



Food caching by a solitary large carnivore reveals importance of intermediate-sized prey

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Pumas (*Puma concolor*) are solitary large carnivores that exhibit high energetic investments while hunting prey that often take multiple days to consume. Therefore, pumas should behave in a way to maximize their energetic gains, including using caching, which is a behavior used by many mammal species to preserve and store food or to conceal it from conspecifics and scavengers to limit their losses. Yet pumas do not always cache their kills. In order to understand caching behavior, we used variables associated with the kills such as prey mass, search time, climate, and habitat to test 20 ecological models (representing four a priori hypotheses: food perishability, resource pulse, consumption time, and kleptoparasitism deterrence) in an information-theoretic approach of model selection to explore factors related to the caching behavior. Models were run with information from tracked radio-collared pumas in California over a 2.5-year period and identified a total of 352 kills. Overall, we documented pumas caching 61.5% of their kills, including 71.6% of Black-tailed Deer (*Odocoileus hemionus columbianus*), their primary prey in the study area. The model with a quadratic effect of adjusted mass of prey on puma caching probability had all of the empirical support ($w = 1.00$). Specifically, pumas were most likely to cache intermediate-sized prey, such as yearling and adult female deer, and also fed from cached kills for longer periods of time. Larger prey may be too large to easily cache, making it less energetically efficient—while small prey can often be consumed quickly enough to not require caching. This suggests that intermediate-sized prey may be the optimal size for caching, allowing a puma to feed for multiple days while not greatly increasing energetic output. The hypotheses we tested were not mutually exclusive and pumas caching their prey may occur for several reasons; nevertheless, our study demonstrated that pumas use caching to extend their foraging time and maximize energetic gains when preying on intermediate-sized prey.

Key words: cache, foraging ecology, kleptoparasitism, optimal foraging theory, *Puma concolor*, scavenging

El esconder comida es un comportamiento utilizado por muchas especies, entre ellos los carnívoros, para conservar y almacenar alimentos u ocultarlos de congéneres y de carroñeros. Los pumas (*Puma concolor*) son grandes carnívoros solitarios que invierten gran cantidad de energía en cazar sus presas, que a menudo tardan varios días en consumir. Por lo tanto, los pumas deberían comportarse de manera que puedan maximizar sus ganancias energéticas, incluyendo el esconder su comida para reducir las pérdidas a manos de vertebrados carroñeros; sin embargo, los pumas no siempre esconden sus presas. En California rastreamos pumas con radio collares durante 2 años y medio, e identificamos 352 presas cazadas. Usando variables asociadas a las cacerías, probamos 20 modelos, que representan 4 hipótesis a priori (alimento-caducidad, recurso-pulso, consumo-tiempo y cleptoparasitismo-disuasión), con un enfoque teórico de la información para explorar factores relacionados con el comportamiento de esconder el alimento. En general, documentamos que los pumas escondieron el 61,5% de sus presas, de las cuales 71,6% eran de ciervo de cola negra (*Odocoileus hemionus columbianus*), su principal presa en el área de estudio. El modelo con efecto cuadrático de la masa corporal de la presa ajustada (proporción

de peso de presa:peso de puma) sobre la tasa de escondido de presa del puma tuvo todo el soporte ($w = 1,00$). Específicamente, era más probable que los pumas escondieran presas de tamaño intermedio, como ciervos jóvenes de un año y hembras adultas, y los pumas también se alimentaban de las presas escondidas durante períodos de tiempo más largos, lo que respalda la hipótesis de que este comportamiento incrementa la energía ganada. Las presas más grandes pueden ser demasiado grandes para esconderlas fácilmente, haciendo que la actividad sea menos eficiente desde el punto de vista energético, mientras que las presas pequeñas a menudo se pueden consumir lo suficientemente rápido como para no requerir ser escondidas. Esto sugiere que las presas de tamaño intermedio pueden ser el tamaño óptimo para ser escondidas, lo que permite que un puma se alimente durante varios días sin ser energéticamente costoso. Las hipótesis que probamos no son mutuamente excluyentes, por lo que el esconder las presas puede ocurrir por varias razones. Nuestro estudio ilustra cómo los pumas suelen esconder su alimento para extender su tiempo de alimentación y maximizar las ganancias energéticas al consumir presas de tamaño intermedio.

Palabras clave: barrido, cleptoparasitismo, ecología de forrajeo, *Puma concolor*, teoría del forrajeo óptimo

Foraging success directly impacts individual fitness. Optimal foraging theory thus describes foraging as an adaptive strategy to maximize the net energy individual animals gain from their food (MacArthur and Pianka 1966). Foraging can be optimized during decisions made around four aspects of foraging: food selection, foraging space, foraging period, and foraging group size (Schoener 1971). For example, choosing optimal food allows for the greatest energy gain while minimizing the energetic costs associated with the time and effort spent searching for this food. Nevertheless, food consumption, and the associated energetic value of food, may be impacted by what occurs after the food is procured (Krofel et al. 2012; Allen et al. 2021a). Understanding how and when animals exhibit specific behaviors to extend their use of the food that they have acquired is therefore an important extension of current optimal foraging theory.

Caching (also called storing or hoarding) is a widespread behavior used to preserve food from spoilage, store surplus food, and hide food from conspecifics and potential scavengers (Macdonald 1976; Careau et al. 2007; Inman et al. 2012; Balme et al. 2017; Krofel et al. 2021). Caching strategies vary among species. Some species use multiple caches spread out in space (e.g., scatter hoarding) while others use caches close together (e.g., larder hoarding; van der Veen et al. 2020). In some species, food is transported before storing (e.g., Arctic Fox, *Vulpes lagopus*; Careau et al. 2007) while others generally cache in situ (e.g., Eurasian Lynx, *Lynx lynx*; Krofel et al. 2021). Food can also be cached for relatively short or long periods; for example, pumas (*Puma concolor*) cache prey that is too large to be consumed in a single feeding event (Elbroch et al. 2015), while arctic foxes store food for use during seasons of resource scarcity (Careau et al. 2007; Samelius et al. 2007).

Caching is of particular importance to solitary carnivores, as they eat prey that is energetically costly to catch and subdue, and meat spoils quickly. Previous research has led to the development of four nonmutually exclusive hypotheses explaining carnivore caching behavior. The *food perishability hypothesis* posits that individuals cache prey to reduce food losses to decomposition. For example, wolverines (*Gulo gulo*) cache food to extend their supply of food through winter (Inman et al. 2012; van der Veen et al. 2020). The *resource pulse hypothesis*

predicts that individuals cache prey to take advantage of ephemeral pulses of high prey availability by storing food for later consumption (Samelius et al. 2007). For example, arctic fox will cache bird eggs and other food items during resource pulses (Careau et al. 2007). Many animals cache food items that take longer to consume than cache, and thereby maximize their energetic gain (*consumption time hypothesis*; Jacobs 1992). Among large carnivores, many species cache large ungulate carcasses to extend their consumption time and energetic gain (Cristescu et al. 2014; Allen et al. 2021b). Finally, the *kleptoparasitism deterrence hypothesis* predicts that caching will reduce prey losses to kleptoparasitism by competitors (Elbroch et al. 2017b). For example, leopards (*Panthera pardus*) appear to cache prey in trees to avoid kleptoparasitism by spotted hyenas (*Crocuta crocuta*; Balme et al. 2017).

Pumas are solitary carnivores that typically kill prey that takes multiple days to consume (Murphy and Ruth 2009) and pumas often cache these prey short-term while they are actively feeding on them. As an ambush predator, pumas generally exhibit long search times while hunting, followed by energetically expensive, explosive chases and grappling to subdue prey (Bryce et al. 2017). In order to forage optimally pumas thus need strategies to preserve prey and prolong feeding, specifically by limiting their losses to decomposers and vertebrate scavengers (including conspecifics and dominant scavengers; Bischoff-Mattson and Mattson 2009; Elbroch et al. 2017a; Barry et al. 2019; Allen et al. 2021a). For example, caching by pumas in open habitats delays detection by avian scavengers, allowing them to consume more of their prey (Elbroch and Wittmer 2013). Caching, however, has not been found to be an effective strategy against kleptoparasitism from American black bears (*Ursus americanus*) in mostly forested habitats (e.g., Elbroch et al. 2015), the losses from which can be so large that pumas are forced to increase their kill rates (Allen et al. 2021a). Why and when pumas cache their kills is thus an important aspect of understanding their foraging ecology that needs to be studied in more depth.

We monitored seven GPS-collared pumas and documented kill and caching sites during a multiyear study of puma foraging ecology in northern California with the ultimate goal of understanding the factors related to whether pumas cache

a kill or not. Specifically, we evaluated a series of 20 models (Table 1), representing multiple variable combinations derived from the four overarching a priori hypotheses introduced above.

MATERIALS AND METHODS

Study area.—We conducted our study across approximately 1,000 km² centered on the Mendocino National Forest located in northern California at the southern edge of the Cascade Mountain Range (Fig. 1). Terrain was variable and rugged and

covered an altitudinal range from 396 to 2,466 m. Mean daily temperatures ranged from −1°C to 24°C across seasons and mean annual precipitation was 132 cm. Forested habitats dominated the study area, but species composition varied with elevation. For a more complete physical description of the study area, see Allen et al. (2015). Black-tailed deer (*Odocoileus hemionus columbianus*) were the only resident ungulate and the primary prey of local pumas (Allen et al. 2015).

Field methods and covariates.—We captured seven pumas ($n_{\text{male}} = 2$, $n_{\text{female}} = 5$) from June 2010 to November 2012 using a combination of hounds and box traps (Allen et al.

Table 1.—A list of the 20 a priori models, sorted alphabetically, that we used to determine the top model predicting whether pumas would cache killed prey. We list the variables in the model, the reason behind each model, and which of the hypotheses the model is associated with. The four main hypotheses include the food perishability hypothesis (Mattson et al. 2007; Bischoff-Mattson and Mattson 2009; Barry et al. 2019), resource pulse hypothesis (Samelius et al. 2007), consumption time hypothesis (Careau et al. 2007; Mattson et al. 2007; Cristescu et al. 2014), and the kleptoparasitism deterrence hypothesis (Laundré and Hernández 2003; Balme et al. 2017; Elbroch et al. 2017a; Allen et al. 2021a). Terms with a superscript “2” (e.g., adjusted mass²) indicate a quadratic relationship between probability of caching and the predictor covariate. All models, including the null model, allow the intercept to vary randomly across individual pumas.

Variables	Reason	Associated hypotheses
Adjusted mass	Pumas are more likely to cache prey that is large compared to them, because large prey is more likely to be discovered by scavengers, competitors, and decomposers.	Consumption time, food perishability, kleptoparasitism deterrence
Adjusted mass + Adjusted mass ²	Pumas are more likely to cache kills that are of the optimal prey size to extend feeding for the individual.	Consumption time, food perishability, kleptoparasitism deterrence
Adjusted mass × Search time	Pumas are more likely to cache large kills when they are hungrier after searching longer for prey.	Consumption time, food perishability, kleptoparasitism deterrence
Canopy cover	Pumas are more likely to cache kills in areas with low canopy cover to protect from the sun and higher temperatures to mitigate decomposition.	Food perishability
Canopy cover + Temperature + Precipitation	Pumas are more likely to cache kills in warmer weather with less precipitation and canopy cover to mitigate losses due to decomposition.	Food perishability
Double kills	Pumas are more likely to cache kills when they make two kills near each other so they can extend their feeding time.	Consumption time, food perishability, resource pulse
Elevation × Temperature	Pumas are more likely to cache kills in warmer microclimates in the mountainous study area.	Food perishability
Fawn season	Pumas are more likely to cache during fawn season to extend the resource pulse of when prey abundance is highest.	Resource pulse
Location	Pumas are more likely to cache kills near the edge of their home range where other pumas are more likely to detect and scavenge from them.	Kleptoparasitism deterrence
Mass	Pumas are more likely to cache larger prey because larger prey will take longer to consume and are therefore more likely to be discovered by scavengers, competitors, and decomposers.	Consumption time, food perishability, kleptoparasitism deterrence
Mass + Location	Pumas will be more likely to cache large prey that are in the vicinity of other pumas and more likely to be discovered.	Consumption time, food perishability, kleptoparasitism deterrence
Mass + Mass ²	Pumas are more likely to cache intermediate-sized prey, as they take longer to consume but are energetically efficient to cache. As such they are the optimal prey size to use caching to extend feeding and energetic gains.	Consumption time, food perishability, kleptoparasitism deterrence
Mass × Temperature	Pumas are more likely to cache larger kills in warmer temperatures to mitigate losses to decomposition.	Consumption time, food perishability, kleptoparasitism deterrence
Null	No variables will explain selection of kills cached by pumas.	Unsupported hypotheses
Precipitation	Pumas are more likely to cache in dry weather to preserve the carcass and mitigate decomposition.	Food perishability
Search time	Pumas are more likely to cache prey when they searched longer for prey, due to greater hunger.	Consumption time
Search time + Search time ²	Pumas are more likely to cache prey when they have killed it after an ideal search time in order to maximize their energetic intake.	Consumption time
Temperature	Pumas are more likely to cache kills in warmer weather to mitigate losses to decomposition.	Food perishability
Temperature + Temperature ²	Pumas are more likely to cache kills in warmer weather to mitigate decomposition, but not bother caching kills in the hottest weather.	Food perishability
Temperature × Precipitation	Pumas are more likely to cache kills in warmer weather with less precipitation to mitigate decomposition.	Food perishability

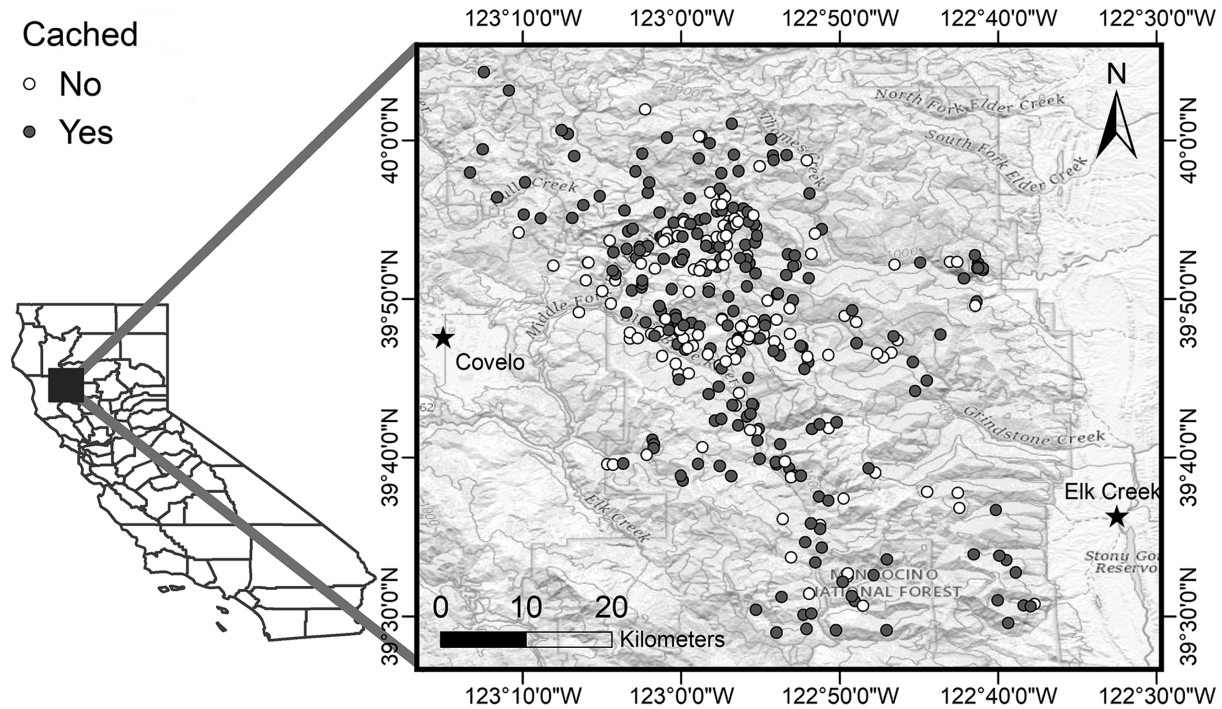


Fig. 1.—The study area in Mendocino National Forest, California and the location of puma kills, with colors indicating whether individual kills were cached or not.

2015). Capture methods were approved by the independent Institutional Animal Care and Use Committee at the University of California, Davis (Protocols 15341 and 16886), and by the Wildlife Investigations Laboratory of the California Department of Fish and Wildlife. We fit pumas with GPS satellite collars (Lotek 7000SAW, New Market, Ontario, Canada) programmed to collect GPS locations every 2 h and downloaded locations via satellite at 3-day intervals.

We identified potential kills as clusters of activity with ≥ 5 GPS locations (i.e., a minimum of 8 h between first and last locations) within 150 m of each other, that contained at least one crepuscular or nocturnal location to distinguish kills from day beds (Allen et al. 2015). We investigated potential kill sites ($n = 598$ out of a possible 609) throughout the year for predation events, and identified remains (bones, hair/feathers) to determine the prey species killed by pumas ($n = 352$ sites). During investigations, we would travel to the centroid of the GPS locations and perform a grid search until finding animal sign to investigate further. We investigated satellite-relayed potential kills within $\bar{x} = 6.78$ (± 8.18 SD) days, which we assumed to be sufficient to recognize caching in most cases as caching was often found to be apparent weeks or even months after kills. We documented whether kills were cached with leaves, soil, and other organic matter, and for the sake of this study considered kills with any evidence of caching to have been cached. We documented visual signs of American black bears scavenging at kills including scats and disturbances in the immediate area of the kill, and also documented the terrain and microhabitat characteristics (elevation, slope, aspect, and canopy cover; Allen et al.

2015). We determined the mean temperature and precipitation associated with the day each kill was made using a local weather station (Allen et al. 2015).

We estimated the mass of prey from the literature. We estimated monthly sex-specific weights for deer fawns (<1-year-old, assuming a birth date of 16 June; Allen et al. 2015) and age- and sex-specific weights of adult deer based on Parker et al. (1993), and cementum annuli analysis (Low and Cowan 1963) performed by Matson's Laboratory (Milltown, Montana) or tooth eruption patterns (Heffelfinger 2010). For all other mammals we used the mean mass reported in Jameson and Peeters (2004) and for birds we used the mean mass reported in Sibley (2016). To create an 'adjusted prey mass,' we divided prey mass by the mass of the individual puma making the kill (e.g., Balme et al. 2017).

We defined the feeding time as the entire duration a puma was active at a GPS cluster from making the kill to abandoning it (Krofel et al. 2012), and determined mass and the proportion consumed based on active consumption rates (see details in Allen et al. 2021a). We defined search time as the duration from the time a kill was abandoned to the time the subsequent kill was made (Allen et al. 2021a), calculated in 2-h increments based on the GPS data. In cases of missing values (i.e., search time cannot be calculated for the first documented kill), we interpolated the mean value for the variable. We defined fawn season, when deer and seasonal prey are most abundant in the study area (Allen et al. 2014), to be from June through August. We also considered any time a puma killed multiple prey within 100 m of another kill to be part of a resource pulse.

We estimated puma space use (i.e., home ranges, as both entire time periods the puma was collared and in 3-month intervals) using autocorrelated kernel density estimators (AKDE; Fleming et al. 2015; Fleming and Calabrese 2017) to account for the high levels of temporal autocorrelation in our GPS location data. We estimated AKDE using the *ctmm* package (v. 0.6.1; Calabrese et al. 2016) in program R (version 4.1.1; R Core Team 2021) using perturbative hybrid residual maximum likelihood to fit continuous time movement models (Fleming et al. 2019; Silva et al. 2022) and selected the best model using AICc (Burnham and Anderson 2002). We used the debias option when estimating the AKDE and used weighting to account for temporal sampling bias. Home range sizes calculated from periods of 3 months and over the total monitoring periods were essentially equal, so we used the home ranges from the entire monitoring periods. We considered the 95% isopleth as the home range boundary and measured the distance from each kill site to the home range boundary, which we used as a proxy for potential interactions with neighboring pumas in our conspecific kleptoparasitism deterrence models (Table 1).

Statistical analyses.—We used program R for all statistical analyses. To simplify our data analyses, we lumped prey species other than deer into groups, birds include: American robin (*Turdus migratorius*); California quail (*Callipepla californica*); California towhee (*Melospiza crissalis*); mountain quail (*Oreortyx pictus*); mourning dove (*Zenaidura macroura*); red-breasted sapsucker (*Sphyrapicus ruber*); wild turkey (*Meleagris gallopavo*). Lagomorphs include: black-tailed jack-rabbit (*Lepus californicus*) and brush rabbit (*Sylvilagus bachmani*). Mesocarnivores include: coyote (*Canis latrans*); fisher (*Pekania pennant*); gray fox (*Urocyon cinereoargenteus*); and northern raccoon (*Procyon lotor*). Rodents include: California ground squirrel (*Otospermophilus beecheyi*); Douglas squirrel (*Tamiasciurus douglasii*); golden-mantled ground squirrel (*Callospermophilus lateralis*); Western gray squirrel (*Sciurus griseus*); and dusky-footed woodrat (*Neotoma fuscipes*). Full data on prey species and frequencies are described in detail in Allen et al. (2015a).

We compared our 20 a priori models explaining puma caching behavior based on the information-theoretic approach (Burnham and Anderson 2002). We first tested for correlations among covariates and removed models where two or more variables were highly correlated (>0.70). We then tested models using binomial generalized linear mixed effect models (GLMMs) in the *lme4* package (Bates et al. 2007), using a

logit link and accounting for the individual puma using random intercepts by puma. All predictor variables were z -score standardized. We compared and ranked models based on the AIC model weight (w ; Symonds and Moussalli 2011). We calculated the area-under-the-curve (AUC) as a measure of each model's predictive performance using the *PresenceAbsence* package in R (Freeman and Moisen 2007). To better understand how caching influenced puma feeding time at kills, we fit two post hoc models using energetic days at kill as our response variable. In our first model, we modeled energetic days at kill as a function of whether or not the kill was cached. In the second model, we added an interactive effect between whether or not the kill was cached and a quadratic effect of prey mass. We fit each model using a gamma GLMM with a log link, and random intercepts by puma. Finally, we fit a series of post hoc models to examine seasonal variation in caching rates. Specifically, we calculated the monthly proportion of kills cached for each unique puma-month combination and used these proportions as the response variable in a beta GLMM with logit links and random intercepts of year nested within puma. We fit these models using the *glmmTMB* package (Brooks et al. 2017). We also rescaled our response variable to $0 < y < 1$ to accommodate a beta distribution using the equation $(y \times [n - 1] + 0.5)/n$ following Smithson and Verkuilen (2006). Our predictor variables in these analyses were z -score standardized, and included mean monthly prey mass, total (summed) monthly prey mass, mean time between kills, mean days spent at kill, and mean monthly temperature.

RESULTS

We documented 352 puma kill sites, including 289 of black-tailed deer (Fig. 1). Overall we documented pumas caching 61.5% ($SD = 0.13$, coefficient of variation = 0.21) of all kills they made, with individual pumas caching between 38.3–75.0% of their kills (Table 2). This included caching 71.6% of black-tailed deer kills, 55.6% of mesocarnivores kills, and 37.5% of lagomorph kills, but only 2.8% of rodent kills and 0.0% of bird kills (Table 2).

The model of mass with a quadratic effect was the top model ($w = 1.00$) for predicting whether a puma would cache a kill (Table 3). The model had high predictive ability ($AUC = 0.84 \pm 0.02 SD$), with mass having a positive effect ($\beta = 0.88 \pm 0.16 SE$) and the quadratic effect having a negative effect ($\beta = -1.23 \pm 0.22 SE$; Fig. 2A). The second-ranked model ($\Delta AIC = 11.9$, $w = 0.00$) was a similar model of adjusted mass

Table 2.—A summary of the prey killed and cached by each individual puma in the study. We present the name (with first letter indicating sex) and age class of each puma, followed by the percent of kills that were cached and number of kills in parentheses for each prey species/type.

Puma	Age class	Total kills	Black-tailed deer	Black bear	Birds	Lagomorphs	Mesocarnivores	Rodents
F1	Adult	65.8% (76)	76.7% (60)	0.0% (1)	0.0% (4)	16.7% (6)	75.0% (4)	0.0% (1)
F17	Subadult	66.1% (56)	72.5% (51)	— (0)	0.0% (1)	— (0)	0.0% (1)	0.0% (3)
F19	Adult	60.0% (25)	75.0% (20)	— (0)	— (0)	— (0)	0.0% (1)	0.0% (4)
F23	Adult	38.3% (47)	65.4% (26)	100.0% (1)	0.0% (1)	— (0)	— (0)	0.0% (19)
F43	Adult	53.2% (62)	57.9% (57)	— (0)	— (0)	— (0)	— (0)	0.0% (5)
M33	Adult	74.3% (70)	77.3% (66)	— (0)	0.0% (1)	— (0)	— (0)	33.3% (3)
M36	Subadult	75.0% (16)	88.9% (9)	— (0)	0.0% (1)	100.0% (2)	66.7% (3)	0.0% (1)
All pumas		61.6% (352)	71.6% (289)	50.0% (2)	0.0% (8)	37.5% (8)	55.6% (9)	2.8% (36)

with a quadratic effect, which also had high predictive ability (AUC = 0.82 ± 0.03 SD) and a similar relationship with probability of caching (Fig. 2B), with adjusted mass having a high positive effect (β = 7.32 ± 1.02 SE) and the quadratic effect having a negative effect (β = -3.28 ± 0.60 SE). No other model or variable we considered explained puma caching behavior (Table 3).

Caching was associated with significantly greater feeding time at kills (β = 0.44 ± 0.08 SE, P < 0.0001; Fig. 3). All coefficients in our second post hoc model were significant (P ≤ 0.007) including the interaction between caching and both the linear (β = -0.33 ± 0.08 SE, P < 0.0001) and the quadratic effect of prey mass (β = -0.38 ± 0.10 SE, P < 0.0001; Fig. 3).

Table 3.—The results for our 20 a priori models for determining reasons for why pumas cache kills as well as the null model. We report the AIC scores, change in AIC score from top model (ΔAIC), and AIC model weight (w).

Variables	AIC	ΔAIC	w
Mass + Quadratic	340.3	0.0	1.00
Adjusted mass + Quadratic	352.2	11.9	0.00
Mass + Location	372.3	32.0	0.00
Mass	375.0	34.7	0.00
Mass × Temperature	376.9	36.6	0.00
Adjusted mass	381.1	40.8	0.00
Adjusted mass × Search time	383.8	43.5	0.00
Canopy cover + Temperature + Precipitation	455.4	115.1	0.00
Fawn season	458.7	118.4	0.00
Canopy cover	461.4	121.1	0.00
Elevation × Temperature	461.9	121.6	0.00
Temperature	462.9	122.6	0.00
Temperature × Precipitation	463.3	123.0	0.00
Precipitation	463.3	123.0	0.00
Temperature + Quadratic	466.5	126.2	0.00
Null	466.9	126.6	0.00
Resource pulse	467.5	127.2	0.00
Search time	468.1	127.8	0.00
Location	468.4	128.1	0.00
Search time + Quadratic	468.8	128.5	0.00

The proportion of kills cached varied by month, being highest in April and May and lowest in August (Fig. 4). The monthly proportion of caching was not significantly associated with total mass of kills (β = 0.13, P = 0.40) or interkill interval (β = -0.20, P = 0.13). Monthly caching rates had significant positive relationships with the mean mass of kills (β = 0.64, P < 0.0001) and time spent at kills (β = 0.45, P = 0.0147). There was a marginally significantly negative relationship between monthly caching rate and mean monthly temperature (β = -0.28, P = 0.0690), suggesting higher caching rates during cooler months.

DISCUSSION

We found that pumas most often cached prey of intermediate size (essentially yearling and adult female black-tailed deer in our study system), and mass was the single best predictor of whether pumas cached a kill or not. The model that included a curvilinear relationship with mass + received all the empirical support among our a priori candidate models, and the only other model that could possibly be considered competitive was a similar model of the curvilinear relationship with adjusted mass. At cached kills, pumas spent more time feeding at intermediate-sized kills (Fig. 3), which suggests that caching may at least in part be explained by the potential energetic benefits of concealing or protecting kills of some threshold size for an extended period. Larger prey on the other hand may simply be too time- and energy-consuming to easily cache, as puma feeding time at uncached kills increased directly in relation to the overall prey mass (Fig. 3). This counterintuitively suggests that caching does not increase feeding time at large kills even though pumas fed for longer at cached kills. Our results therefore suggest that caching allows a puma to feed for multiple days on intermediate-sized kills, and as such caching behavior can be used to increase energetic gains from procured food. We were, however, unable to account for individual variation in

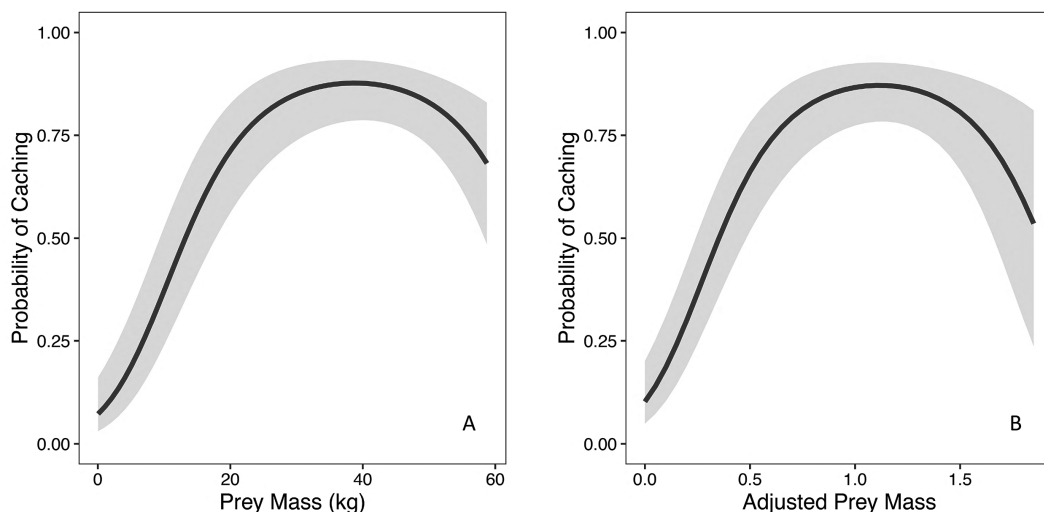


Fig. 2.—Model-based predicted probabilities (±95% CI) of puma caching behavior as a function of the quadratic curvilinear relationship with (A) mass of prey, and (B) adjusted mass (ratio of prey mass to individual puma mass).

caching behavior, and individuals may vary in how often they cache prey and the factors that affect why they cache a given kill or not.

Unexpectedly, we found that pumas were less likely to cache their largest kills and models based simply on absolute prey mass and absolute adjusted mass had consistently low empirical support. This pattern seems counterintuitive, but brown bears (*U. arctos*) and leopards also most frequently cache

intermediate-sized ungulates (Cristescu et al. 2014; Balme et al. 2017). In the case of leopards, their preference for ‘caching’ intermediate-sized prey—which is more often hoisting prey into trees to escape ground scavengers rather than covering prey—is explained by their physical limitations (i.e., their inability to lift the largest prey into trees; Stein et al. 2015; Balme et al. 2017). Pumas have not developed the hoisting behavior of leopards, possibly because the dominant scavengers in much of their range are spectacled bears (*Tremarctos ornatus*) and American black bears, both of which are capable climbers. But the act of gathering material and caching prey can also take effort, as does moving larger carcasses to ideal locations for caching, and it may not be energetically efficient to cover larger prey. This seems to be the most likely explanation for why a brown bear or puma is less likely to cache large prey, which they theoretically should utilize as long as possible to maximize their energetic gains. Ideal prey sizes may also be driven by the feeding capacity of solitary carnivores, as they sometimes reach satiation before consuming large kills entirely, and could vary among individuals.

The probability of being discovered by competitors that can injure or harm pumas at large kills may also contribute to their decisions as to whether to cache prey. Nevertheless, we found little direct evidence that caching was used primarily as a deterrent to kleptoparasitism, including scavenging by other pumas and dominant black bears (Allen et al. 2021a). Specifically, we found little direct evidence that caching was effective at reducing detection of carcasses by dominant black bears, as black bears scavenged from 61.1% of cached kills, compared to 27.4% of uncached kills, and scavenging by black bears was more likely at larger kills. We also found that pumas

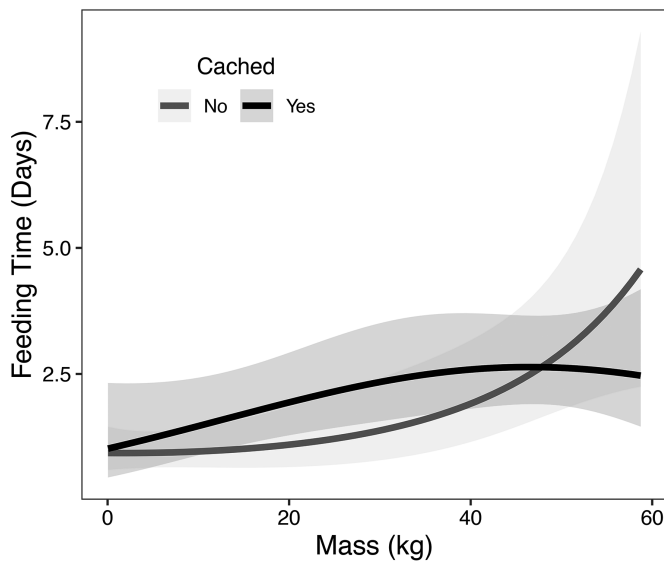


Fig. 3.—Model-based predicted probabilities ($\pm 95\%$ CI) of the relationship between puma caching behavior and puma feeding time (days) with an interaction of quadratic mass.

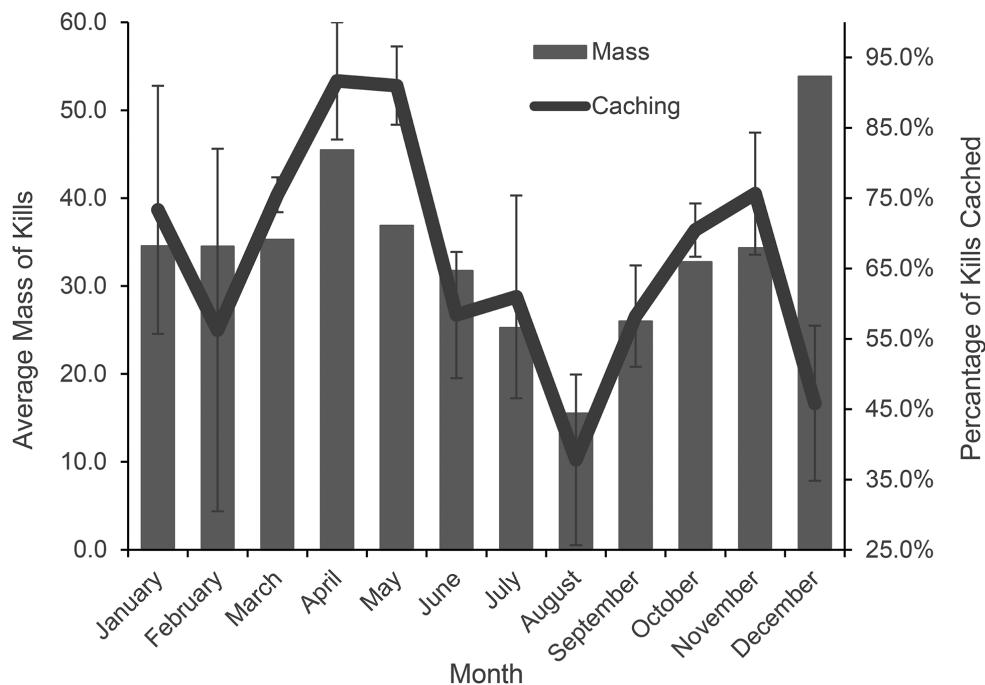


Fig. 4.—Seasonality of caching, represented by a line showing the proportion of kills that are cached each month (with error bars representing *SE*). We also show the average mass of kills by month.

cache more of their kills in months with fewer black bears on the landscape, which allows them to consume more of the prey they kill in these months (Allen et al. 2021a). The high proportion of kills found by black bears unfortunately meant that we could not model how caching affected detection by black bears accurately. The proximity of a kill to the home range boundary of a puma, which we used as a measure of potential conspecific kleptoparasitism, had little empirical support (Table 3). When this distance was combined with mass, it became much more informative, and an improvement on the model of just mass alone. Conspecific kleptoparasitism, however, may not be entirely negative, and may provide adaptive advantages such as reciprocal sharing, especially when carcasses are too large for a single puma to consume (Elbroch et al. 2017a). We acknowledge that data on conspecific space use or density (e.g., Balme et al. 2017) may be more appropriate for determining risk of conspecific kleptoparasitism. Yet such data were unavailable for our study and are often difficult to collect for solitary carnivores, and this hypothesis needs further testing.

Contrary to our predictions, environmental variables and resource pulses had far less predictive ability to determine whether pumas would cache kills or not compared to adjusted prey mass. Furthermore, the relationship of caching with temperature was contrary to our expectation, with temperature having a significant negative effect on caching probability and caching being least frequent in the warmest months. One possible explanation for this counterintuitive result is that black-tailed deer fawns were also readily available during the summer fawn pulse. Puma often exploit summer fawn pulses (Knopff et al. 2010; Clark et al. 2014) and pumas also kill more small prey during summer that may not require caching (due to their small size and relatively quick consumption time) despite much warmer temperatures (Allen et al. 2021a). However, the fawn season model (i.e., *food pulse hypothesis*) had low empirical support suggesting that reduced caching for fawns in our study is better explained by their small body size and the *consumption time hypothesis*. We also found little relationship of caching with times when pumas made multiple kills. Caching relatively small prey such as fawns, or multiple kills is less consistent with the *consumption time hypothesis* or optimal foraging theory, as fawns are consumed quickly and do not necessarily need caching and multiple large kills may spoil or be stolen by scavengers before being able to be consumed despite caching. Consistent with this reasoning, brown bears also do not cache fawns or double kills more frequently than other prey (Cristescu et al. 2014). While previous carnivore studies (e.g., Teurlings et al. 2020) have linked caching to delayed invertebrate activity that slows decomposition, the sole study investigating this effect in pumas (Bischoff-Mattson and Mattson 2009) buried ungulate carcasses to simulate caching and monitored carcass decomposition compared to unburied carcasses rather than monitoring actual puma kills.

Our study illustrates how pumas use caching to extend their foraging time, maximizing the energetic gains from optimal-sized prey. Black-tailed deer were the primary prey of pumas in our study area, both in numbers and prey biomass

(Allen et al. 2015). The frequency of puma caching behaviors and longer duration of feeding at kills of intermediate-sized deer suggest that they are their most important prey, and that pumas often use caching as a means to increase their consumption time. Our hypotheses are not mutually exclusive, however, and our observational study makes it difficult to determine the causal mechanisms behind puma caching. For example, our results were less consistent with the hypotheses that caching in puma were primarily to deter scavengers and decomposers, but these hypotheses still received more empirical support than our null model. Our findings—in addition to similar findings among other solitary carnivores (Cristescu et al. 2014; Balme et al. 2017)—suggest that further studies into caching behaviors including multiple study sites with a greater variety in size of prey species, may provide further insights into our understanding of what constitutes optimal prey, as well as the decisions individual predators make when selecting prey. Ultimately, food caching by pumas and other carnivores may serve multiple purposes, each with the overall goal of extending the immediate food supply from fresh kills.

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