Caching reduces kleptoparasitism in a solitary, large felid

Guy A. Balme*[1,2] (iD), Jennifer R. B. Miller[1,2,3] (iD), Ross T. Pitman[1] and Luke T. B. Hunter[1,4]

[1]*Panthera, 8 West 40th Street, New York, NY 10018, USA;* [2]*Institute for Communities and Wildlife in Africa, Department of Biological Sciences, University of Cape Town, Private Bag X3, Rondebosch, Cape Town 7701, South Africa;* [3]*Department of Natural Resources, Cornell University, 111 Fernow Hall, Ithaca, NY 14853, USA; and* [4]*School of Life Sciences, Westville Campus, University of KwaZulu-Natal, Durban 4000, South Africa*

Summary

1. Food caching is a common strategy used by a diversity of animals, including carnivores, to store and/or secure food. Despite its prevalence, the drivers of caching behaviour, and its impacts on individuals, remain poorly understood, particularly for short-term food cachers.

2. Leopards *Panthera pardus* exhibit a unique form of short-term food caching, regularly hoisting, storing and consuming prey in trees. We explored the factors motivating such behaviour among leopards in the Sabi Sand Game Reserve, South Africa, associated with four not mutually exclusive hypotheses: food-perishability, consumption-time, resource-pulse and kleptoparasitism-avoidance.

3. Using data from 2032 prey items killed by 104 leopards from 2013 to 2015, we built generalized linear mixed models to examine how hoisting behaviour, feeding time and the likelihood of a kill being kleptoparasitized varied with leopard sex and age, prey size and vulnerability, vegetation, elevation, climate, and the immediate and long-term risk posed by dominant competitors.

4. Leopards hoisted 51% of kills. They were more likely to hoist kills of an intermediate size, outside of a resource pulse and in response to the presence of some competitors. Hoisted kills were also fed on for longer than non-hoisted kills. At least 21% of kills were kleptoparasitized, mainly by spotted hyaenas *Crocuta crocuta*. Kills were more likely to be kleptoparasitized at lower temperatures and if prey were larger, not hoisted, and in areas where the risk of encountering hyaenas was greatest. Female leopards that suffered higher rates of kleptoparasitism exhibited lower annual reproductive success than females that lost fewer kills.

5. Our results strongly support the kleptoparasitism-avoidance hypothesis and suggest hoisting is a key adaptation that enables leopards to coexist sympatrically with high densities of competitors. We further argue that leopards may select smaller-sized prey than predicted by optimal foraging theory, to balance trade-offs between kleptoparasitic losses and the energetic gains derived from killing larger prey.

6. Although caching may provide the added benefits of delaying food perishability and enabling consumption over an extended period, the behaviour primarily appears to be a strategy for leopards, and possibly other short-term cachers, to reduce the risks of kleptoparasitism.

Key-words: competition, consumption time, food perishability, kleptoparasitism avoidance, optimal foraging, *Panthera pardus*, resource pulse, short-term caching, spotted hyaena

Introduction

Food caching is an evolutionary strategy adopted by a wide range of animals to store and/or secure food (Smith & Reichman 1984; Vander Wall 1990). Food caching is defined as the handling of food to conserve it for future use; in this context, the terms hoarding and storing are synonymous with caching (Vander Wall 1990). Cached food may be consumed minutes to hours after caching (short-term caching), or months to years after caching

*Correspondence author. E-mail: gbalme@panthera.org

(long-term caching). Methods of caching are similarly diverse; most animals bury food item(s), but food can also be stored in specially constructed receptacles (e.g., several species of bees and wasps), impaled on exposed thorns and barbs (e.g., *Lanius* spp.), wedged into bark and rock crevices (e.g., *Sitta* spp.), covered in plant litter (e.g., numerous carnivores), or submerged underwater (e.g., spotted hyaena *Crocuta crocuta*) (reviewed in Vander Wall 1990). The method used to cache food, as well as the time taken to consume food, appears to be a complex interaction between the morphology and nutritional needs of the forager, the foraging environment, and the type(s) of food that is cached (Smith & Reichman 1984; Vander Wall 1990).

Several not mutually exclusive hypotheses have been proposed to explain why animals cache food. Long-term cachers generally store food to survive periods of food scarcity. Such periods may be prolonged and predictable (e.g., North American fox squirrels *Sciurus niger* accumulate food in the fall for use during an energy-demanding winter; Cahalane 1942), or intermittent and unpredictable (e.g., pika *Ochotona princeps* store hay as a safeguard against extreme climatic conditions that preclude foraging; Conner 1983). The motivation for short-term cachers to store food appears more diverse and is less understood. The *food-perishability hypothesis* postulates that short-term cachers store food primarily to avoid or delay food spoilage (Neuschulz *et al.* 2015). Cougars *Puma concolor* in Arizona cache a greater proportion of kills at lower elevations where temperature and humidity is higher, and where food spoils more rapidly (Bischoff-Mattson & Mattson 2009). Animals may also choose to cache less perishable foods. Arctic foxes *Alopex lagopus* bury a greater proportion of eggs than live-caught prey, assumedly because eggs contain antimicrobial agents that retard spoilage (Careau, Giroux & Berteaux 2007). The time required to consume food may also affect an animal's decision to cache. The *consumption-time hypothesis* suggests that caching should be favoured when the time taken to cache (and retrieve) food is short relative to the time required to consume food (Jacobs 1992). Pumas and grizzly bears *Ursus arctos*, for example, primarily cache prey that cannot be consumed in a single sitting (Mattson *et al.* 2006; Cristescu, Stenhouse & Boyce 2014). In this context, caching may enable animals to optimize foraging, by allowing them to invest time in other activities such as sourcing more food or nursing dependent young (Jorge, Brown & van der Merwe 2012). This is particularly true for animals feeding on temporarily abundant food resources. The *resource-pulse hypothesis* proposes that by prioritizing food caching over consumption, animals can maximize short-lived resource peaks (Careau *et al.* 2008). Coyotes *Canis latrans* in Canada increase caching rates during periods of high snowshoe hare *Lepus americanus* abundance (O'Donoghue *et al.* 1998). Several bird species similarly increase caching rates in response to temporary peaks in resource abundance (Stephens & Krebs 1986). Finally, the *kleptoparasitism-avoidance hypothesis* posits that animals cache food to reduce the risk of kleptoparasitism (MacDonald 1976). This may seem counter-intuitive, as animals that defer feeding increase the time over which food can be discovered and pilfered. However, in some instances, caching allows animals to delay feeding until dominant competitors are absent (e.g., Cowie, Krebs & Sherry 1981), or to relocate food to sites where the potential for kleptoparasitism is low (e.g., Muñoz & Bonal 2011; Steele *et al.* 2013). Kleptoparasitism can have profound impacts on individuals, populations and entire ecosystems (Gorman *et al.* 1998; Krofel, Kos & Jerina 2012; Moleón *et al.* 2014); consequently, behaviours that reduce the risk of kleptoparasitism may be strongly selected.

Food caching is common among carnivores of all sizes and has been documented in species from at least five families, including the Canidae, Felidae, Hyaenidae, Mustelidae and Ursidae (Smith & Reichman 1984; Vander Wall 1990). However, despite its prevalence, few studies have explored the drivers of caching behaviour in free-ranging carnivores or its impacts on individuals (but see Careau, Giroux & Berteaux 2007; Cristescu, Stenhouse & Boyce 2014). Here we explore the motivation for food caching in a solitary, large felid: the leopard *Panthera pardus*. Leopards exhibit a unique form of short-term food caching by regularly hoisting, storing and consuming prey in trees (Fig. 1). No other carnivore displays similar behaviour, at least at the frequency observed in leopards. Caching rates appear to vary significantly both within and between leopard populations, from 0% to 84% of food cached (Smith 1977; Bothma & le Riche 1984; Stander *et al.* 1997; Karanth & Sunquist 2000; Bailey 2005; Stein, Bourquin & McNutt 2015; Miller, Jhala & Jena 2016). Previous studies have been limited by small sample sizes and an inability to account for potentially confounding factors (e.g., the distribution and abundance of competitors, but see Stein, Bourquin & McNutt 2015); accordingly, the motivations for food caching by leopards, as well as its consequences, remain largely untested.

Using a dataset of >2000 kills, we examined the demographic, ecological, environmental and climatic factors affecting caching behaviour (hereafter referred to as hoisting) in leopards in the Sabi Sand Game Reserve (SSGR), South Africa, considering the four explanatory hypotheses described above. We made the following not mutually exclusive predictions in support of each hypothesis.

Food-perishability hypothesis

Food spoilage is retarded by low temperatures and humidity and high wind speeds (Braack 1986; Watson & Carlton 2005; Bischoff-Mattson & Mattson 2009), conditions positively associated with height, even at a microscale (Rosenberg, Blad & Verma 1983). Leopards are therefore more likely to hoist kills in conditions that hasten spoilage (i.e., at high temperatures and humidity and at low wind speeds). Leopards should also preferentially

Fig. 1. An adult male leopard hoists a juvenile impala kill in the Sabi Sand Game Reserve, South Africa (photo credit: Villiers Steyn).

hoist larger prey (within the bounds of their physical capabilities), as smaller prey can be consumed before it spoils. Finally, leopards should be able to feed on hoisted kills for longer than non-hoisted kills due to their assumedly slower rates of decomposition. Leopards are obligate carnivores, and thus food type should not affect caching behaviour.

Consumption-time hypothesis

Leopards are expected to hoist larger kills that cannot be consumed in a single sitting. Leopards should also engage in other activities while feeding on hoisted kills; for example, they may resume hunting, in which case leopards which hoist should have multiple concurrent kills. Hoisting may also facilitate nursing for adult females with dependent offspring.

Resource-pulse hypothesis

Leopards should preferentially hoist kills during periods of high prey abundance or vulnerability. In subtropical regions, such as in our study area, this will likely coincide with the birthing and mating seasons of their principal prey (Owen-Smith 2008).

Kleptoparasitism-avoidance hypothesis

Leopards are more likely to hoist kills in areas where the likelihood of kleptoparasitism is high; in areas where the risk of encountering a dominant competitor is high and/

or in open habitats where kills are more likely to be detected. Large prey take more time to consume than small prey, and are thus more vulnerable to detection by competitors. Leopards should therefore preferentially hoist larger kills. Finally, if hoisting effectively safeguards kills from competitors, leopards should be able to feed on hoisted kills for longer than non-hoisted kills.

To better gauge the effectiveness of hoisting as a means of safeguarding kills from competitors, we examined the factors influencing kleptoparasitism risk in more detail and explored the possible impacts of kleptoparasitism on leopard behaviour and fitness. Our study provides insight on the drivers of caching behaviour among carnivores, as well as other short-term food cachers in general.

Materials and methods

STUDY AREA

The SSGR is situated in the lowveld region of Mpumalanga Province, South Africa (midpoint: 31°29′E, 24°49′S). The SSGR is a 625 km^2 conservancy with no internal fences and a fenceless eastern boundary that abuts the Kruger National Park, allowing animals to range freely across a protected landscape >22 000 km^2. The prevailing vegetation is open to semi-wooded savanna dominated by *Acacia*, *Combretum* and *Terminalia* species, interspersed with grasslands and wooded grasslands. Topography is generally flat; elevation ranges from 260 to 504 m a.s.l. Mean monthly temperatures vary from 28 °C in January to 17 °C in July. The area receives an average of 620 mm of rain each year, which falls mainly during the wet season from October to March. Most extant indigenous mammal species are present on the reserve, including the entire large carnivore guild, as well as the primary prey base of this guild (Radloff & du Toit 2004). Estimated leopard, lion *Panthera leo*, and spotted hyaena densities within the study area were $12·2 \pm 0·1$ leopards per 100 km^2, $10·8 \pm 0·2$ lions per 100 km^2 and $13·0 \pm 0·2$ hyaenas per 100 km^2, respectively (G.A. Balme unpublished data; Mills, Juritz & Zucchini 2001).

DATA COLLECTION

The SSGR hosts a number of ecotourism lodges for high-end photographic safaris which provided detailed observation data on animal distribution, behaviour and kills. Clients are taken on two 'game-drives' daily (c. 06.00–09.30 and 15.30–19.00 h) conducted by an experienced guide accompanied by a skilled tracker. Charismatic species such as leopards are highly sought-after and sightings are frequent; on average, $14·5 \pm 0·1$ different leopards are seen per day (range = 3–28 leopards; excluding dependent cubs) and 6428 ± 914 leopard sightings recorded each year (range = 5453–8255 sightings). Due to the high frequency of sightings, leopards have become habituated to the presence of game-drives and guides are familiar with the individuals that use their traversing area (Balme *et al.* 2013). Guides are required to record sightings of leopards and other large carnivore species after each game-drive.

Records date back to the mid-1970s, but we restricted our analyses to 1 January 2013 to 31 December 2015 when data collection protocols were standardized across lodges through the implementation of sightings capture software (Peak Performance

International, Cape Town, South Africa). Data include the identity of the leopard (if known), its location (recorded on a geo-referenced map), whether it had a kill, the species, sex, and age class (juvenile, subadult, and adult) of the prey, whether the kill was hoisted, the presence of other large carnivores within sight of the kill, whether the kill was kleptoparasitized, and other behaviours (e.g., intra and interspecific interactions). To assess the accuracy of the guides' ability to identify individual leopards, we asked them to submit photographs with the putative identity of the leopard from a random subset of sightings; they correctly identified the individual in all photos ($n = 112$).

STATISTICAL ANALYSIS

We used generalized linear mixed models (GLMMs) to explore hypotheses and determine the factors affecting: (i) the probability of a leopard hoisting its kill; (ii) the duration of time that a leopard was observed feeding on its kill; and (iii) the likelihood of a kill being kleptoparasitized. For all analyses, we excluded scavenged food items. In cases where hunting or scavenging was uncertain, we assumed that the food item was hunted unless there was evidence to suggest otherwise (e.g., the presence of an agitated subordinate predator near the kill).

The following variables, or combinations thereof, were included in GLMMs (see sections below for detail on model structure).

Sex and age of the leopard: We only included leopards of known identity in the analyses. Leopard litters in the SSGR are typically discovered at a young age (mean = 49 ± 4 days; Balme *et al.* 2013), ensuring that our age estimates were reliable.

Ratio of prey body mass to leopard body mass: We used the size of prey relative to the leopard's size (rather than simply prey body mass), as this took into account likely disparities in strength (and hence hoisting ability) between male and female, and adult and subadult leopards. We also considered the quadratic function of prey to leopard body mass in some models to test whether leopards favoured hoisting intermediate-sized kills (Stein, Bourquin & McNutt 2015). Estimates of adult male and female prey body mass were taken from Radloff & du Toit (2004), Owen-Smith & Mills (2008) and Skinner & Chimimba (2005). In the absence of growth curves for all prey species, we approximated subadult mass by multiplying adult male or female mass by 0·7, and approximated juvenile mass by multiplying mean adult mass by 0·3 (Radloff & du Toit 2004). Estimates of leopard body mass were derived from a von Bertalanffy growth curve calculated using measurements taken from immobilized leopards during a long-term radio-telemetry study in nearby KwaZulu-Natal, South Africa (Fattebert 2014). Due to the opportunistic nature of data collection, it was possible that larger kills were over-represented (Owen-Smith & Mills 2008). Accordingly, we used a one-way analysis of covariance to compare the sizes of kills located once the leopard had already begun feeding to kills that were observed directly (i.e., from the start to the finish of the hunt, hereafter observed kills), controlling for the sex of the leopard.

Whether the kill occurred during a period of prey abundance or vulnerability: Impala *Aepyceros melampus* are the primary year-round prey of leopards in the SSGR (Fig. S1, Supporting Information). However, their relative contribution to leopard diet increases significantly between November and January, during and soon after the impala birthing season, and in April and May, during the impala rut (Fig. S1; Owen-Smith 2008). We therefore assumed that these two periods represented an inter-annual resource pulse for leopards (cf. Cristescu, Stenhouse & Boyce 2014).

Immediate and long-term competitor risk: We defined immediate competitor risk as a binominal variable indicating the presence (1) or absence (0) of an adult male leopard, any lion(s), or any spotted hyaena(s) (hereafter hyaena) at a kill (in addition to the leopard responsible for the kill). These carnivores were responsible for 98% of kleptoparasitism events (see Results). Like leopards, lions and hyaenas were habituated to the presence of game-drives. However, there was no evidence that they associated vehicles with leopard (or other predator) kills; animals tolerated vehicles but did not approach them. Long-term competitor risk was derived using ranging data of adult male leopards ($n = 3179$ sightings), lions ($n = 3988$ sightings) and hyaenas ($n = 1513$ sightings) collected by guides during 2015. We calculated kernel density estimates (KDEs) for all known individual male leopards ($n = 27$) and lion prides ($n = 9$) in the SSGR using the Spatial Analsist extension in ArcGIS 10.1 (ESRI, Redpath, CA, USA). Few unknown male leopards were viewed in the study area in 2015, and no unknown lion prides. Importantly, no kills were kleptoparasitized by unknown leopards or lions; only by individuals for which we had ranging data. Guides did not distinguish between individual hyaenas in the sightings reports. As such, we calculated KDEs for all hyaena sightings combined; sampling effort (i.e., the number of game-drives) was constant across the study area throughout 2015 ($\chi^2_{11} = 4.954$, $P = 0.933$). We rasterized KDEs (100×100 m resolution), summed the raster maps for individual male leopards and lion prides (separately for each species), and then clipped the species maps to the area intersected by all three species maps. The value of each pixel in the final species-specific maps (Fig. S2) represented the long-term risk of leopards encountering each of these dominant competitors (Broekhuis *et al.* 2013).

Environmental and climate variables: To measure vegetation density at each kill site, we extracted the value of woody cover from each cell containing a kill site using data from the 2009 National Mosaic Land-Cover (10×10 m resolution; South African National Biodiversity Institute 2009). We have no data on temporal variation in cover, but this is likely to be less than spatial variation in woody cover (Scholes, Bond & Eckhardt 2003), which we assessed. Mean daily temperatures, humidity levels and wind speeds were sourced from the South African Weather Service. Elevation (Jarvis *et al.* 2008) was measured at each kill site due to its potential effects on climatic factors.

All statistical analyses were performed in the R statistical environment (R Core Team 2015). Prior to including variables in each GLMM, we screened for correlation using a cut-off of $|r| = 0.70$. We scaled all continuous variables around a mean of 0 and variance of 1 to facilitate comparison. The leopard's identity and the year the kill occurred were included as random factors to account for pseudoreplication (Bolker *et al.* 2009). We used Akaike's Information Criterion corrected for sample sizes (AIC$_c$) to select the most parsimonious models (Burnham & Anderson 2002). When candidate models were within ΔAIC$_c$ <2, we performed model averaging using the R package *glmulti* (Calcagno & de Mazancourt 2010) to estimate unbiased parameter coefficients. Odds ratios were used to gauge effect size, where larger values indicated greater likelihood of the variable effect.

HOISTING BEHAVIOUR

We used GLMMs with a binomial error structure and logit link function to assess the factors influencing the likelihood of a leopard hoisting its kill (1 = hoisted; 0 = remained on the ground).

We only had complete data on the distribution of dominant competitors throughout our study area from the start of 2015; hence, we ran two separate analyses to address this question. The first included the full dataset (2013–2015) and tested the food-perishability, consumption-time and resource-pulse hypotheses. The following explanatory variables were considered in the models: leopard sex, leopard age, ratio of prey body mass to leopard body mass[2], whether the kill occurred during a prey resource pulse, extent of woody cover, elevation, ambient temperature, humidity and wind speed. The second analysis, to test the kleptoparasitism-avoidance hypothesis, featured only data from 2015. We included variables from the first analysis deemed to have a significant effect on hoisting probability, as well as factors relating to the immediate and long-term risk posed by dominant competitors. Finally, we ran both analyses again using kills from only female leopards while including the presence of nursing cubs (≤4 months old) as an additional variable in the models to determine whether nursing behaviour affected hoisting probability.

FEEDING TIME

Guides did not record how much of the kill had been consumed upon detection. Accordingly, we used the number of game-drives that a leopard was observed at its kill as a proxy for feeding time, acknowledging that this is an underestimate of true feeding time. We used GLMMs with a Poisson error structure and logit link function to assess the factors influencing the number of game-drives that a leopard was observed at its kill. Feeding time was only associated with the food-perishability and kleptoparasitism-avoidance hypotheses. As such, the only variables included in the models were: ratio of prey to leopard body mass, woody cover, elevation, ambient temperature, humidity, wind speed, whether the kill was hoisted and whether the kill was kleptoparasitized.

KLEPTOPARASITISM RISK

We used GLMMs with a binomial error structure and logit link function to assess the factors affecting the likelihood of a leopard kill being kleptoparasitized (1 = kleptoparasitized; 0 = voluntarily abandoned). We only included kills from 2015 when we had ranging data on dominant competitors. Explanatory variables included in models were: leopard sex, leopard age, ratio of prey to leopard body mass, whether the kill occurred during the resource pulse, woody cover, elevation, ambient temperature, humidity, wind speed, the long-term risk posed by dominant competitors and whether the kill was hoisted. We did not include the immediate risk posed by competitors as this was implicitly linked to kleptoparasitism risk (i.e., a kill could not be kleptoparasitized if a competitor was not present).

We also undertook an exploratory analysis to assess the impact(s) of kleptoparasitism on leopard fitness, specifically on the annual reproductive success (ARS) of females. We did not assess male ARS since we could not unequivocally assign paternity to all litters without genetic data. Female ARS was calculated as the total number of offspring raised to independence divided by the observed reproductive longevity of females (defined as the period from the birth of a mother's first litter to the independence of her final recorded litter; Packer *et al.* 1988). Estimates of ARS included litters born before 2013, but kill data were limited to the study period. We used linear regression to compare the proportion of kills lost by females to their ARS, restricting our analysis to females with ≥10 kill records. Data were arcsine transformed.

Results

Excluding dependent cubs, 104 leopards were seen feeding on 2215 food items, of which 2032 were considered killed by the leopard (mean number of kills per individual = 19·5 ± 2·2, range = 1–117). Scavenged items (n = 183) were kleptoparasitized mainly from other leopards (89%), but also from lion (3%), hyaena (1%), African wild dog *Lycaon pictus* (1%), cheetah *Acinonyx jubatus* (<1%), Nile crocodile *Crocodylus niloticus* (<1%) and martial eagle *Polemaetus bellicosus* (<1%) kills, as well as scavenged from animals that died from causes other than predation (4%). Leopards killed at least 41 species (5 bird species, 5 reptile species, 31 mammal species), ranging in size from a juvenile Natal spurfowl *Pternistis natalensis* (≈135 g) to a juvenile giraffe *Giraffa camelopardalis* (≈303 kg) (Table S1). Male leopards typically killed larger prey than females (males: mean = 44·6 ± 1·2 kg, range = 0·2–303·0 kg; females: mean = 33·1 ± 0·7 kg, range = 0·2–180·0 kg; $z = -8.065$, $P < 0.001$); however, females killed larger prey relative to their own body size than males (males: mean = 0·7 ± 0·1, range = 0·1–4·3; females: mean = 0·9 ± 0·1, range = 0·1–6·1; $z = -10.064$, $P < 0.001$). There was no difference in the size of observed kills (n = 264) and those located after the leopard had begun feeding (n = 1768; $F_{1,2032} = 0.532$, $P = 0.466$). As such, we included all documented kills in our analyses. Leopards were recorded with multiple concurrent kills on only 15 occasions (1% of total kills).
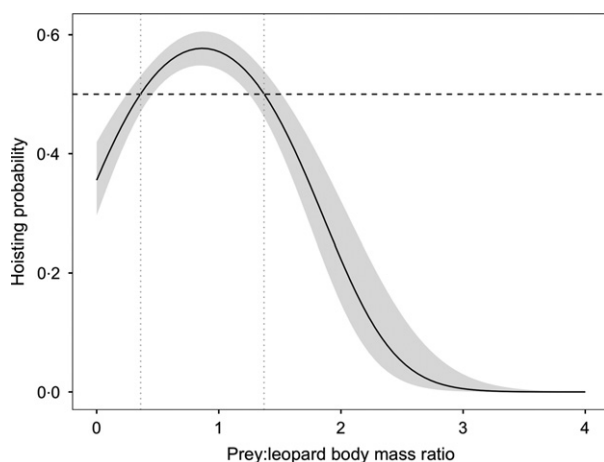
HOISTING BEHAVIOUR

Leopards hoisted 51% of kills. Eight models in our full GLMM (including kills from 2013 to 2015; n = 2032) assessing hoisting probability qualified for model averaging (Table S2). The only factors significantly affecting whether a leopard hoisted its kill were the quadratic function of prey to leopard body mass and whether the kill occurred during the resource pulse (Table 1). Leopard sex approached significance ($P = 0.060$); the odds of a male leopard hoisting its kill were 33% greater than a female (odds ratio = 1·330). Leopards had a >50% probability of hoisting kills that were 40% to 140% of their body mass (Fig. 2). The largest kill hoisted by a leopard in our study was a juvenile African buffalo *Syncerus caffer* (≈166 kg). Contrary with expectations, a leopard was 23% less likely to hoist its kill during the resource pulse than outside the pulse (odds ratio = 0·768). No factors relating to habitat or climate had a significant effect on hoisting probability.

A reduced GLMM (using kills from 2015 only; n = 930) suggested that the immediate risk posed by some competitors also increased the likelihood of a kill being hoisted. Five models had ΔAIC_c <2 (Table S2), though model averaging suggested the only factors significantly affecting hoisting probability were the quadratic function of prey to leopard body mass, the presence of a male leopard at a kill, and the presence of a hyaena at a kill (Table 1). Kills were 2·6 times more likely to be hoisted if a male leopard

Table 1. Results from generalized linear mixed models assessing the (a) likelihood of a leopard hoisting its kill (data from 2013 to 2015; testing the food-perishability, consumption-time and resource-pulse hypotheses), (b) likelihood of a leopard hoisting its kill (2015; kleptoparasitism-avoidance hypothesis), (c) feeding time (2013–2015; food-perishability and kleptoparasitism-avoidance hypotheses) and (d) kleptoparasitism risk (2015; kleptoparasitism-avoidance hypothesis) in the Sabi Sand Game Reserve, South Africa. Model-averaged β estimates with standard error, odds ratios, and z and P values are shown for parameters in models with a $\Delta AIC_c <2$

Parameter	β ± SE	Odds ratio	z	P
(a) Hoisting behaviour (food-perishability, consumption-time, resource-pulse hypotheses)				
Prey : leopard body mass^2	−0·313 ± 0·068	0·731	4·602	<0·001*
Resource pulse	−0·264 ± 0·097	0·768	2·721	0·007*
Leopard sex (male)	0·285 ± 0·152	1·330	1·880	0·060
Leopard age	−0·094 ± 0·068	0·911	1·375	0·169
Humidity	−0·057 ± 0·051	0·944	1·128	0·259
Temperature	−0·037 ± 0·052	0·963	0·725	0·469
Elevation	−0·041 ± 0·064	0·960	0·641	0·521
(b) Hoisting behaviour (kleptoparasitism-avoidance hypothesis)				
Prey : leopard body mass^2	−0·317 ± 0·091	0·728	3·467	<0·001*
Male leopard – immediate risk	0·940 ± 0·282	2·560	3·330	<0·001*
Hyaena – immediate risk	0·431 ± 0·157	1·538	2·746	0·006*
Hyaena – long-term risk	0·120 ± 0·073	1·128	1·637	0·102
Lion – immediate risk	−0·710 ± 0·463	0·492	1·532	0·125
Resource pulse	−0·171 ± 0·139	0·843	1·230	0·219
Male leopard – long-term risk	0·063 ± 0·071	1·065	0·884	0·377
(c) Feeding time (food-perishability and kleptoparasitism-avoidance hypotheses)				
Kill kleptoparasitized	−0·233 ± 0·044	0·792	5·252	<0·001*
Kill hoisted	0·222 ± 0·034	1·248	6·547	<0·001*
Prey : leopard body mass	0·138 ± 0·016	1·148	8·856	<0·001*
Temperature	−0·047 ± 0·017	0·954	2·818	0·005*
Wind speed	0·014 ± 0·017	1·014	0·828	0·407
Humidity	−0·003 ± 0·017	0·997	0·197	0·844
(d) Kleptoparasitism risk (kleptoparasitism-avoidance hypothesis)				
Kill hoisted	−1·115 ± 0·182	0·328	6·128	<0·001*
Prey : leopard body mass	0·586 ± 0·089	1·797	6·545	<0·001*
Temperature	−0·368 ± 0·092	0·692	4·007	<0·001*
Hyaena – long-term risk	0·237 ± 0·094	1·268	2·512	0·012*
Elevation	0·201 ± 0·106	1·223	1·894	0·058
Leopard sex (male)	−0·411 ± 0·251	0·663	1·635	0·102

*$P < 0.05$.

Fig. 2. Probability (solid black line) of a leopard hoisting its kill in relation to prey size (represented as the prey to leopard body mass ratio). The shaded area represents the 95% confidence interval, the horizontal dashed line indicates a hoisting probability of 50%, and vertical dashed lines indicate the lower and upper estimates of prey size corresponding to a hoisting probability of 50%.

was observed near the kill (odds ratio = 2·560), and 1·5 times more likely to be hoisted if a hyaena was seen at the kill (odds ratio = 1·538). The immediate risk posed by lions had no influence on hoisting probability, and neither did the long-term risk posed by any competitors.

Models which only included kills made by female leopards suggested that the presence of nursing cubs had no effect on female hoisting probability ($P > 0.05$).

FEEDING TIME

Several factors had a significant influence on the duration of time that a leopard was observed at its kill (Tables 1 and S2). Unsurprisingly, leopards spent more time on larger kills (odds ratio = 1·148) and less time on kills that were kleptoparasitized (odds ratio = 0·792). Leopards were also observed on hoisted kills for 25% longer than on non-hoisted kills (odds ratio = 1·248). Finally, the time that leopards spent feeding on kills decreased with increasing temperature (odds ratio = 0·954).
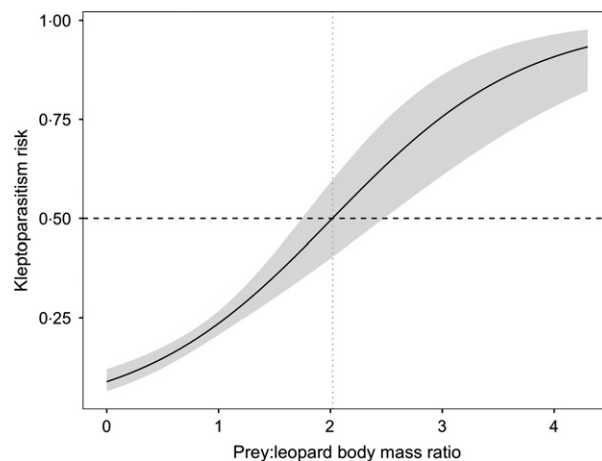
KLEPTOPARASITISM

At least 21% of leopard kills were kleptoparasitized (Table S1). Hyaenas were the most common perpetrators (accounting for 50% of kleptoparasitized kills), followed by other leopards (39%), lions (9%), African wild dogs (1%), Nile crocodiles (<1%) and chacma baboons *Papio ursinus* (<1%). Male leopards were responsible for 143 of the 162 (88%) kills kleptoparasitized by conspecifics. Three models in our GLMM assessing kleptoparasitism risk qualified for model averaging (Table S2); however, the only factors significantly affecting whether a kill was kleptoparasitized were the ratio of prey to leopard body mass, whether the kill was hoisted, the long-term risk posed by hyaena and ambient temperature (Table 1). Larger kills had a higher probability than smaller kills of being kleptoparasitized (odds ratio = 1·797). Indeed, prey larger than twice the leopard's body mass had a >50% likelihood of being kleptoparasitized (Fig. 3). A hoisted kill was 67% less likely to be kleptoparasited than a kill on the ground (odds ratio = 0·328). Male leopards and lions could kleptoparasitize most kills, regardless of whether it was hoisted or not, whereas hyaenas mainly kleptoparasitized kills on the ground (Table 2). Despite this, the likelihood of a kill being kleptoparasitized increased with hyaena density (odds ratio = 1·268), but not by male leopard or lion density. Kleptoparasitism risk was inversely related to temperature (odds ratio = 0·692), with more kills pilfered in colder months (Fig. 4).

Twenty-four adult females were recorded feeding on ≥10 kills during the study. These females gave birth to 197 cubs in 109 litters over 138·6 leopard-years. Mean ARS was 0.4 ± 0.1 independent cubs per year (range = 0–1·0 independent cubs per year). On average, these females lost 23% of their kills to other competitors (range = 5% to 45%). Females that suffered higher rates of kleptoparasitism exhibited lower ARS than females that lost fewer kills ($F_{1,23} = 12.005$, $r^2 = 0.353$, $P = 0.002$; Fig. 5).

Discussion

Our results mainly support the kleptoparasitism-avoidance hypothesis to explain caching behaviour in leopards. Consistent with its predictions, hoisting reduced the risk of kleptoparasitism, kills were more likely to be hoisted in the presence of dominant competitors, larger kills were more likely to be hoisted than smaller kills, and hoisted kills were generally fed on for longer than non-hoisted kills. The finding that prey size was a significant determinant of hoisting probability also supports the consumption-time hypothesis. However, there were few examples of leopards with multiple concurrent kills, which would be expected if leopards hoisted kills to resume foraging. Females also did not increase hoisting rates to facilitate nursing; they were equally likely to hoist kills with or without young cubs.
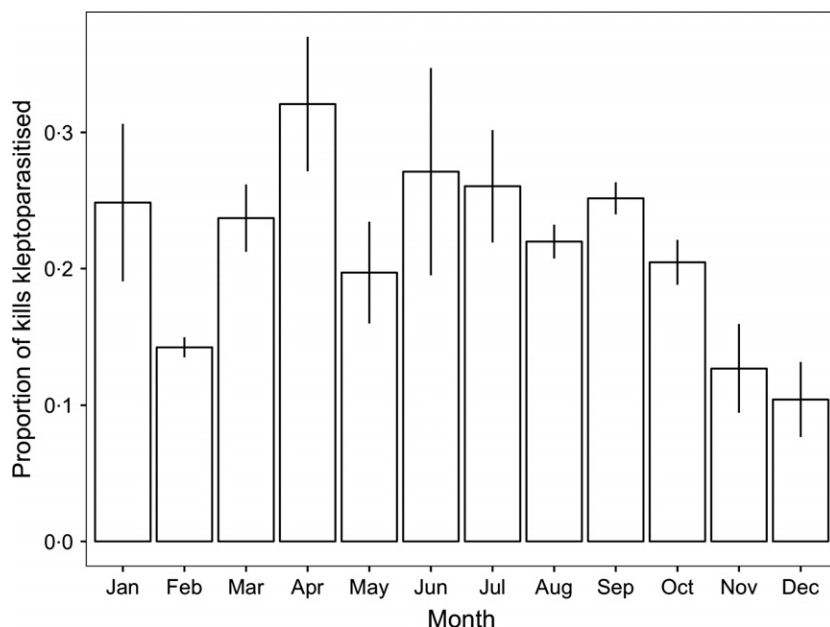

Fig. 3. Probability (solid black line) of a leopard's kill being kleptoparasitized in relation to prey size (represented as the prey to leopard body mass ratio). The shaded area represents the 95% confidence interval, the horizontal dashed line indicates a kleptoparasitism risk of 50%, and the vertical dashed line indicates the estimated prey size corresponding to a kleptoparasitism risk of 50%.

Table 2. Number of occasions that adult male leopards, spotted hyaenas, and lions were detected at and kleptoparasitized hoisted and non-hoisted leopard kills ($n = 930$) in the Sabi Sand Game Reserve, South Africa, in 2015
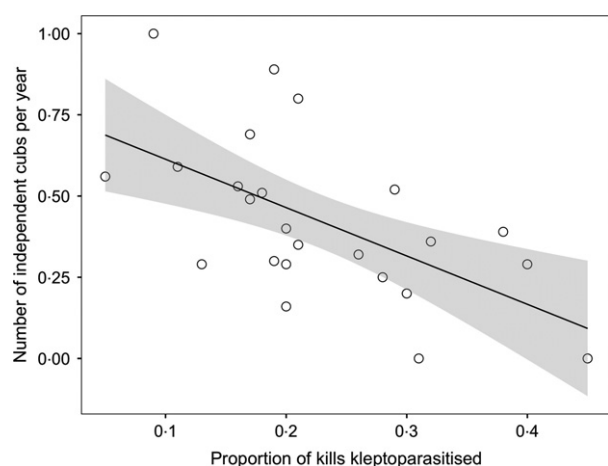
	Kills		
	Hoisted	Not hoisted	Total
Male leopard			
Detected at kill	56	17	73
Kill kleptoparasitized	56	16	72
Spotted hyaena			
Detected at kill	200	91	291
Kill kleptoparasitized	39	80	119
Lion			
Detected at kill	8	14	22
Kill kleptoparasitized	5	14	19

Leopards generally hoisted kills of intermediate size, ranging from 40% to 140% of their body mass. Smaller prey was usually consumed in one sitting; hence, the likelihood of a competitor discovering and kleptoparasitiszing a small kill was low. In contrast, very large kills (i.e., kills greater than twice their body mass) were rarely hoisted, probably because it was beyond the capabilities of the leopard, or at least too energetically prohibitive to warrant hoisting.

Our results were consistent with those from northern Botswana (Stein, Bourquin & McNutt 2015) in showing that male leopards generally hoisted a greater proportion of kills than females. Due to male leopards' larger size, a greater proportion of their kills fall within the preferred prey–leopard size range for hoisting. Female leopards may also have less motivation to hoist kills, as they

Fig. 4. Mean monthly proportion of leopard kills kleptoparasitized by dominant competitors. Vertical lines represent standard error.

Fig. 5. Annual reproductive success of female leopards, measured by the number of independent cubs raised per year, in relation to the proportion of kills lost to kleptoparasitism. Open circles show raw data and shaded area the 95% confidence interval.

suffered higher rates of intraspecific kleptoparasitism, against which hoisting is ineffective. Indeed, our results showed that kleptoparasitic male leopards were more likely to be observed at hoisted kills than non-hoisted kills. Leopards and other felids typically rely on visual rather than olfactory cues to detect and hunt prey (Sunquist & Sunquist 2002), which presumably applies also to scavenging. Consequently, it may have been easier for male leopards to locate hoisted kills because they were more visible than kills on the ground (cf. Stander *et al.* 1997). Male leopards may have also been more likely to discover hoisted kills simply because hoisted kills were fed on for longer than non-hoisted kills. The strong positive relationship between the immediate risk posed by male leopards and hoisting probability is thus likely a consequence of hoisting, rather than a motivation for hoisting.

In contrast, leopards were often seen to hoist kills in direct response to the arrival of a hyaena at a kill, and hoisting effectively protected kills from hyaenas (the 39 hoisted kills kleptoparasitized by hyaenas all fell from the tree, often dislodged by inexperienced cubs). As such, the immediate risk posed by hyaenas at kills is more likely a driver of hoisting behaviour. The presence of lions at kills had no effect on hoisting probability. Lions pose a far greater threat to the safety of leopards than hyaenas (Bailey 2005; Balme *et al.* 2013), and in all cases that lions found a leopard with a kill on the ground, the leopard immediately abandoned its kill and fled. Hoisting was also not particularly effective at safeguarding kills from lions (Fig. S3); lions were able to kleptoparasitize 63% of the hoisted kills that they detected.

Our results were consistent with findings from recent studies which suggest that risk avoidance by subordinate competitors is often reactive rather than predictive (Broekhuis *et al.* 2013; López-Bao *et al.* 2016, Swanson *et al.* 2016). Leopards did not increase hoisting rates in areas with higher densities of dominant competitors, instead they responded to the immediate risk posed by some competitors. Leopards may be unable to detect and infer the long-term risk posed by competitors, particularly by hyaenas which are extremely flexible in their foraging strategies (East & Hofer 2013). If leopards could distinguish between risky and less risky hyaena areas, we would have expected them to do so as the relative density of hyaenas was a significant determinant of kleptoparasitism risk.

Optimal foraging theory predicts that predator–prey preference should follow a normal distribution when plotted against prey body mass (Stephens & Krebs 1986; Hayward *et al.* 2006). Some prey species are too small to sustain predators, while others are too large to be safely killed. A meta-analysis of leopard prey preferences from across leopard range showed that preferred prey body

mass is skewed to the left; i.e., leopards generally select smaller prey than expected based on their size (see fig. 3 in Hayward *et al.* 2006). Our study confirmed that leopards are capable of killing prey many times their body mass, but they rarely do. Hayward *et al.* (2006) suggested that this may be due to the solitary nature of leopards; they cannot afford to get injured and therefore target smaller, less dangerous prey. An alternative but not necessarily competing explanation is that leopard select prey that fit within the optimal size range to hoist. The increased risk of kleptoparasitism associated with feeding on the ground may offset the energetic gains that leopards obtain from hunting larger prey, even if such prey can be subdued safely. This interaction between kleptoparasitism risk and prey choice is likely dependent on the local densities of competitors. Pumas typically select smaller prey during periods when black bear *Ursus americanus* densities are high, and hence the risk of kleptoparasitism is greater (Elbroch *et al.* 2015). Leopards may likewise be expected to select smaller prey in areas with high densities of hyaenas, or other sympatric competitors that cannot climb trees (e.g., wolves *Canis lupus*, dholes *Cuon alpinus* and striped hyaenas *Hyaena hyaena* in Asia).

None of the climatic factors that we assessed influenced hoisting probability, reducing support for the food-perishability hypothesis. Braack (1986) showed that in the adjoining Kruger National Park, microbes and arthropods can consume the fleshy tissue from a medium-sized ungulate such as an impala within 5 days during summer and within 14 days during winter. This suggests that, at least during the hot summer months, leopards suffered competition over kills from necrophilous micro-organisms as well as from other large carnivores. It was therefore unsurprising that leopards spent less time on kills as temperatures increased. However, due to the high densities of competitors in our study area, the benefits that leopards gained from hoisting kills in terms of reducing kleptoparasitism, which was more common during cooler periods, likely outweighed the benefits of adjusting hoisting rates to account for food perishability. Hyaenas hunt a greater proportion of their food during summer (Henschel & Skinner 1990), when there is an abundance of vulnerable young prey, likely explaining the decrease in kleptoparasitism rates at this time.

Contrary with the predictions of the resource-pulse hypothesis, leopards decreased hoisting rates during periods of high prey vulnerability and abundance (i.e., the impala birthing and mating seasons; Owen-Smith 2008). This was likely related to the size of prey targeted during these seasons. Newborn impala lambs were typically not hoisted, particularly by male leopards, as they could be consumed in a single sitting. In contrast, male impalas, which appeared disproportionately vulnerable during the rut, were above the preferred size range for female leopards to hoist. An alternative explanation is that leopards hoisted fewer kills during the resource pulse because they could afford to lose food at those times, but kleptoparasitism rates did not increase at this time. In general, animals which prioritize food caching over consumption during resource peaks only do so if the perishability of food is close to or exceeds the duration of the peak (Vander Wall 1990). Leopards would gain little by attempting to store impala beyond the periods they were most vulnerable due to their high perishability (the carcass would decompose within days if left uneaten).

Despite their ability to hoist kills, leopards in our study area suffered high rates of kleptoparasitism (at least 21% of kills were kleptoparasitized). However, without being able to hoist kills, losses of prey to hyaenas would likely create an untenable situation for leopards. Taking into consideration the number of occasions that we observed hyaenas at leopard kills, as well as the relative inability of leopards to defend non-hoisted kills from hyaenas, we estimate that kleptoparasitism rates in the absence of hoisting would reach as high as 38%. Although only exploratory, our results suggested that kleptoparasitism impacted individual fitness even at observed levels. Females that suffered higher rates of kleptoparasitism had lower ARS. Hyaenas and lions collectively account for 42% of leopard cub mortality at our site (Balme *et al.* 2013), some of which occurs during kleptoparasitic events. Offspring survival is also closely tied to food abundance in many large carnivores (Packer *et al.* 1988; Ruth *et al.* 2011), and the loss of kills may increase the risk of leopard cubs dying of starvation (Bailey 2005). Adult leopard survival may also be affected by kleptoparasitism. Large carnivores likely function close to maximum sustained energy outputs (Carbone, Teacher & Rowcliffe 2007); hence, decreased food availability or increased activity may render individuals energetically vulnerable. Predators need to increase kill rates (and importantly, the energetically-costly time spent searching for prey; Williams *et al.* 2014) to compensate for kills lost to competitors (Krofel, Kos & Jerina 2012; Elbroch *et al.* 2015), but ultimately they may still suffer a net loss of food (Krofel, Kos & Jerina 2012). Depending on the hunting approach employed by predators, as well as the relative abundance of prey, this increase in energetic demands may compromise individual survival, and even threaten population persistence (Gorman *et al.* 1998). Therefore, hoisting is likely an important adaption that enables leopard populations to coexist and thrive in environments with dominant competitors, particularly hyaenas, which are poor climbers but reach high densities.

Hoisting rates vary dramatically between leopard populations (Sunquist & Sunquist 2002). Much of this variation can likely be explained by the types and densities of sympatric competitors, as well as possibly habitat structure. Hoisting rates in our study (51%) were comparable to those in northern Botswana (38%) where spotted hyaena densities are similar (Stein, Bourquin & McNutt 2015). In contrast, leopards seldom (<20%) hoist kills in areas where competitors are largely extirpated (e.g., Stein 2008) or naturally scarce (e.g., Smith 1977; Bothma & le Riche 1984; Stander *et al.* 1997). Although woody cover did not influence hoisting probability in our study, vegetation may affect caching at a range-wide scale. Hoisting

appears more prevalent among leopards in Africa than in Asia; for example, leopards rarely hoisted kills in Nagarahole (13%) National Park and never in Kanha NP in India, despite high densities of tigers *Panthera tigris* and dholes (Karanth & Sunquist 2000; Miller, Jhala & Jena 2016). The very dense vegetation in these parks, and across much of Asian leopard range (but which was absent from our study area), likely reduces the ability of competitors to detect leopard kills.

We provide one of the first detailed examinations of caching behaviour in a large carnivore (also see Cristescu, Stenhouse & Boyce 2014). Although caching may have added benefits for leopards in delaying food perishability and allowing individuals to consume food over a longer time, the behaviour appears to be primarily a strategy to reduce the risk of kleptoparasitism. Other carnivores that cache typically do so by burying food (e.g., Artic foxes and wolverines *Gulo gulo*; Careau, Giroux & Berteaux 2007; Inman *et al.* 2012), covering food with plant litter (e.g., pumas and grizzly bears; Mattson *et al.* 2006; Cristescu, Stenhouse & Boyce 2014), or even storing food underwater (e.g., spotted hyaena; Kruuk 1972). Future work could assess the effectiveness of these different caching techniques in safeguarding food against kleptoparasitism, while accounting for different environmental and ecological conditions (particularly the densities and foraging strategies of sympatric competitors). This may provide insight on why hoisting has not evolved among more carnivore species, especially those that can climb trees. Future studies could also assess the impact of caching on predation rates of leopards and other carnivores, and accordingly their impacts on prey populations (Krofel, Kos & Jerina 2012; Elbroch *et al.* 2015). More detailed research is additionally required on the energetic trade-offs associated with food caching (Jorge, Brown & van der Merwe 2012). We were able to demonstrate some of the benefits that leopards obtained from caching, but we could not measure the costs of hoisting kills. Finally, there are few empirical data on the fitness costs (or benefits to perpetrators; García, Becker & Favero 2013) of kleptoparasitism, despite its prevalence in nature and the role it likely plays in structuring ecological communities (Moleón *et al.* 2014; Pereira, Owen-Smith & Moleón 2014).

Authors' contributions

G.B. conceived the ideas, designed the methodology and collected the data; G.B. and R.P. analysed the data; G.B., J.M., R.P. and L.H. contributed critically to the writing of the manuscript and gave final approval for publication.

Acknowledgements

Data accessibility

Data used in this study are archived in the Dryad Digital Repository; https://doi.org/10.5061/dryad.gb794 (Balme *et al.* 2017).

References

Bailey, T.N. (2005) *The African Leopard: Ecology and Behaviour of a Solitary Felid*, 2nd edn. Blackburn Press, Caldwell, NJ, USA.

Balme, G.A., Batchelor, A., Woronin-Britz, N., Seymour, G., Grover, M., Hes, L., Macdonald, D.W. & Hunter, L.T.B. (2013) Reproductive success of female leopards: the importance of top-down processes. *Mammal Review*, **43**, 221–237.

Balme, G. A., Miller, J. R. B., Pitman, R. T. & Hunter, L. T. B. (2017) Data from: Caching reduces kleptoparasitism in a solitary, large felid. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.gb794.

Bischoff-Mattson, Z. & Mattson, D. (2009) Effects of simulated mountain lion caching on decomposition of ungulate carcasses. *Western North American Naturalist*, **69**, 343–350.

Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H. & White, J.S.S. (2009) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution*, **24**, 127–135.

Bothma, J.D.P. & le Riche, E.A. (1984) Aspects of the ecology and the behaviour of the leopard in the Kalahari Desert. *Koedoe*, **27**, 259–279.

Braack, L.E.O. (1986) Arthropods associated with carcasses in the northern Kruger National Park. *South African Journal of Wildlife Research*, **16**, 91–98.

Broekhuis, F., Cozzi, G., Valeix, M., McNutt, J.W. & Macdonald, D.W. (2013) Risk avoidance in sympatric large carnivores: reactive or predictive? *Journal of Animal Ecology*, **82**, 1098–1105.

Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multimodal Inference: A Practical Information-Theoretic Approach*, 2nd edn. Springer, New York, NY, USA.

Cahalane, V.H. (1942) Caching and recovery of food by the western fox squirrel. *The Journal of Wildlife Management*, **6**, 338–352.

Calcagno, V. & de Mazancourt, C. (2010) glmulti: an R package for easy automated model selection with (generalized) linear models. *Journal of Statistical Software*, **34**, 1–29.

Carbone, C., Teacher, A. & Rowcliffe, J.M. (2007) The costs of carnivory. *PLoS Biology*, **5**, e22.

Careau, V., Giroux, J.F. & Berteaux, D. (2007) Cache and carry: hoarding behavior of arctic fox. *Behavioral Ecology and Sociobiology*, **62**, 87–96.

Careau, V., Lecomte, N., Bêty, J., Giroux, J.F., Gauthier, G. & Berteaux, D. (2008) Hoarding of pulsed resources: temporal variations in egg-caching by arctic fox. *Ecoscience*, **15**, 268–276.

Conner, D.A. (1983) Seasonal changes in activity patterns and the adaptive value of haying in pikas. *Canadian Journal of Zoology*, **61**, 411–416.

Cowie, R.J., Krebs, J.R. & Sherry, D.F. (1981) Food storing by marsh tits. *Animal Behaviour*, **29**, 1252–1259.

Cristescu, B., Stenhouse, G.B. & Boyce, M.S. (2014) Grizzly bear ungulate consumption and the relevance of prey size to caching and meat sharing. *Animal Behaviour*, **92**, 133–142.

East, M.L. & Hofer, H. (2013) Spotted hyena. *The Mammals of Africa; Vol. V: Carnivores, Pangolins, Equids and Rhinoceroses* (eds J. Kingdon & M. Hoffmann), pp. 272–281. Bloomsbury Publishing, London, UK.

Elbroch, L.M., Lendrum, P.E., Allen, M.L. & Wittmer, H.U. (2015) Nowhere to hide: pumas, black bears, and competition refuges. *Behavioral Ecology*, **26**, 247–254.

Fattebert, J. (2014) Spatial ecology of a leopard population recovering from over-harvest. PhD thesis, University of KwaZulu-Natal, Durban, South Africa.

García, G.O., Becker, P.H. & Favero, M. (2013) Intraspecific kleptoparasitism improves chick growth and reproductive output in common terns. *Ibis*, **155**, 338–347.

Gorman, M.L., Mills, M.G., Raath, J.P. & Speakman, J.R. (1998) High hunting costs make African wild dogs vulnerable to kleptoparasitism by hyaenas. *Nature*, **391**, 479–481.

Hayward, M.W., Henschel, P., O'brien, J., Hofmeyr, M., Balme, G. & Kerley, G. I. H. (2006). Prey preferences of the leopard. *Journal of Zoology*, **270**, 298–313.

Henschel, J.R. & Skinner, J.D. (1990) The diet of the spotted hyaenas in Kruger National Park. *African Journal of Ecology*, **28**, 69–82.

Inman, R.M., Magoun, A.J., Persson, J. & Mattisson, J. (2012) The wolverine's niche: linking reproductive chronology, caching, competition, and climate. *Journal of Mammalogy*, **93**, 634–644.

Jacobs, L.F. (1992) The effect of handling time on the decision to cache by grey squirrels. *Animal Behaviour*, **43**, 522–524.

Jarvis, A., Reuter, H.I., Nelson, A. & Guevara, E. (2008) *Hole-filled Seamless SRTM Data V4*. International Centre for Tropical Agriculture (CIAT). Available at: http://srtm.csi.cgiar.org (accessed 15 November 2016).

Jorge, M.L.S., Brown, J.S. & van der Merwe, M. (2012) Handling time and the evolution of caching behavior. *Behavioral Ecology*, **23**, 410–417.

Karanth, K.U. & Sunquist, M.E. (2000) Behavioural correlates of predation by tiger, leopard and dhole in Nagarahole, India. *Journal of Zoology*, **250**, 255–265.

Krofel, M., Kos, I. & Jerina, K. (2012) The noble cats and the big bad scavengers: effects of dominant scavengers on solitary predators. *Behavioral Ecology and Sociobiology*, **66**, 1297–1304.

Kruuk, H. (1972) *The Spotted Hyena: A Study of Predation and Social Behavior*. University of Chicago Press, Chicago, IL, USA.

López-Bao, J.V., Mattisson, J., Persson, J., Aronsson, M. & Andrén, H. (2016) Tracking neighbours promotes the coexistence of large carnivores. *Scientific Reports*, **6**, 23198.

MacDonald, D.W. (1976) Food caching by red foxes and some other carnivores. *Zeitschrift für Tierpsychologie*, **42**, 170–185.

Mattson, D., Hart, J., Miller, M. & Miller, D. (2006) Predation and other behaviors of mountain lions in the Flagstaff Uplands. *Mountain Lions of the Flagstaff Uplands* (ed. D. Mattson), pp. 31–42. USGS Open-File Report 2007-1062. Available at: http://pubs.usgs.gov/of/2007/1062/of 2007-1062.pdf (accessed 5 April 2016).

Miller, J.R.B., Jhala, Y.V. & Jena, J. (2016) Livestock losses and hotspots of attack from tigers and leopards in Kanha Tiger Reserve, Central India. *Regional Environmental Change*, **16**, 17–29.

Mills, M.G.L., Juritz, J.M. & Zucchini, W. (2001) Estimating the size of spotted hyaena populations through playback recordings allowing for non-response. *Animal Conservation*, **4**, 335–343.

Moleón, M., Sánchez-Zapata, J.A., Selva, N., Donázar, J.A. & Owen-Smith, N. (2014) Inter-specific interactions linking predation and scavenging in terrestrial vertebrate assemblages. *Biological Reviews*, **89**, 1042–1054.

Muñoz, A. & Bonal, R. (2011) Linking seed dispersal to cache protection strategies. *Journal of Ecology*, **99**, 1016–1025.

Neuschulz, E.L., Mueller, T., Bollmann, K., Gugerli, F. & Böhning-Gaese, K. (2015) Seed perishability determines the caching behaviour of a food-hoarding bird. *Journal of Animal Ecology*, **84**, 71–78.

O'Donoghue, M., Boutin, S., Krebs, C.J., Zuleta, G., Murray, D.L. & Hofer, E.J. (1998) Functional responses of coyotes and lynx to the snowshoe hare cycle. *Ecology*, **79**, 1193–1208.

Owen-Smith, N. (2008) Changing vulnerability to predation related to season and sex in an African ungulate assemblage. *Oikos*, **117**, 602–610.

Owen-Smith, N. & Mills, M.G.L. (2008) Predator-prey size relationships in an African large-mammal food web. *Journal of Animal Ecology*, **77**, 173–183.

Packer, C., Herbst, L., Pusey, A.E., Bygott, J.D., Hanby, J.P., Cairns, S.J. & Borgerhoff Mulder, M. (1988) Reproductive success of lions. *Reproductive Success: Studies of Individual Variations in Contrasting Breeding Systems* (ed. T.H. Clutton-Brock), pp. 363–383. University of Chicago Press, Chicago, IL, USA.

Pereira, L.M., Owen-Smith, N. & Moleón, M. (2014) Facultative predation and scavenging by mammalian carnivores: seasonal, regional and intra-guild comparisons. *Mammal Review*, **44**, 44–55.

R Core Team (2015) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. Available at: https://www.r-project.org/ (accessed 1 February 2016).

Radloff, F.G. & du Toit, J.T. (2004) Large predators and their prey in a southern African savanna: a predator's size determines its prey size range. *Journal of Animal Ecology*, **73**, 410–423.

Rosenberg, N.J., Blad, B.L. & Verma, S.B. (1983) *Microclimate: The Biological Environment*, 2nd edn. Wiley, Chichester, UK.

Ruth, T.K., Haroldson, M.A., Murphy, K.M., Buotte, P.C., Hornocker, M.G. & Quigley, H.B. (2011) Cougar survival and source-sink structure on Greater Yellowstone's Northern Range. *The Journal of Wildlife Management*, **75**, 1381–1398.

Scholes, R.J., Bond, W.J. & Eckhardt, H.C. (2003) Vegetation dynamics in the Kruger ecosystem. *The Kruger Experience: Ecology and Management of Savanna Heterogeneity* (eds J.T. Du Toit, K.H. Rodgers & H.C. Biggs), pp. 242–262. Island Press, Washington, DC, USA.

Skinner, J.D. & Chimimba, C.T. (2005) *The Mammals of the Southern African Sub-Region*. Cambridge University Press, Cambridge, UK.

Smith, R.M. (1977) Movement patterns and feeding behaviour of leopard in the Rhodes Matopos National Park, Rhodesia. *Arnoldia Rhodesia*, **8**, 1–16.

Smith, C.C. & Reichman, O.J. (1984) The evolution of food caching by birds and mammals. *Annual Review of Ecology and Systematics*, **15**, 329–351.

South African National Biodiversity Institute (2009) *2009 National Mosaic Land-Cover*. Available at: http://bgis.sanbi.org/landcover/project.asp (accessed 1 March 2016).

Stander, P.E., Haden, P.J., Kaqece, II & Ghau, II (1997) The ecology of asociality in Namibian leopards. *Journal of Zoology*, **242**, 343–364.

Steele, M.A., Contreras, T.A., Hadj-Chikh, L.Z., Agosta, S.J., Smallwood, P.D. & Tomlinson, C.N. (2013) Do scatter hoarders trade off increased predation risks for lower rates of cache pilferage? *Behavioral Ecology*, **25**, 206–215.

Stein, A.B. (2008) Ecology and conservation of the leopard in Northcentral Namibia. PhD thesis, University of Massachusetts, Amherst, MA, USA.

Stein, A.B., Bourquin, S.L. & McNutt, J.W. (2015) Avoiding intraguild competition: leopard feeding ecology and prey caching in northern Botswana. *African Journal of Wildlife Research*, **45**, 247–257.

Stephens, D.W. & Krebs, J.R. (1986) *Foraging Theory*. Princeton University Press, Princeton, NJ, USA.

Sunquist, M. & Sunquist, F. (2002) *Wild Cats of the World*. University of Chicago Press, Chicago, IL, USA.

Swanson, A., Arnold, T., Kosmala, M., Forester, J. & Packer, C. (2016) In the absence of a "landscape of fear": how lions, hyenas, and cheetahs coexist. *Ecology and Evolution*, **6**, 8534–8545.

Vander Wall, S.B. (1990) *Food Hoarding in Animals*. University of Chicago Press, Chicago, IL, USA.

Watson, E.J. & Carlton, C.E. (2005) Insect succession and decomposition of wildlife carcasses during fall and winter in Louisiana. *Journal of Medical Entomology*, **42**, 193–203.

Williams, T.M., Wolfe, L., Davis, T., Kendall, T., Richter, B., Wang, Y., Bryce, C., Elkaim, G.H. & Wilmers, C.C. (2014) Instantaneous energetics of puma kills reveal advantage of felid sneak attacks. *Science*, **346**, 81–85.

Supporting Information

Details of electronic Supporting Information are provided below.

Fig. S1. Relative monthly contributions (proportion of kills) of prey species to leopard diet in the Sabi Sand Game Reserve, South Africa, from 2013 to 2015.

Fig. S2. Long-term risk of leopards encountering an adult male leopard, a spotted hyaena(s), and a pride of lions in the Sabi Sand Game Reserve, South Africa, based on their relative densities derived from species-specific ranging data collected in 2015.

Fig. S3. A female lion kleptoparasitizes a hoisted juvenile kudu kill from an adult female leopard.

Table S1. Prey species killed by leopards in the Sabi Sand Game Reserve, South Africa, from 2013 to 2015.

Table S2. Model selection results from generalized linear mixed models assessing the (a) likelihood of a leopard hoisting its kill (data from 2013 to 2015; testing the food-perishability, consumption-time and resource-pulse hypotheses), (b) likelihood of a leopard hoisting its kill (2015; kleptoparasitism-avoidance hypothesis), (c) feeding time (2013–2015; food-perishability and kleptoparasitism-avoidance hypotheses) and (d) kleptoparasitism risk (2015; kleptoparasitism-avoidance hypothesis) in the Sabi Sand Game Reserve, South Africa.