

# Reports

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## Hunting on a hot day: effects of temperature on interactions between African wild dogs and their prey

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**Abstract.** As global temperatures increase, interactions between species are affected by changes in distribution, abundance and phenology, but also by changes in behavior. The heat dissipation limitation hypothesis suggests that the ability to dissipate heat commonly limits the activity of endotherms, a problem that should be particularly acute for cursorial predators and their prey in equatorial ecosystems. Allometric relationships suggest that heat dissipation should be a stronger constraint for larger species, so that (smaller) predators should be less affected than (larger) prey. We used data from 266 complete days of direct observation of African wild dogs (*Lycaon pictus*) in five packs over a period of 2 yr to test how deviations of temperature from that expected for the time of day affected eight measures of hunting effort and success. We found that higher temperatures disadvantaged the prey of wild dogs more than the dogs themselves, with increased hunting success and shorter pursuits on warmer days. Broadly, our results demonstrate that effects of temperature on behavior can alter interactions between species, exacerbating or offsetting the direct effects of climate change.

**Key words:** African wild dog; hunting; *Lycaon pictus*; predation; temperature.

### INTRODUCTION

As global temperatures increase, interactions between species are affected. It is well-established that temperature-dependent changes in species' distribution, abundance and phenology can alter trophic relationships, with consequences for population dynamics (Walther et al. 2002, Pearson and Dawson 2003, Edwards and Richardson 2004). Temperature also has obvious effects on behavior in most animal species, which suggests that changes in behavior could play an important role in determining the effect of rising temperatures on interactions between species. In particular, predators and their prey commonly have very different body sizes, morphology, physiology, and behavior — making it likely that a change in temperature might affect them differently and thus alter their interactions (Harley 2011, Grigaltchik et al. 2012, Allan et al. 2015).

Several studies of vertebrate predators hunting invertebrate prey show that higher temperatures increase

hunting success by altering the activity or availability of poikilothermic prey (Avery and Krebs 1984, Avery 1985, Rodenhouse 1992). In interactions between pairs of fish species, predators and prey do not necessarily acclimate to temperature changes in the same manner even though both are ectothermic, and this can affect attack rates, escape speeds, and the intensity of predation (Grigaltchik et al. 2012, Allan et al. 2015). The expected effect of temperature on predator-prey interactions between pairs of endotherms is not intuitively obvious (though some human populations are known to have changed the species, location, and time that they hunt in response to climate change: Berkes and Jolly 2002). Understanding the effect of increasing temperature on the dynamics of large carnivores and their antelope prey is important because both groups are in global decline (Estes et al. 2011, Ripple et al. 2015), and the African wild dog (*Lycaon pictus*) studied here is among the world's most endangered large carnivores.

Speakman and Krol (2010) found that the ability to dissipate heat often limits the activity of endotherms, and large African carnivores and the antelopes that they hunt possess a range of adaptations to reduce the problem of

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FIG. 1. African wild dogs and their prey both possess adaptations to tolerate or dissipate the heat generated by sustained fast running, including morphological adaptations such as long, slender limbs and large, vascularized ears.

overheating during sustained pursuit or flight (Fig. 1). For example, the carotid rete allows the tremendous heat generated by sustained high-speed running to be better tolerated (Taylor and Lyman 1972, Baker and Chapman 1977, Owen-Smith 1998), and long, slender limbs and large ears serve to dissipate heat (Speakman and Krol 2010). Despite such adaptations, high temperatures are a constraint on activity for tropical ungulates and carnivores (Owen-Smith 1998, Speakman and Krol 2010, Shrestha et al. 2014), and mean temperature in Southern Africa has risen  $0.2^{\circ}\text{C}$  per decade since 1960 (Kruger and Shongwe 2004). As mean temperature rises, interactions among these species are likely to be affected by differences in response.

African wild dogs are among the most cursorial of predators, traveling more than 10 km/d in search of suitable hunting opportunities and pursuing prey at high speeds over long distances (Estes and Goddard 1967, Fanshawe and Fitzgibbon 1993, Creel and Creel 1995, Gorman et al. 1998, Speakman et al. 2015). Given the limiting effect of heat accumulation on running performance, one might predict that high temperatures should decrease their hunting activity or success, but it is also possible that heat is a greater constraint for their prey than for the dogs themselves. Wild dogs commonly cooperate to kill antelopes more than 10 times their own mass (Creel and Creel 1995), and well-described allometric relationships suggest that the lower surface area to volume ratio of larger prey should cause them to overheat more rapidly than smaller predators, through effects on all pathways of heat flux (Schmidt-Nielsen 1984, Porter and Kearney 2009, Speakman and Krol 2010). Indeed, recent data confirm that activity patterns are more strongly constrained by high temperature in large antelopes relative to smaller antelopes (Shrestha et al. 2014). On the other hand, larger species generally show less increase in metabolic rate (and consequent heat) as running speed increases (Taylor et al. 1970). Because

different allometric effects on heat balance run in opposite directions, the net effect of temperature deviation on predator-prey interactions is difficult to predict with certainty, increasing the value of empirical tests.

To address this question empirically, we used continuous direct observations of five wild dog packs on 266 complete d over 2 yr to test the effect of temperature on eight measures of hunting effort and success. Specifically, we first determined the “temperature deviation” for a given day by relating temperature to time. We then determined whether hunts occurred under hotter or cooler conditions than expected for the time of day and tested how each measure of hunting success or effort was affected. Wild dogs hunt virtually every day, concentrating their activity into two periods at dawn and dusk (Mills and Biggs 1993, Creel and Creel 2002, Cozzi et al. 2012, Rasmussen and Macdonald 2012), which for the Selous population studied here summed to a mean of 3.9 active h per day (Creel and Creel 2002). This crepuscular pattern of activity reduces the likelihood of nocturnal encounters with lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*), both larger competitors that commonly steal carcasses from wild dogs or even kill them (Estes and Goddard 1967, Fanshawe and Fitzgibbon 1993, Mills and Biggs 1993, Creel and Creel 1996, Broekhuis et al. 2013). In theory, wild dogs could respond to day-to-day variation in temperature in two ways, either by altering the time at which they hunt to maintain relatively constant temperature, or by hunting at relatively fixed times and thus experiencing variation in temperature. Prior research on wild dogs has described peaks of hunting activity at dawn and dusk that are stable year-round (Mills and Biggs 1993, Creel and Creel 2002), and there was no detectable effect of temperature on the time at which they hunted (see results herein). Consequently, wild dogs in Selous experienced substantial day-to-day temperature variation while hunting in relatively fixed time windows, providing an opportunity to test the

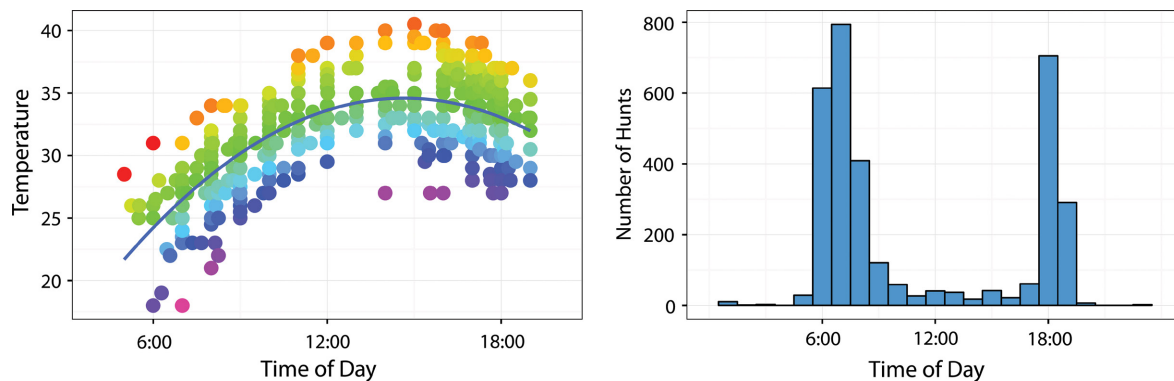


FIG. 2. Left: Ambient shaded temperatures recorded while following African wild dogs in the Selous Game Reserve showed that time of day explained 45% of the observed variation in temperature, but there is substantial variation in temperature at a given time of day. Shading shows the 95% confidence limits for the second order polynomial regression. Residuals from this polynomial regression provide a measure of temperature deviation from the conditions expected on an average day (here scaled to the color spectrum). Right: Hunting activity was concentrated into two crepuscular periods, peaking near dawn and dusk, year-round. Wild dogs experienced considerable day-to-day variation in temperature while hunting within these time windows.

effects of temperature variation on hunting effort and success.

#### METHODS

We gathered data on hunting success and temperature from wild dogs in five radio-collared packs over a period of 2 yr (1992–1994) in the Selous Game Reserve, Tanzania. Observations were evenly distributed across all months except March, April, and the first 2 weeks of May. Detailed methods for observation of hunts have been described previously (Creel and Creel 1995, 2002). Briefly, we used VHF telemetry to locate wild dogs and followed them continuously to record encounters with prey, hunts, and kills by direct observation. We recorded chase distances using a combination of the vehicle odometer (with units of 0.05 km) and a laser rangefinder to measure distances run by the dogs but not followed with the vehicle. Distances recorded in this manner are more accurate than can be obtained from less-direct methods such as GPS collars, because the start and finish are observed directly, and hunts typically do not follow straight lines over the interval between GPS fixes (Creel et al. 2013). Adults are the primary hunters in wild dog packs (Creel and Creel 1995), and the size of packs in this study ranged from 3 to 20 adults ( $\bar{X} = 8.2 \pm 0.20$  SE). Of 17 species hunted, the most common targets were impala (*Aepyceros melampus*,  $N = 293$  hunts), wildebeest (*Connochaetes taurinus*,  $N = 266$ ) and warthog (*Phacocoerus africanus*,  $N = 88$ ). For the data analyzed here, the mean mass of killed prey ( $87.9 \text{ kg} \pm 14.8$  SE) was more than triple that of a wild dog. The data in this paper are restricted to 266 d on which we followed a pack continuously through all activity ( $\bar{X} = 3.9 \pm 0.2$  SE hours of hunting and  $12.3 \pm 0.5$  SE kilometers moved in 24 h), providing data on (1) the daily number of “chases” or “hunts;” operationally defined by pursuit at a fast run for >50 m, bringing prey to bay or making a kill; (2) daily

number of kills; (3) daily mean distance of chases; and (4) mean distance of successful chases that ended in a kill; (5) daily hours of hunting activity, (6) kilometers traveled daily; (7) mean kill mass; and (8) daily kilograms of meat obtained per dog.

During wild dog follows on the 266 d just described, we recorded shaded ambient air temperature (outside the vehicle) and the time of observation on 943 occasions ( $\bar{X} = 3.5$  observations per day) distributed representatively.

#### Statistical analysis

To determine a daily “temperature deviation” that quantified how hot or cold a specific day was in comparison to the temperature expected for that time of day, we regressed temperature on time of day, fitting a polynomial regression via ordinary least squares with the `lm()` function of the base stats package in R. We confirmed the model’s assumptions and fit using quantile-quantile, scale-location, and residual-fitted plots (here and throughout). We then used the residuals from this regression as a measure of temperature deviation from expectation in units of °C (Fig. 2). We used polynomial regression to confirm that most (76%) of this variation in temperature was unrelated to the day of year.

With temperature deviation as the independent variable of interest, we used generalized linear mixed models (GLMMs) to examine effects on each of the eight measures of hunting effort and success. Pack size is known to affect hunting effort and success and packs differ in patterns of prey selection, so our inferences are based on GLMMs that controlled for fixed effects of pack size and random effects of pack identity. We fit GLMMs using the `glmer()` function of the `lme4` package, with a Poisson distribution for models of the number of hunts and kills, and a Gaussian distribution for models of chase distance, successful chase distance, kilometers

traveled, mass of food obtained, and duration of hunting activity. For each dependent variable, we confirmed that the regression coefficient for the effect of temperature deviation was stable across a set of regression models including the GLMM just described, a GLM including only fixed effects of pack size and temperature deviation, and a GLMM including only a fixed effect of temperature deviation and a random effect of pack identity. Inferences about the effect of temperature deviation were stable across these models for all response variables. For all dependent variables, AIC scores consistently supported models that estimated effects of temperature while controlling effects of pack size and pack identity (minimum  $\Delta\text{AIC} \geq 6.1$ , compared to univariate models with the temperature deviation effect only). Using models of the number of hunts as an example,  $\Delta\text{AIC} = 0$  for the full GLMM with temperature, pack size and pack identity, 15.7 for the GLMM with temperature and pack identity, 84.3 for the GLM with temperature and pack size, and 215.3 for the GLM with temperature only. No inferences about the significance of temperature were altered by the choice of model, for any of the dependent variables.

## RESULTS

As expected, temperature showed a quadratic relationship to time of day (Fig. 2), with time explaining 45% of the variance in temperature. Temperatures typically ranged from the mid-20s during the morning hunting period, peaked in the mid-30s in the afternoon, and dropped into the low 30s during the evening hunting period. Within this basic pattern, there was considerable variation, with the coldest and warmest days differing by approximately 15°C across all times of day (Fig. 2). Because the study site is equatorial and coastal, most of this variation was due to factors other than season ( $r^2 = 0.24$  for a third-order polynomial regression of temperature deviation on Julian date). Wild dogs did not detectably alter the time of day at which they hunted in response to temperature deviation ( $b = -0.40 \pm 0.86$  SE,  $z = -0.47$ ,  $P = 0.64$ ) in either the morning or evening hunting period (interaction of temperature deviation X am/pm:  $b = -0.21 \pm 1.10$  SE,  $z = -0.18$ ,  $P = 0.85$ ), suggesting that the timing of hunts is more directly linked to time than to temperature. Consequently, wild dogs experience considerable day-to-day variation in the temperatures at which they hunt.

Examining the relationship of hunting effort and success to temperature deviation, the daily number of hunts and kills both increased on hotter than expected days (Fig. 3: hunts:  $b = 0.015 \pm 0.007$  SE,  $z = 2.16$ ,  $P = 0.031$ , kills:  $b = 0.049 \pm 0.010$  SE,  $z = 4.76$ ,  $P < 0.001$ ). While there was considerable variation among packs (with large packs hunting and killing more often), these multiplicative effects indicate that the number of hunts per day increased on average by 1.5% per °C, while the number of kills per day increased by 4.9% per °C. The

effect of temperature deviation on the number of kills made was consistently positive for all packs. As suggested by the larger increase in killing rate than in hunting rate, hunting success (the ratio of kills to hunts) increased under hotter than expected conditions ( $b = 0.060 \pm 0.031$  SE,  $t = 1.91$ ,  $P = 0.056$ ).

The distance of chases decreased on hotter than average days ( $b = -0.05 \pm 0.008$  SE,  $z = -7.00$ ,  $P < 0.0001$ ), particularly for successful chases that ended in a kill ( $b = -0.09 \pm 0.011$  SE,  $z = -8.51$ ,  $P < 0.0001$ ) (Fig. 3). There was again substantial variation among packs (with large packs making shorter chases), but these additive effects indicate that chases were on average 55 m shorter per °C (a 9.5% reduction relative to the mean of  $570 \pm 30$  m), and successful chases were 90 m shorter per °C (an 11.0% reduction relative to the mean of  $840 \pm 50$  m). The effect of temperature deviation was consistently negative for all but one pack (which was quite large and thus had relatively short chases).

The daily duration of hunting activity ( $b = -0.038 \pm 0.024$  SE,  $z = -1.60$ ,  $P = 0.14$ ), daily distance traveled ( $b = -0.102 \pm 0.108$  SE,  $z = -0.95$ ,  $P = 0.51$ ) and kilograms of meat obtained per individual ( $b = 0.083 \pm 0.065$  SE,  $z = 1.27$ ,  $P = 0.21$ ) were not detectably related to temperature deviation (Fig. 3). Consistent with the observation that number of kills increased with temperature deviation but kilograms of meat obtained per individual did not, the mean mass of killed prey tended to decrease under hotter conditions ( $b = -0.735 \pm 0.432$  SE,  $z = -1.70$ ,  $P = 0.089$ ), though the effect was not strong.

The relationships shown in Fig. 3 all show some variation among packs. While the effects of temperature deviation described above are from models that control for variation in pack size and pack identity, these models did not include an interaction between temperature deviation and pack size, which the data suggest might exist. Post hoc, we fit a model that added this interaction to each model with a significant main effect of temperature deviation, and in every case, the main effect of temperature deviation on hunting effort or success was greatly strengthened (hunts:  $b = 0.0578 \pm 0.014$  SE,  $t = 4.02$ ,  $P < 0.0001$ , kills:  $b = 0.128 \pm 0.021$  SE,  $t = 6.22$ ,  $P < 0.0001$ , chase distance:  $b = -0.075 \pm 0.015$  SE,  $t = 5.01$ ,  $P < 0.0001$ , successful chase distance:  $b = -0.158 \pm 0.022$  SE,  $t = 7.12$ ,  $P < 0.0001$ ). Because these coefficients were estimated by models that included an interaction suggested by the data, our discussion below focusses on effect sizes from the original models. If inference from models including the interaction term was preferred, the influence of temperature deviation on hunting effort and success would be substantially stronger, increasing by factors ranging from 1.4-fold to 3.9-fold.

Relatively little of the variation in temperature deviation could be explained by time of year, because the site is close to the equator and ocean. Although 76% of the variation in temperature was day-to-day rather than seasonal, 24% of the observed variation could be explained

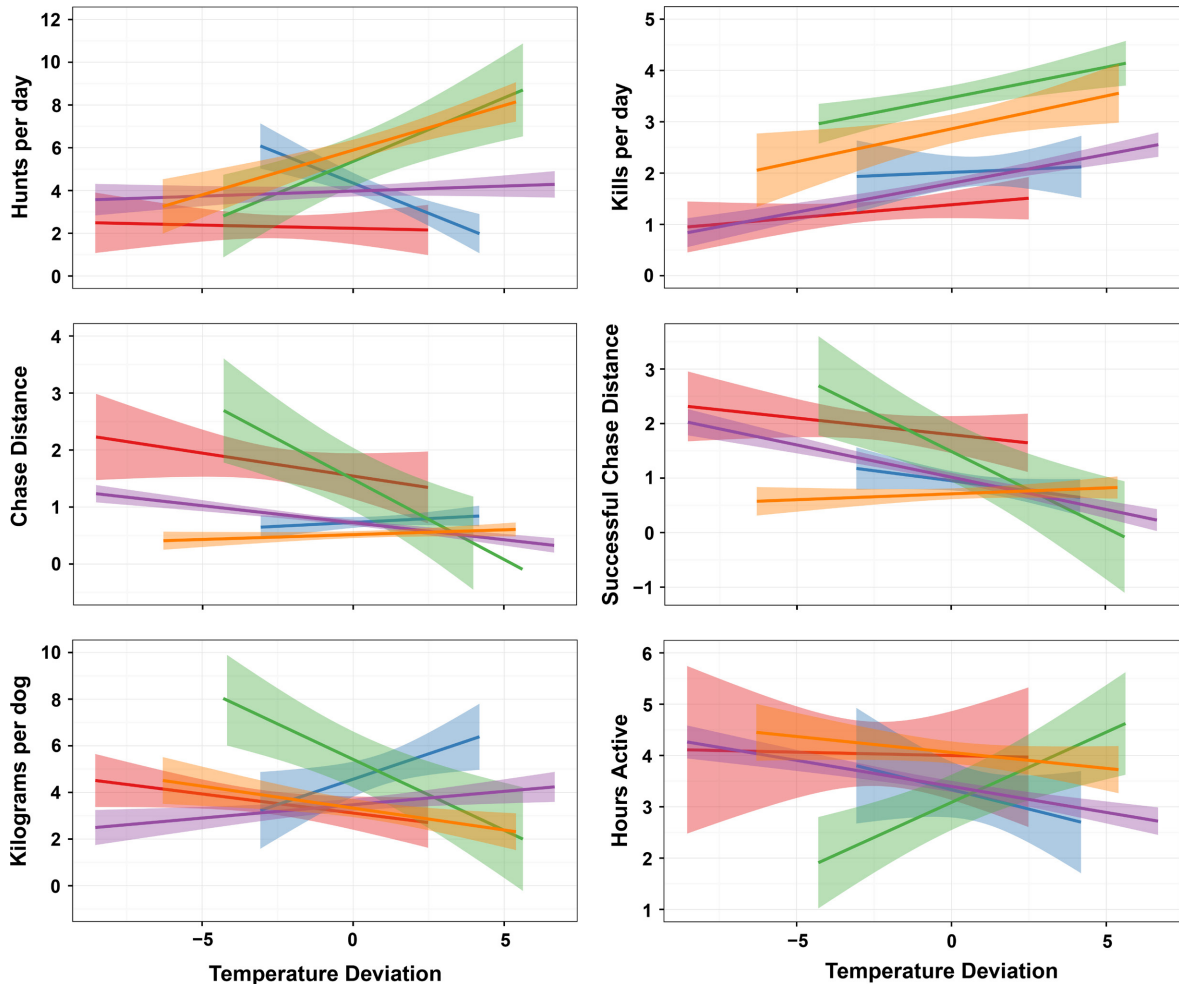


FIG. 3. Relationships of wild dog hunting effort and hunting success to temperature deviation (positive values are hotter than typical for the time of day; negative values are colder than typical). Data from five packs are denoted consistently across panels by color. Mean pack sizes (adults) over the 2 yr of observation were: red = 4.9, purple = 5.3, blue = 8.0, orange = 13.2, green = 14.0. Top row: the number of hunts and kills per day increased with warmer conditions (controlling effects of pack size and identity, here and throughout). Middle row: the distance of pursuits of prey, and particularly successful pursuits, decreased with warmer conditions. Bottom row: the mass of food obtained per day and the number of active hours were not detectably related to temperature deviation.

by the day of year. Thus, some fraction of the observed effects of temperature deviation could potentially be caused by other factors that co-vary with temperature (e.g., the availability of juvenile prey). Contrary to this hypothesis, the regression of mean daily mass of prey killed on day of year detected no relationship ( $b = 0.0062 \pm 0.011$ ,  $t = 0.53$ ,  $P = 0.59$ ), nor was any effect detected with 2nd or 3rd order polynomial regression.

#### DISCUSSION

Speakman and Krol (2010) have recently suggested that the ability to dissipate heat (rather than the supply of energy) often limits the activity of endotherms, and that this limit should operate more strongly for larger animals. African wild dogs and their prey engage in sustained high

speed running in a hot environment, exposing them to severe problems of heat dissipation. Allometric theory and data generally suggest that larger species should be more constrained by overheating (Schmidt-Nielsen 1984, Porter and Kearney 2009, Speakman and Krol 2010), and our data largely confirm that positive temperature deviations favor wild dogs in their interactions with (larger) prey. On days that were hotter than expected, wild dogs hunted and killed more often, their chases decreased in length, and this effect was twice as strong for chases that ended in a kill. All of these effects, but particularly the 11% decrease (per °C) in the length of successful chases, suggest that heat dissipation limits the escape of prey more than it limits pursuit by wild dogs.

We did not detect an increase in prey mass with positive temperature deviation, nor did we detect a decrease

in hours of activity, but the weight of evidence generally suggests that warmer temperature disadvantages prey more than it disadvantages the dogs. As temperatures rise in sub-Saharan Africa (Kruger and Shongwe 2004), the climatic envelope for both large carnivores and their prey is likely to contract, exacerbating already pervasive declines from anthropogenic effects (Estes et al. 2011, Ripple et al. 2015). Superimposed on this grim pattern, the effects of heat dissipation are likely to favor wild dogs in their predatory interactions with larger prey, providing a mild ray of hope for one of Africa's most endangered large carnivores.

Neither the time of day at which wild dogs hunted nor the duration of activity were detectably related to temperature deviation — suggesting that other factors such as light conditions (Cozzi et al. 2012, Rasmussen and Macdonald 2012) and avoidance of competitors (Mills and Biggs 1993, Creel and Creel 1996, Broekhuis et al. 2013) have strong effects on the time window for hunting. This inference is reinforced by the observation that morning and evening hunting activity peaks occur under very similar light conditions at dawn and dusk (06:00 and 18:00 in this equatorial population), but at substantially different mean temperatures (Fig. 2). Superimposed on this broad pattern, the warmer conditions during the evening hunting window might explain why it is typically shorter, as revealed by differences in the width of the two peaks in Fig. 2 (right panel).

It is reasonable to hypothesize that the relationship of heat dissipation to body size could obliquely favor cooperative hunting in hot environments. Because cooperation allows predators to kill larger prey, cooperative hunters might be at an advantage when heat dissipation constrains hunting success, relative to non-cooperative hunters that typically kill prey closer to their own size (or smaller). In wild dogs, pack size is positively related to the mass of prey killed (Creel and Creel 1995), which in Selous was mainly due to a shift from predation focused on impala to predation focused on wildebeest (Creel and Creel 2002). Variation in the species hunted might explain why we found a weak tendency for the mass of prey killed to decrease under hotter conditions, rather than the increase that would be expected if heat dissipation is more problematic for larger prey (Speakman and Krol 2010, Shrestha et al. 2014). Small prey respond to wild dog hunts almost exclusively by running, but large prey often stand their ground and defend themselves (Creel and Creel 1995). Limitation by heat dissipation is probably weaker for antipredator responses that do not involve sustained high speed running (Taylor et al. 1970), so interactions with large prey may be less affected by temperature than interactions with smaller prey, for which flight is the only effective defense. This hypothesis would be weakened if the heat generated by struggling to subdue prey is appreciable relative to the heat generated by pursuit (and thus we would expect different patterns for stalking predators).

Broadly, our results confirm that effects of temperature on behavior can modify predatory interactions between species, exacerbating or offsetting the direct effects of climate change. Although the effects described here are subtle and difficult to study, prior research on the energetics of hunting has shown that wild dogs are strongly affected by changes in hunting efficiency of this magnitude (Gorman et al. 1998). Thus it is reasonable to hypothesize that an 11% reduction in the distance of successful chases (with a 1°C increase in mean temperature) is large enough to affect a wild dog's fitness when compounded over thousands of hunts in a lifetime. The effects of temperature on the behavioral aspects of species' interactions warrant attention, together with better-understood consequences of climate change.

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