. A1). Using these values gave a best-fit equation to determine CEV from prey mass (m_p) as follows:

$$\text{CEV} = \text{EV} \times m_p = \left(U + \frac{L - U}{1 + e^{(90.4 - m_p)/13.4}} \right) \times m_p. \quad (9)$$

Using this equation, each kill was assigned a CEV, enabling potential HP intake to be established. Accounting for the pack size–dependent probability of making a kill during an HP (p_C), the pack daily energetic intake (PDEI) was given as follows:

$$\text{PDEI} = \text{CEV} \times p_C \times n_{HP}. \quad (10a)$$

Because of a finite stomach capacity, smaller foraging groups may thus be unable to consume a whole prey item. In these cases, a conservative estimate of 10 kg of meat per hunting individual was allowed for at the respective EV. This resulted in an alternative expression to calculate PDEI for smaller packs when stomach capacity became a limiting factor to intake:

$$\text{PDEI} = (\text{EV} \times 10 \times n_H) \times p_C \times n_{HP}. \quad (10b)$$

To assess daily intake at the individual level, one has to account for the number of individuals in the pack sharing the food (n_S), which may be different from n_H, since some individuals—the lactating female, pups, and/or pup guard—may be waiting for food to be regurgitated at the den. This was determined relative to parturition as follows: (1) 0–4 weeks: number of adults and yearlings plus one to account for additional intake by the lactating female; (2) 5–10 weeks: number of adults and yearlings plus half the number of pups; and (3) ≥11 weeks: total number of adults, yearlings, and pups.

Thus, individual daily energetic intake was DEI = PDEI/n_S. Because DEI differed between the denning and nomadic periods (^{D}DEI and ^{N}DEI), the annual mean daily energetic intake (^{A}DEI) was given by the following equation:

$$^A\text{DEI} = \frac{^D\text{DEI} \times {}^D D + {}^N\text{DEI} \times (364 - {}^D D)}{364}. \quad (11)$$

Net Rate of Energy Intake

The per capita daily net rate of energy intake was obtained by subtracting equation (8) from equation (11): ^{A}DEI − ^{A}DEE.

Data Analysis

Because most of the above equations work at the individual level and vary with pack size, relationships between model parameters and pack size were analyzed to provide values for these parameters. Best-fit regressions were sought for the above variables relative to pack size using SPSS and GraphPad Prism. With the analysis of pups born, maternal parity was included as a covariate, and pack was treated as a repeated measure running a general linear model on SAS software. Where no significant relationship was evident with respect to pack size, mean values for the parameters in question were used.

Results

Pack Size Relationships

Data showed a dichotomous relationship between pack size, the length of the denning season, and the probability of pup guarding: packs with $n_{AY} \leq 5$ denned for 16 weeks ($^{D}D = 112$), and packs with $n_{AY} > 5$ denned for 12 weeks ($^{D}D = 84$), with the probability of a pup guard remaining at the den being 0.38 for packs with $n_{AY} \leq 5$ and 0.97 for packs with $n_{AY} > 5$. A significant relationship was found between n_{AY} and n_{AYP} (table 1). Relationships between the number of adults, yearlings, foraging group size, and the number of supported pups were therefore as follows: $^{D}n_{AY} \leq 5$: $n_{H} = {}^{D}n_{AY} - 0.38$; $^{D}n_{AY} > 5$: $n_{H} = {}^{D}n_{AY} - 0.97$; $^{N}n_{H} = {}^{N}n_{AY}$; and $n_{AYP} = 3.80 + 1.22 \times n_{AY}$.

Energetic Expenditure

Daily resting energetic expenditure (DEE$_r$; eq. [1]). Because there was no significant relationship between pack size and HPT, a mean HPT was used as follows: ^{D}HPT = 151 min (2.51 h), and ^{N}HPT = 133 min (2.20 h; table 1). The n_{HP}'s were significantly different for the denning and nomadic periods ($F = 55.7$, df $= 1, 861$, $P < .001$) and were thus treated separately ($^{D}n_{HP}$ and $^{N}n_{HP}$; fig. 1A).

Daily walking and chasing energetic expenditures (DEE$_w$ and DEE$_c$; eqq. [2]–[7]). Using $v_{w} = 8.37$ km/h (table 1), $m_{d} = 25$ kg, and the above HPT yielded baseline HPE$_w$ and HPE$_c$ (eqq. [4], [5]) for $n_{AY} = 15$ to be, respectively, ^{D}HPE$_w$ = 2,070 kJ/h, ^{N}HPE$_w$ = 1,820 kJ/h, ^{D}HPE$_c$ = 5,810 kJ/h, and ^{N}HPE$_c$ = 5,090 kJ/h.

Estimation of Z. Two wild dogs from the sample of six in the study of Gorman et al. (1998) had a DEE that was 10,370 kJ lower than the others, prompting the authors to speculate that these individuals had not chased, thus giving insight into the actual energetic costs of chasing. Using our values for v_{w} and equations (2) and (3) gave only 7,980 kJ for a 3.45-h hunt. This indicates that our

figures for chasing may be too low and probably are a reflection of the measurement of chase distance. Proportionally, they were 77% lower; therefore, Z was set at 1.30 (i.e., 1.00/0.77).

The HPDs were significantly different between the denning and nomadic periods ($F = 153.6$, df $= 1, 455$, $P < .0001$; table 1); thus, the sample was split into ^{D}HPD and ^{N}HPD. No significant difference was found for CD according to period of the year ($F = 0.30$, df $= 1, 250$, $P = .57$); thus, the regression for CD was used for both periods (fig. 1B).

The CD enabled the range of C_{1-15} for respective n_{H} to be derived at 2.20–1.00, as well as respective walking distances. Consequently, W_{1-15} was calculated to be within the range of 0.93–1.00. These data then enabled DEE$_w$ and DEE$_c$ (eqq. [6], [7]) to be calculated for pack size ranges $n_{AY} = 2$–15.

These results allowed for ^{A}DEE to be calculated relative to pack size (eq. [8]; fig. 2A). Extrapolating these data to a pack size of $n_{AY} = 21$ resulted in DEE = 15,500 kJ, which concurs closely with Gorman et al.'s value of 15,300 kJ.

Energetic Gain

Pack intake. There was a significant difference between CEVs during denning and nomadic periods ($F = 7.5$, df $= 1, 631$, $P = .006$), with mean hunt period ^{D}CEV being 62,000 kJ higher than ^{N}CEV (table 1), thus justifying splitting the sample into the respective periods. The CEVs per HP (^{D}CEVn_{H} and ^{N}CEVn_{AYP}) were determined according to equations in figure 1C. Inspection of resultant ^{D}CEVn_{H} revealed that up to a pack size of $n_{AY} = 5$, the size of the stomach became a limiting factor during the denning season, since food intake was limited to those hunting and carrying meat back to the den. Kill and den sites were 3.7 ± 2.5 km (mean $\pm$ SD; $N = 188$) apart, thus thwarting the possibility for wild dogs to compensate

Table 1: Foraging parameters for wild dogs in the Hwange region, Zimbabwe, 1994–2002

Parameter	Relationship with pack size	N	Mean	Maximum	Minimum	df	F	P	r²
n_{AYP}	$3.80 + 1.22 \times n_{AY}$	1,123				1	813.1	<.001	.42
^{D}HPT	NS	260	150.6	340	25				
^{N}HPT	NS	225	132.6	295	40				
v_{w}	NA	164	8.37	28.0	1.1				
^{D}HPD	NS	193	9.40	23.7	.6				
^{N}HPD	$6.66 - 0.023 \times n_{AYP} - 0.018 \times (n_{AYP})^2 + 0.00047 \times (n_{AYP})^3$	264				3	12.3	<.001	.12
$\overline{X}$ ^{D}CEV	NA	202	398.3	1,286	81				
$\overline{X}$ ^{N}CEV	NA	430	336.3	1,286	30				
EV	$7,309.0 - 49.9 \times n_{AY}$	631				1	53.9	<.001	.08

Note: n_{AYP} = total number of adults, yearlings, and pups; n_{AY} = total number of adults and yearlings; ^{D}HPT = denning hunt period time (min); ^{N}HPT = nomadic hunt period time (min); v_{w} = walking speed (km/h); ^{D}HPD = denning hunt period distance (km); ^{N}HPD = nomadic hunt period distance (km); $\overline{X}$ ^{D}CEV = denning mean carcass energetic value (mJ); $\overline{X}$ ^{N}CEV = nomadic mean carcass energetic value (mJ); EV = energetic value of carcass (kJ/kg) relative to n_{AY}; NS = not significant; NA = not applicable.
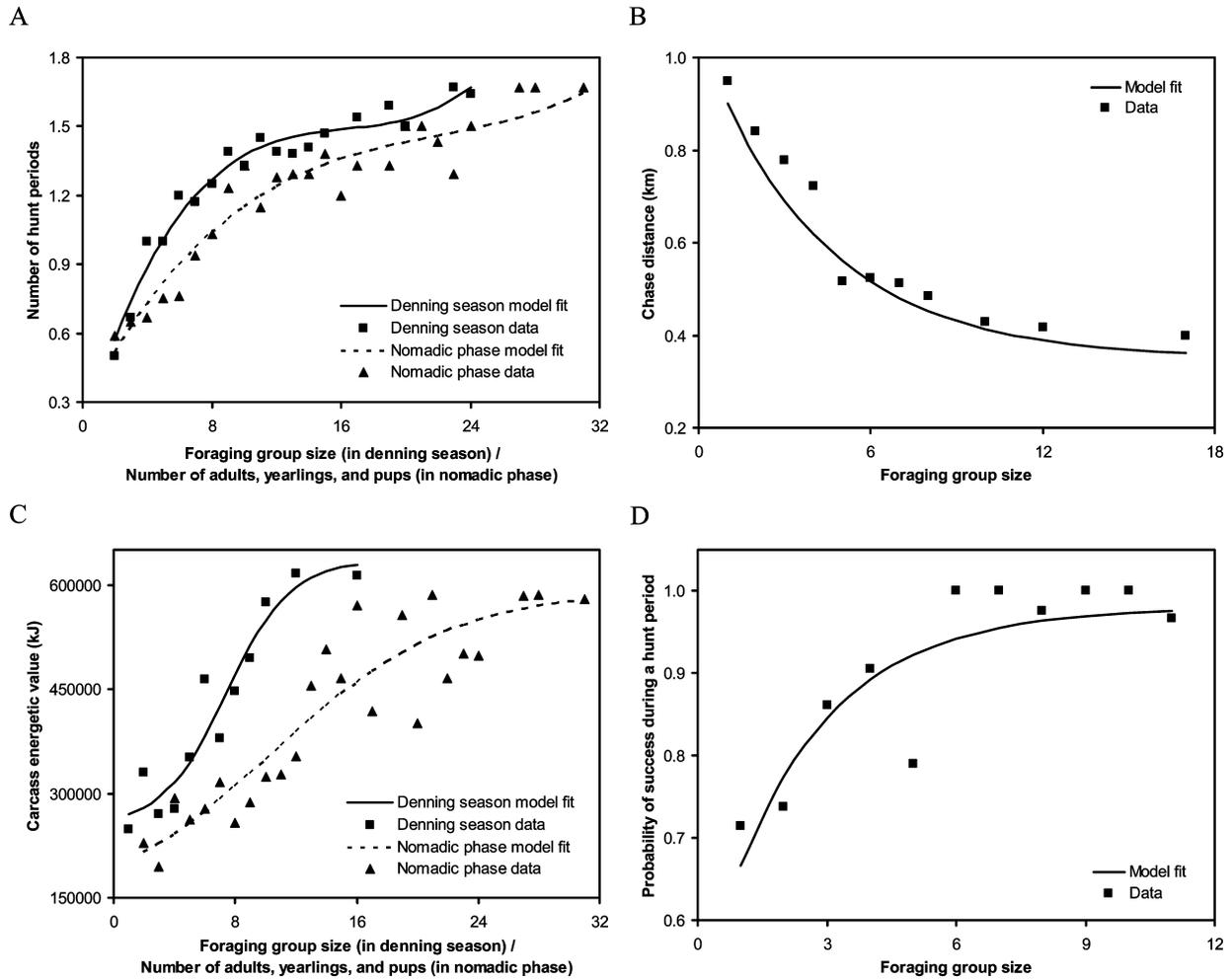
Figure 1: Relationship between pack or foraging group size and (*A*) number of hunt periods per day (denning season [$F = 12.7$, df $= 3, 318$, $P < .01$]: $^{D}n_{HP} = 0.16 + 0.23 \times (n_{AY}) - 0.014 \times (n_{AY})^2 + 0.00028 \times (n_{AY})^3$; nomadic phase [$F = 31.4$, df $= 3, 545$, $P < .01$]: $^{N}n_{HP} = 0.27 + 0.14 \times (n_{AYP}) - 0.0060 \times (n_{AYP})^2 + 0.000083 \times (n_{AYP})^3$), (*B*) mean chase distance per hunt period ($N = 251$, df $= 8$, $r^2 = 0.96$; $^{DN}CD = 0.36 + 0.87 \times e^{-0.28 \times n_H}$), (*C*) carcass energetic value of prey (denning season [$N = 202$, df $= 8$, $r^2 = 0.92$]: $^{D}CEV = 253{,}120 + 381{,}744/[1 + 10^{(7.42 - n_H) \times 0.21}]$; nomadic phase [$N = 430$, df $= 21$, $r^2 = 0.84$]: $^{N}CEV = 129{,}777 + 462{,}358/[1 + 10^{(10.64 - n_{AYP}) \times 0.074}]$), and (*D*) probability of success during a hunt period ($N = 461$, df $= 10$, $r^2 = 0.77$; $p_C = 0.50 + 0.48 \times (1 - e^{-0.42 \times n_H})$) for wild dogs in the Hwange region, Zimbabwe, 1994–2002.

for limited stomach capacity by returning to a kill before being kleptoparasitized. Intake data by species revealed no significant difference between prey frequencies derived from fecal and visual assessments (Wilcoxon signed-rank test: $N = 11$, $Z = -0.12$, $P = .91$).

The probability of making a kill during a hunt period (p_C) increased with pack size (fig. 1*D*); however, there was no relationship between pack size and the likelihood of success once a chase had been initiated ($F = 2.6$, df $= 1, 13$, $P = .13$). Consequently, PDEI was calculated using equation (10a) during the nomadic phase and for pack size $n_{AY} > 5$ during the denning season. Equation (10b) was used for pack size $n_{AY} \leq 5$ during the denning season.

Individual intake. The DEI was determined according to the number of wild dogs sharing and according to the number of weeks that had elapsed since parturition. It was then evaluated at the annual level to provide ^{A}DEI (eq. [11]; fig. 2*B*).

Net Rate of Energy Intake

The per capita daily net rate of energy intake (^{A}DEI $- ^{A}$DEE) is shown in figure 2*C*, supporting our prediction that, up to a certain limit, individuals in larger packs experience increased net foraging returns. Figure 2*C* also illustrates the hypothetical case of stomach capacity not

A

B

C
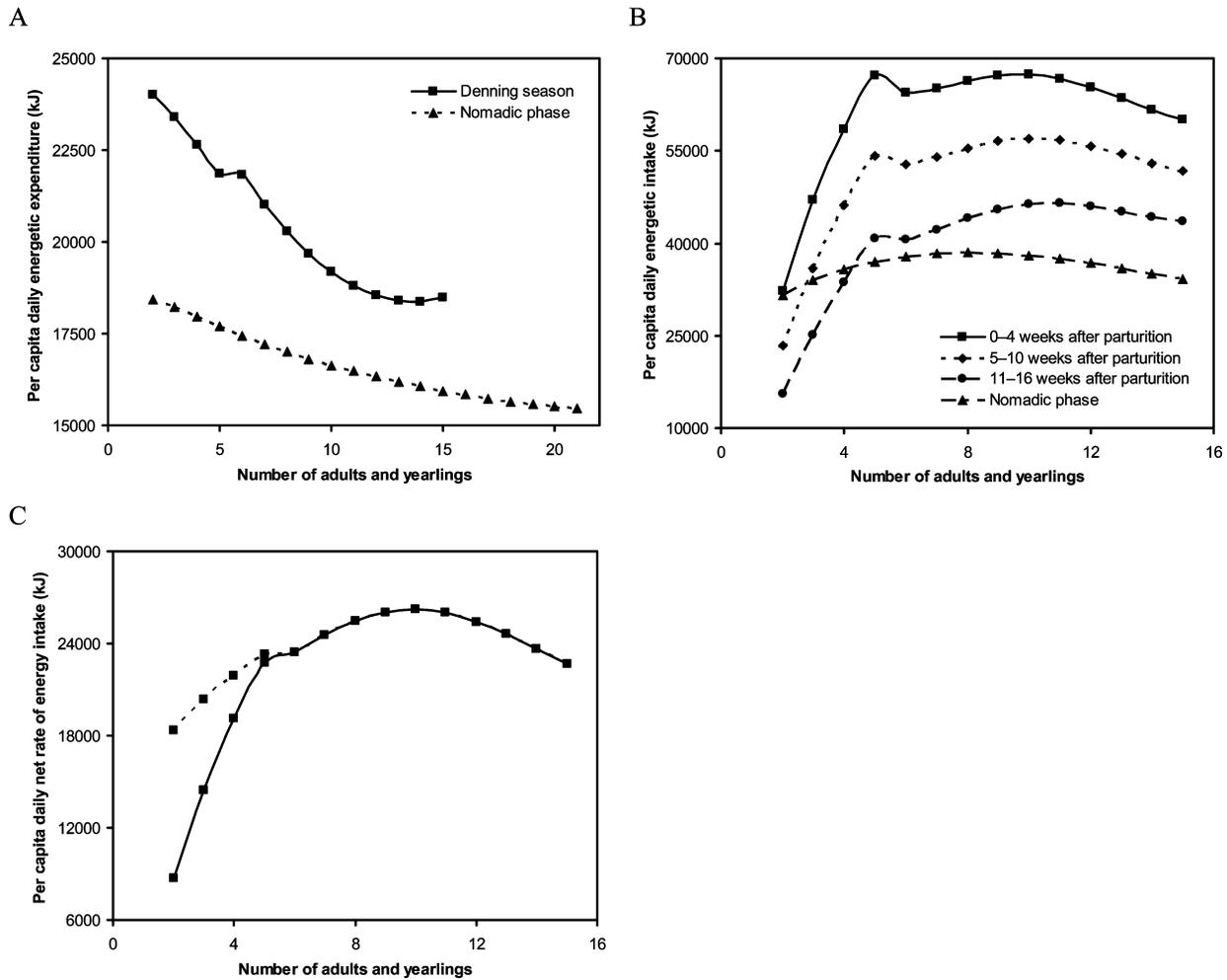
Figure 2: Energetic cost/benefit analysis of cooperative hunting in wild dogs. *A*, Per capita daily energetic expenditure (DEE). *B*, Per capita daily energetic intake (DEI). *C*, Per capita daily net rate of energy intake (DEI − DEE). Also shown is the hypothetical case (*dashed line*) when stomach capacity is not a limiting factor to food intake during the denning season.

being a limiting factor to food intake during the denning season. This highlights the morphological constraint induced by hypercursoriality, limiting food intake in packs with $n_{AY} \leq 5$.

Reproductive Life-History Trade-Off

Pup age when first counted was 6.0 ± 2.7 weeks (mean ± SD; minimum = 2, maximum = 11; N = 36). Weekly pup mortality (calculated as mortality/number of weeks observed) was 0.04 ± 0.09 (mean ± SD; minimum = 0.00, maximum = 0.50; N = 36).

We observed only a single subordinate female giving birth, with the two litters being treated separately. Maternal parity as a covariate did not affect the number of pups born (N = 36, χ^2 = 1.5, P = .68), and a significant positive relationship between mean pack size the year before and litter size was found (N = 36, B = 3.5, t = 3.6, P = .001, r^2 = 0.36; fig. 3).

Weekly pup mortality rate relative to number of dogs in the pack during the denning period (calculated as weekly pup mortality/number of pups born) was not related to pack size (N = 36, B = 3.5, t = 3.6, P = .19, r^2 = 0.06). The slope was positive, possibly indicating a bias toward larger packs losing proportionally more pups. To test the effect of this, on the assumption that weekly mortality rates observed were constant, numbers of pups first seen were accordingly adjusted to give a "projected number of pups born." Because this strengthened the relationship (N = 36, B = 3.2, t = 3.5, P = .001, r^2 =
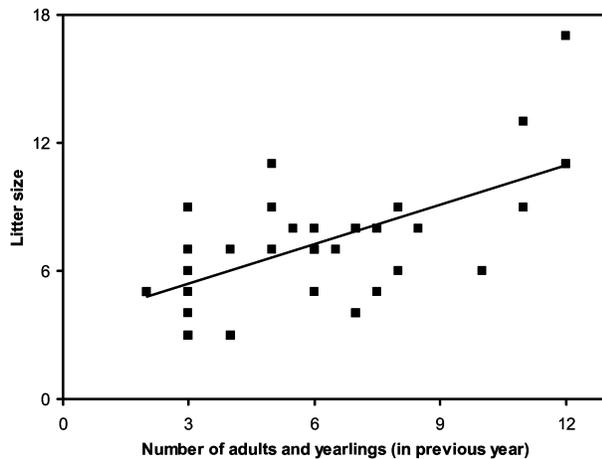
Figure 3: Reproductive life-history trade-off (i.e., smaller litters) resulting from cooperative hunting in wild dogs ($N = 36$, $B = 3.5$, $t = 3.6$, $P = .001$, $r^2 = 0.36$).

0.43), it is deemed unlikely that the inability to obtain an exact head count at birth has affected the result, supporting our prediction that small packs, energetically compromised by higher maintenance costs, exhibit reduced reproductive output.

Discussion

Our model integrates the energetic costs and benefits of cooperative hunting in wild dogs under natural conditions and evaluates the life-history consequences thereof. Under the conditions in our study area, we found a positive relationship between pack size and the net rate of energy intake up to a pack size of 10. We also showed that smaller packs have a lower reproductive output, most likely as a consequence of their lower energetic intake. In tandem, our study empirically tests two widely accepted ecological assumptions: (1) that one of the drivers for the evolution of sociality can be foraging benefits and (2) that if energetic maintenance costs increase, reproductive investment will decrease.

If social animals live in an aggregation economy that was accrued to foraging (Giraldeau and Caraco 2000), individuals should initially experience higher foraging payoffs with increasing group size G that reach a peak at G^* and then fall with further increases in group size. In our study, we indeed found such a dome-shaped relationship, with $G^* = 10$ (fig. 2*C*). Because group foraging is favored in such an economy, G is predicted to equilibrate around the optimal size G^*, at which each group member would maximize its net energy gain from cooperative hunting (Giraldeau and Caraco 2000). While the observed

median pack size of six ($N = 22$ packs) in our study population does not match G^*, it does match the point at which the rate of increase in benefits greatly reduces (fig. 2*C*). While it may be argued that the optimum group size for hunting may not be the overriding factor determining pack size and that other aggregation benefits could shape pack size, we argue that because net energy is the minimum mappable ecological unit, it can be deemed a valid indicator of individual fitness. Consequently, the size of G suggests not only that wild dogs in our study population may be energetically compromised and close to falling into an energetic poverty trap but also that a comparison of G^* with the actual group size can provide a conservation tool to indicate the energetic condition of a population.

While three other studies of widely foraging predators also report net benefits of cooperative hunting (Boesch 1994; Creel 1997; Vucetich et al. 2004), Huey et al. (2001) suggested that hypercursoriality is a precarious lifestyle, with predators that occupy the "widely foraging" niche risking "running on empty." Foraging mode belies a number of ecological consequences with respect to body plan and lifestyle (Huey and Pianka 1981; Perry and Pianka 1997), with our study highlighting the morphological trade-off between running and a stomach capacity that maximizes foraging returns. This study thus adds to our mechanistic understanding of the energetic constraints on the diet of carnivores (Carbone et al. 1999, 2007; McNab 2000). Furthermore, as a result of the excessive costs of chasing revealed by this study, we found that the tangible energetic benefits of group foraging start to accrue only at a pack size of five (fig. 2*C*). In this case, sociality becomes an obligate necessity and can consequently become an Achilles' heel under suboptimal environmental conditions.

These results also provide a mechanistic example of how pervasive selection for maximal body size (Cope's rule) can lead to a macroevolutionary ratchet locking animals into a trend of increased morphological and physiological specialization, thus resulting in premature clade and taxa extinctions, as documented in fossil canids (hespercyonines and borophagines). Here, none of the hypercarnivorous species persisted for more than 6 million years, whereas more omnivorous species endured up to 11 million years, with it being hypothesized that hypercursorial Permian therapsids, creodonts, amphicyonids, and hyaenids followed the same path (Van Valkenburgh et al. 2004*a*). In the case of wild dogs, to compete at the top of the African predator guild alongside spotted hyenas (*Crocuta crocuta*) and lions (*Panthera leo*), they have indeed specialized to the extreme to occupy the "widely foraging" niche. These include the m1P4 trenchant heel, a skull length to breadth ratio giving them one of the highest bite forces for a mammal relative to its mass (Wroe et al. 2005), an absence of metacarpel 1, a stomach capacity that

equates to nearly 40% of their body weight, and unique turbinates thought to facilitate maximal oxygen intake (Van Valkenburgh et al. 2004*b*). Conversely, energetically frugal lions at the "sit-and-wait" end of the foraging continuum lack constraints on stomach capacity, which enables the net rate of intake to be maximized in pairs (Packer and Ruttan 1988) and highlights that other aggregation benefits contribute to their sociality. This thought process leads us to speculate as to where spotted hyenas fit in. Through a clan system, while they do scavenge, they also rank as a top cursorial predator and, where advantageous, hunt in groups, though they mostly do so in singletons or pairs (Holekamp et al. 1997, 2000). Consequently, rather than being obligate hunters, they can be termed facultative social foragers, able to profit from either energetically expensive hypercursorial hunting or frugal scavenging. Large body size and the ability to evoke the collective ability of the clan when essential, coupled with craniodental morphology that enables them to access energetically rich pickings accrued from bone cracking, substantially contribute to ensure that they can maximally utilize forage gains, and hopefully they have avoided the precarious niche.

In our study, we found no relationship between pack size and the likelihood of success once a chase had been initiated. This indicates that with the excessive costs of chasing at stake, smaller packs use an all-or-nothing strategy once energetic investment has commenced. This would also explain why smaller packs have longer chase distances (fig. 1*B*) and the overall high hunting success (fig. 1*D*), as generally found in wild dogs when compared with other large predators (Hayward et al. 2006). Similarly, Carbone et al. (2005) found that smaller packs of wild dogs spend more time feeding than do larger packs and consume more of a carcass, including the energetically poorest sections. This also indicates that small packs are under more severe energetic stress and are of concern regarding the wild dog, which is considered endangered by the International Union for Conservation of Nature (Woodroffe et al. 2004) and prone to multiple Allee effects at small pack size (Courchamp et al. 1999, 2000, 2002; Courchamp and Macdonald 2001; Berec et al. 2007). As an illustration, Courchamp et al. (2002) found that the threshold pack size at which leaving a pup guard becomes economic when embarking on a hunt is around five. Strikingly, our model (fig. 2*C*) revealed that the same minimum pack size was required to capitalize on the energetic benefits of group foraging.

It seems that small wild dog packs are energetically compromised, leading to less energy being available for reproduction, a constraint that, in turn, predicts a decrease in litter size. We found that smaller packs did indeed have significantly smaller litters (fig. 3), suggesting a reproductive life-history trade-off and validating foundation ecological theory (Odum 1953). Changes in litter size may be attributed primarily to differences in food availability in a number of canid species (Macdonald et al. 2004). Our study thus illustrates how an energetic poverty trap can drive a process leading to a characteristic extinction vortex, with reduction in group size resulting in lower net foraging gains and smaller litters and eventually in group extirpation. This has important management implications regarding, for example, the potential benefits of artificial group augmentation (Graf et al. 2006), setting of hunting quotas, and limiting ecotourism activities involving hypercursorial cooperative hunters (Courchamp et al. 2006).

The evolution of sociality has been a dominant issue in the study of animal behavior, with cooperative hunting being regarded as one of the most widely distributed forms of cooperation among predatory mammals (Packer and Ruttan 1988), including humans (King 1975). Anthropologists have even speculated that convergent factors underlie the social evolution in hominids and *Lycaon* (Mellinger 1982). Our study indicates that, up to a certain limit, net benefits of cooperative hunting offset increased food demands of larger groups. Conversely, group size can fall below a critical threshold where daily energy requirements can barely be met, resulting in a reproductive life-history trade-off. Overall, it becomes apparent that where cooperative hunting is causal to the evolution of sociality, it is the foraging mode that is the driver of sociality rather than group foraging per se. Intriguingly, there are few obligate social, hypercursorial species, highlighting the potentially precarious nature of this niche.

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Appendix from G. S. A. Rasmussen et al., "Achilles' Heel of Sociality Revealed by Energetic Poverty Trap in Cursorial Hunters"

(Am. Nat., vol. 172, no. 4, p. 508)

Relationships between Prey Mass and Energetic Value Available to *Lycaon pictus*

Table A1
Mean mass (kg) of prey eaten by wild dogs in the Hwange region, Zimbabwe, 1994–2002

Prey	Adult			Subadult			Young		
	Male	Female	Sex unknown	Male	Female	Sex unknown	Male	Female	Sex unknown
Bat-eared fox	4.1	4.1	4.1						
Bushbuck	45.0	30.0	37.5						
Bushpig	62.0	60.0	61.0						
Duiker	18.7	20.7	19.7						
Eland		460.0					126.3	134.8	130.5
Grysbok	10.3	10.3	10.3						
Impala	45.7	38.5	42.1	35.6	31.4	33.5	22.7	17.7	20.2
Kudu	227.8	157.4	192.6	85.5	98.7	92.1	44.3	46.1	45.2
Sable		185.0					32.0	43.5	37.8
Springhare			3.5						
Steenbok	11.1	11.1	11.1						
Warthog							10.0	10.0	10.0
Waterbuck		209.1							42.7
Wildebeest									51.0
Zebra									95.0

Note: Sources are Skinner and Smithers (1990), the Hwange Ungulate Project (Centre Nationale de la Recherche Scientifique), and the Natural History Museum Zimbabwe.

1
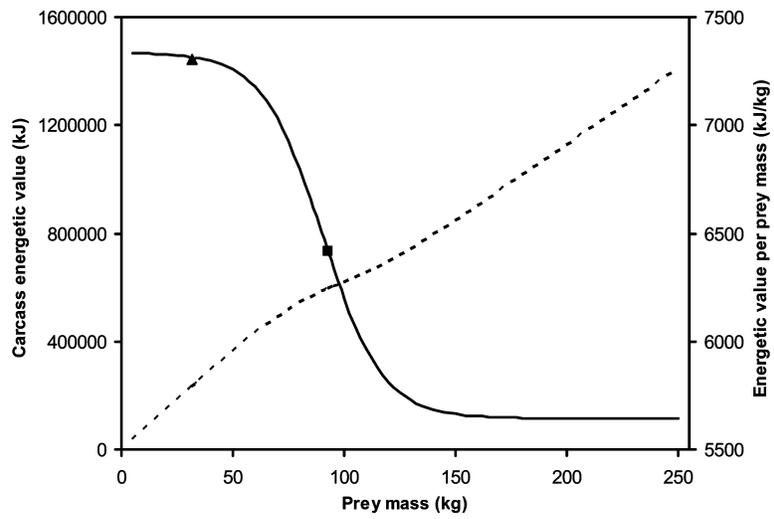
Figure A1: Relationship between prey mass, energetic value per prey mass (*solid line*), and total available carcass energetic value of prey (*dashed line*) eaten by wild dogs in the Hwange region, Zimbabwe, 1994–2002. Symbols indicate values for impala (*triangle*) and wildebeest (*square*) from Creel and Creel (2002).