

# Stage-dependent puma predation on dangerous prey

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## Keywords

beaver; porcupine; *Puma concolor*; risk-taking; stage-dependent foraging; prey size; optimal hunting; predation.

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Editor: Matthew Hayward

Received 21 April 2016; revised 7 December 2016; accepted 14 December 2016

doi:10.1111/jzo.12442

## Abstract

Predators likely assess their risk of injury with regards to hunting different prey types, while deciding whether to initiate an attack or to avoid dangerous prey. Risk-taking is age-, stage- and state-dependent, and foraging theory predicts that juvenile predators, individuals of lower social rank, and less-experienced predators that are hungry are among those most likely to engage dangerous prey. In carnivores that optimally hunt prey larger than themselves, however, juveniles may also select for smaller, suboptimal prey as they refine their hunting skills. Thus, in the case of predators that exhibit age-specific prey selection, there may be multiple factors influencing decision-making about prey selection. We compared puma (*Puma concolor*) predation on dangerous adult ungulates and safer juvenile ungulates, as well as two similar-sized rodent species: the more dangerous North American porcupine (*Erethizon dorsatum*) and the more vulnerable American beaver (*Castor canadensis*). We found that dispersing, subadult pumas with limited hunting experience and without territories avoided dangerous but optimally sized adult ungulates, and instead hunted dangerous, suboptimal porcupines more than resident, territorial adults. In contrast, there was no difference in puma predation on beavers between dispersers and residents. Small prey (e.g. not ungulates) formed a large portion of dispersing puma diets of both sexes, and this stage-dependent foraging pattern might be important in describing the ecology of the species, as well as in modeling potential dispersal habitat that could see puma expansion east in North America across hostile matrices where their primary prey has been reduced through anthropogenic effects.

## Introduction

Predation is inherently risky, yet attacking some prey is riskier than others (Mukherjee & Heithaus, 2013). Thus predators should assess their risk of injury with regards to hunting different prey types, before deciding whether to initiate an attack or to avoid dangerous prey all together (Berger-Tal *et al.*, 2009). Foraging theory predicts that juvenile predators, individuals of lower social rank, and hungry, less-experienced predators are among those more likely to take additional risks and engage dangerous prey (Brown, 1992; Cresswell, 1994; Mukherjee & Heithaus, 2013). In contrast, pregnant females would incur the highest costs from risk of injury and therefore are predicted to avoid dangerous prey most often (Clark, 1994). Risk-taking, however, is likely sex-, stage- and state-dependent (McNamara & Houston, 1996; Jaeger *et al.*, 2014). The health, age and social status of the predator in the moment they encounter prey may influence their decisions and behaviors. For example in carnivores that optimally hunt prey larger than themselves, inexperienced juveniles often select for smaller, slower suboptimal prey as they continue to refine their hunting skills (Kitchener, 1999; Hayward *et al.*, 2007). Thus, in the case of

predators that exhibit age-specific prey selection, there may be multiple factors influencing decision-making about prey selection. The data needed to explore and test these assumptions in natural systems, however, are rarely available (Mukherjee & Heithaus, 2013).

Pumas (*Puma concolor*) are widespread solitary predators that exhibit distinct age-specific behavioral classes and that hunt prey much larger than themselves. Puma kittens are dependent upon their mothers for up to 2 years, when they disperse away from their natal ranges to create territories as independent adults (Logan & Sweanor, 2010). Dispersing pumas, sometimes called 'transients,' travel through unfamiliar terrain with unknown prey distributions, suffer low social rank in encounters with resident adults, and exhibit greater mortality rates than established adults (Logan & Sweanor, 2010; Ruth *et al.*, 2011).

Hunting pumas are also occasionally killed when pierced or crushed by antlers or horns of large ungulates (e.g. deer, *Odocoileus* spp.; elk, *Cervus elaphus*; bighorn sheep, *Ovis canadensis*), or when thrown and subsequently slammed into trees or punctured by tree limbs (Ross, Jalkotzy & Daoust, 1995; Murphy & Ruth, 2010). They are also sometimes killed

as a consequence of hunting smaller porcupine species (*Erethizon dorsatum*, *Spiggurus mexicanus*, *Coendou mexicanus*) (Mukherjee & Heithaus, 2013; Elbroch, Hoogesteijn & Quigley, 2016a). Porcupines differ from other mammals in North and South America, in that they wear weapons to deter potential predators. North American porcupines are covered by approximately 30 000 quills—sharp, rigid, hollow hairs 2–10 cm long, and each tipped with 700–800 barbs (Cho *et al.*, 2012). Thus, porcupines pose a much higher risk to pumas and other carnivores than other small prey (Kukka & Jung, 2015; Elbroch *et al.*, 2016a).

In wild felids, the larger the discrepancy between the size of the predator and their larger prey, the longer the learning process for juveniles to acquire efficient hunting skills (Kitchener, 1999). Hunting skills are learned both socially through watching siblings and mothers (John *et al.*, 1968), as well as through opportunities created by mothers for dependent young to participate in operant learning (Caro & Hauser, 1992; Elbroch & Quigley, 2013). Hunting large prey is dangerous, and requires practice and experience to master. In African lions, for example Hayward *et al.* (2007) reported that juvenile animals that lacked the skills or confidence to bring down large prey, contradicted prey size predictions based on optimal foraging theory by disproportionately selecting for smaller, suboptimal prey.

Pumas may also exhibit age-specific prey selection (e.g. Knopff *et al.*, 2010), though this question has not been directly tested in published literature. While the optimal prey size for pumas is adult deer (*Odocoileus* spp.) and juvenile elk (*Cervus canadensis*) (Carbone *et al.*, 1999; Husseman *et al.*, 2003), pumas hunt a great range of prey, including larger ungulates such as moose (*Alces alces*) and smaller mammals and bird species (Knopff *et al.*, 2010; Murphy & Ruth, 2010). It may be that juvenile pumas hunt small prey more than adult pumas to increase their hunting proficiency while simultaneously reducing risks associated with hunting adult ungulates. Puma populations are also increasingly being described as a collective of individuals that select different prey (Elbroch *et al.*, 2016b), providing opportunities to assess intraspecific differences in their consumption of different dangerous prey.

Our objective was to examine age- and sex-specific puma predation upon ungulates, North American porcupines and American beavers (*Castor canadensis*). The porcupine (4–18 kg; Woods, 1973) and beaver (11–26 kg, sometimes more; Jenkins & Busher, 1979) are two members of the Order Rodentia that overlap in size, and are both common secondary prey for pumas (Knopff *et al.*, 2010; Murphy & Ruth, 2010). Whereas porcupines are dangerous prey because of their quills, beavers are not, thus providing a potentially useful comparison. We hypothesized that because pumas hunt prey up to eight times their size (e.g. bull elk, or moose), experience would influence prey selection and pumas would exhibit age-specific prey selection for ungulates. Specifically, we predicted that juvenile, dispersing pumas of both sexes would select against more dangerous adult ungulates, whereas there would be no pattern explaining which pumas selected against safer juvenile ungulates. Second, we hypothesized that young male, dispersing pumas would disproportionately hunt porcupines, a dangerous small prey, whereas resident adults and females would not.

We expected dispersers to consider the potential energetic gains they might obtain from attacking dangerous small prey they encountered worth the potential risk of injury they might incur. Third, we predicted that all pumas, regardless of sex or residency status, would select for safer beavers equally because beavers do not pose a high risk of injury to pumas.

## Materials and methods

### Study sites and field methods

We conducted our research in western Colorado (February 2010 to March 2013) and northwest Wyoming (April 2012 to July 2015) in the Rocky Mountains, USA. The species assemblages at each site were overlapping, but the Colorado site was drier and supported a greater diversity of small and medium carnivores, but fewer megafauna. Complete study area descriptions for Colorado are found in Elbroch *et al.* (2014), and for Wyoming, in Elbroch *et al.* (2013).

Following capture protocols approved by the Institutional Animal Care and Use Committee (IACUC) at the University of California, Davis (Protocols 15341) and Jackson IACUC (Protocol 027-10EGDBS-060210), pumas were captured and fitted with global positioning system (GPS) collars (Lotek Iridium and Globalstar collars, Newmarket, Ontario; Vectronics Globalstar Plus, Berlin, Germany); all collars were equipped with automatic drop-off mechanisms, and researchers collected collars from the field without recapturing the animals. GPS collars acquired location data at 30 min, 1-, or 2-h intervals. GPS clusters were identified visually in ArcGIS. In Colorado, GPS clusters were defined as any  $\geq 2$  locations occurring within 150 meters and spanning  $\geq 2$  h, and containing a minimum of one GPS location recorded during crepuscular or nocturnal periods (Elbroch *et al.*, 2014). In Wyoming, GPS clusters were defined as any  $\geq 2$  locations occurring within 150 meters and spanning  $\geq 4$  h, at all times of day. Puma location data were transferred to handheld GPS units to locate clusters in the field. Prey remains, including hair, skin, rumen, and bone fragments, were used to identify prey species, and the state of prey remains, presence and location of bite marks and body parts consumed were used to determine whether the puma had killed the animal or was scavenging (Elbroch *et al.*, 2014).

### Determining selection and testing stage-dependent variables

We defined ‘dispersers’ as unaccompanied, marked subadult pumas exhibiting GPS trajectories in one direction away from their natal areas with potential consequences for gene flow, and ‘residents’ as pumas that confined their movements (as determined with GPS data) to established territories (Ronce, 2007; Logan & Sweanor, 2010). We transitioned dispersers to residents following their first month in an established territory; for their first month in newly established territories, we defined these individuals as dispersers to reflect the time needed to learn local prey patterns. Dispersers that established a territory ( $n = 4$ ) were not included a second time as residents to avoid unequal sampling that might complicate interpreting results.

**Table 1** Individual puma prey selection in Wyoming and Colorado, including observed and expected frequency of kills, Bonferroni confidence intervals and the type of selection exhibited by each individual for each prey category

PumaID	Site	Res/Dispe	Total kills	Prey	% Obs	% Exp	Bonf low	Bonf high	Selection
F47	WY	Resident	91	Adult ungulates	0.240	0.275	0.127	0.353	None
				Juvenile ungulates	0.650	0.552	0.524	0.776	None
				Beaver	0.000	0.037	0.000	0.000	Against
				Porcupine	0.010	0.052	-0.016	0.038	Against
				Other small prey	0.110	0.083	0.028	0.192	None
F49	WY	Resident	81	Adult ungulates	0.238	0.275	0.112	0.363	None
				Juvenile ungulates	0.438	0.552	0.291	0.584	None
				Beaver	0.099	0.037	0.016	0.182	None
				Porcupine	0.111	0.052	0.024	0.198	None
				Other small prey	0.111	0.083	0.024	0.198	None
F51	WY	Resident	95	Adult ungulates	0.319	0.275	0.192	0.446	None
				Juvenile ungulates	0.585	0.552	0.451	0.719	None
				Beaver	0.053	0.037	-0.005	0.110	None
				Porcupine	0.000	0.052	0.000	0.000	Against
				Other small prey	0.042	0.083	-0.009	0.094	None
F61	WY	Resident	202	Adult ungulates	0.279	0.275	0.195	0.362	None
				Juvenile ungulates	0.612	0.552	0.521	0.703	None
				Beaver	0.035	0.037	0.002	0.067	None
				Porcupine	0.005	0.052	-0.007	0.017	Against
				Other small prey	0.069	0.083	0.025	0.114	None
F109	WY	Resident	81	Adult ungulates	0.494	0.275	0.347	0.640	For
				Juvenile ungulates	0.420	0.552	0.275	0.565	None
				Beaver	0.025	0.037	-0.018	0.068	None
				Porcupine	0.000	0.052	0.000	0.000	Against
				Other small prey	0.062	0.083	-0.005	0.129	None
M29	WY	Resident	65	Adult ungulates	0.200	0.275	0.069	0.331	None
				Juvenile ungulates	0.708	0.552	0.559	0.857	For
				Beaver	0.046	0.037	-0.019	0.111	None
				Porcupine	0.000	0.052	0.000	0.000	Against
				Other small prey	0.046	0.083	-0.019	0.111	None
M85	WY	Resident	72	Adult ungulates	0.338	0.275	0.190	0.486	None
				Juvenile ungulates	0.507	0.552	0.350	0.664	None
				Beaver	0.000	0.037	0.000	0.000	Against
				Porcupine	0.000	0.052	0.000	0.000	Against
				Other small prey	0.153	0.083	0.047	0.259	None
F07	CO	Resident	73	Adult ungulates	0.384	0.306	0.233	0.534	None
				Juvenile ungulates	0.616	0.479	0.466	0.767	None
				Beaver	0.000	0.037	0.000	0.000	Against
				Porcupine	0.000	0.052	0.000	0.000	Against
				Other small prey	0.000	0.083	0.000	0.000	Against
F08	CO	Resident	44	Adult ungulates	0.500	0.306	0.301	0.699	None
				Juvenile ungulates	0.455	0.479	0.256	0.653	None
				Beaver	0.000	0.037	0.000	0.000	Against
				Porcupine	0.000	0.052	0.000	0.000	Against
				Other small prey	0.045	0.083	-0.033	0.124	None
F09	CO	Resident	61	Adult ungulates	0.541	0.306	0.373	0.709	For
				Juvenile ungulates	0.443	0.479	0.275	0.611	None
				Beaver	0.000	0.037	0.000	0.000	Against
				Porcupine	0.000	0.052	0.000	0.000	Against
				Other small prey	0.016	0.083	-0.024	0.057	None
F10	CO	Resident	63	Adult ungulates	0.365	0.306	0.205	0.525	None
				Juvenile ungulates	0.492	0.479	0.326	0.658	None
				Beaver	0.000	0.037	0.000	0.000	Against
				Porcupine	0.000	0.052	0.000	0.000	Against
				Other small prey	0.143	0.083	0.033	0.253	None

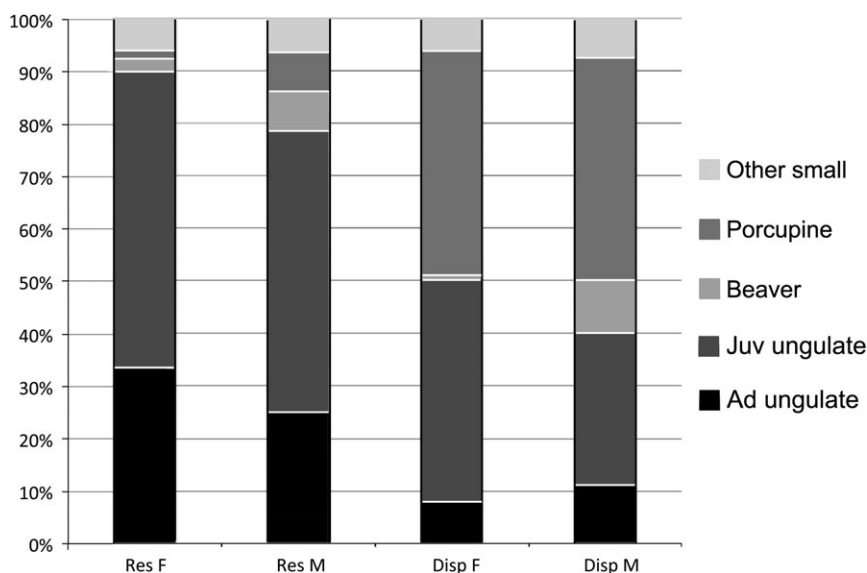
**Table 1** Continued.

PumaID	Site	Res/Dispe	Total kills	Prey	% Obs	% Exp	Bonf low	Bonf high	Selection
F12	CO	Resident	24	Adult ungulates	0.292	0.306	0.047	0.537	None
				Juvenile ungulates	0.625	0.479	0.364	0.886	None
				Beaver	0.083	0.037	-0.058	0.224	None
				Porcupine	0.000	0.052	0.000	0.000	Against
				Other small prey	0.000	0.083	0.000	0.000	Against
M06	CO	Resident	42	Adult ungulates	0.143	0.306	0.000	0.285	Against
				Juvenile ungulates	0.452	0.479	0.250	0.655	None
				Beaver	0.164	0.037	0.065	0.307	None
				Porcupine	0.014	0.052	0.101	0.059	Against
				Other small prey	0.055	0.083	0.049	0.143	None
M13	CO	Resident	39	Adult ungulates	0.385	0.306	0.179	0.590	None
				Juvenile ungulates	0.487	0.479	0.276	0.698	None
				Beaver	0.103	0.037	-0.019	0.224	None
				Porcupine	0.000	0.052	0.000	0.000	Against
				Other small prey	0.026	0.083	-0.038	0.089	None
F96	WY	Disperser	12	Adult ungulates	0.167	0.275	-0.117	0.451	None
				Juvenile ungulates	0.667	0.552	0.307	1.026	None
				Beaver	0.000	0.037	0.000	0.000	Against
				Porcupine	0.000	0.052	0.000	0.000	Against
				Other small prey	0.167	0.083	-0.102	0.436	None
F97	WY	Disperser	28	Adult ungulates	0.037	0.275	-0.059	0.133	Against
				Juvenile ungulates	0.185	0.552	-0.012	0.383	Against
				Beaver	0.036	0.037	-0.052	0.123	None
				Porcupine	0.714	0.052	0.501	0.928	For
				Other small prey	0.000	0.083	0.000	0.000	Against
F90	WY	Disperser	21	Adult ungulates	0.083	0.275	-0.066	0.232	Against
				Juvenile ungulates	0.583	0.552	0.318	0.849	None
				Beaver	0.000	0.037	0.000	0.000	Against
				Porcupine	0.286	0.052	0.039	0.532	None
				Other small prey	0.095	0.083	-0.065	0.255	None
M68	WY	Disperser	25	Adult ungulates	0.280	0.275	0.043	0.544	None
				Juvenile ungulates	0.240	0.552	0.015	0.491	Against
				Beaver	0.200	0.037	0.000	0.400	None
				Porcupine	0.200	0.052	0.000	0.400	None
				Other small prey	0.080	0.083	-0.056	0.216	None
M01	CO	Disperser	40	Adult ungulates	0.025	0.306	-0.040	0.090	Against
				Juvenile ungulates	0.300	0.479	0.109	0.491	None
				Beaver	0.025	0.037	-0.037	0.087	None
				Porcupine	0.650	0.052	0.461	0.839	For
				Other small prey	0.000	0.083	0.000	0.000	Against
M03	CO	Disperser	25	Adult ungulates	0.080	0.306	-0.063	0.223	Against
				Juvenile ungulates	0.320	0.479	0.074	0.566	None
				Beaver	0.120	0.037	-0.042	0.282	None
				Porcupine	0.280	0.052	0.056	0.504	None
				Other small prey	0.200	0.083	0.000	0.400	None

Following Elbroch *et al.* (2016b), we compared prey killed by individual pumas to prey availability as determined by total prey killed by the puma population. We created five categories of prey type (adult ungulates, juvenile ungulates, porcupine, beaver, other small prey), and only included pumas for which we had documented  $\geq 10$  prey in the analyses. Then, we employed chi-square goodness of fit tests to determine differences in individual resource selection. When results of the chi-square tests for a puma were significant, we created Bonferroni confidence intervals (CIs) for each prey type for each puma to

determine which prey proportions were statically different from those selected at the population-level (Byers, Steinhorst & Krausman, 1984; Elbroch *et al.*, 2016b).

Then we employed a series of single multivariate generalized linear models (GLM; SAS 9.3, SAS Institute, Cary, NC, USA) with a binomial distribution (logit link function) to fit our selection parameter (selects against a prey or not) to three independent covariates, study site, territorial status (disperser or resident) or sex, to test whether any of them explained which pumas selected against each prey type. Because our prey



**Figure 1** Mean proportions of diet for five prey types for each behavioral class of pumas. M = male; F = female.

availability was estimated from prey killed by pumas, we focused our analysis on pumas that selected against rather than for each prey type to better capture all pumas that killed prey types, rather than those that only killed them in high abundance. We assessed model performance using pseudo- $R^2$ , a standard method for logistic regression (Baguley, 2012).

## Results

We tracked 25 pumas (11 in CO, 14 in WY) for which we recorded 1390 prey (510 in CO, 880 in WY); for 20 pumas we had sufficient data to include them in analyses (Table 1, Fig. 1). Five pumas selected against adult ungulates, and our model ( $R^2 = 0.641$ ) indicated that they were more often dispersing pumas ( $F_{3,17} = 9.237$ ,  $P = 0.002$ ), but of either sex ( $F_{3,17} = 0.124$ ,  $P = 0.725$ ) or study area ( $F_{3,17} = 2.730$ ,  $P = 0.099$ ). Two pumas selected against juvenile ungulates, and our model ( $R^2 = 0.770$ ) indicated that they were more often dispersing pumas ( $F_{3,17} = 6.03$ ,  $P = 0.014$ ), but again of either sex ( $F_{3,17} = 1.726$ ,  $P = 0.189$ ) or study area ( $F_{3,17} = 3.819$ ,  $P = 0.051$ ). ( $F_{3,17} = 5.074$ ,  $P = 0.24$ ). Fifteen pumas selected against porcupines, and our model ( $R^2 = 0.538$ ) indicated that they were more often resident pumas ( $F_{3,17} = 6.933$ ,  $P = 0.009$ ), but of either sex ( $F_{3,17} = 0.023$ ,  $P = 0.878$ ) or study area ( $F_{3,17} = 1.209$ ,  $P = 0.272$ ). Eight pumas selected against beavers, and our model ( $R^2 = 0.236$ ) suggested that none of our covariates explained selection for this prey: dispersing pumas ( $F_{3,17} = 0.031$ ,  $P = 0.860$ ), sex ( $F_{3,17} = 3.575$ ,  $P = 0.059$ ), or study area ( $F_{3,17} = 0.595$ ,  $P = 0.440$ ) (Table 1, Fig. 1).

## Discussion

Predators weigh the profitability of killing dangerous prey against the potential risk of injury (Berger-Tal *et al.*, 2009),

which can range from temporary reduced mobility to death. Theory predicts that those animals in the greatest need, which varies with the status (e.g. health, age, sex) of the animal at the time, will take the greatest risks (Brown, 1992; Cresswell, 1994; Mukherjee & Heithaus, 2013). There is, however, variation exhibited by carnivores with long-learning processes and age-specific variation in hunting behaviors. For example results from field research on felids that hunt prey as large or larger than themselves show that younger, inexperienced carnivores select safer, suboptimal prey before they gain the experience needed to efficiently kill dangerous, large prey (Hayward *et al.*, 2007). Our results describing puma predation on dangerous adult ungulates and porcupines versus safer juvenile ungulates and beavers (Fig. 1) suggested that puma prey selection supported both foraging theory and other research emphasizing age-specific prey selection in carnivores that optimally hunt prey as large or larger than themselves; puma predation was both predictable and stage-dependent.

As we hypothesized, subadult, dispersing pumas of both sexes avoided dangerous adult ungulates requiring substantial practice and experience to hunt efficiently and instead disproportionately hunted dangerous porcupines (Fig. S1). Porcupines are slow on the ground and likely an attractive, easy prey for hungry pumas dispersing through areas with which they are unfamiliar and thus do not know where primary prey are found. In contrast, our model exploring puma selection against beavers, a more vulnerable prey, performed poorly and was unable to identify covariates that might explain beaver selection, supporting the concept that risk of injury influences foraging decisions. Beaver selection may be explained by variables other than risk of injury, including prey size-profitability trade offs (Gómez-Ortiz *et al.*, 2011), heterogeneity in prey availability across territories (but see Lowrey, Elbroch & Broberg, 2016), or intraspecific variation in prey preferences (Pettorelli *et al.*, 2015; Elbroch *et al.*, 2016b). Or it may be



that the unpredictable, opportunistic aspects of natural predation sometimes muddle patterns of intraspecific prey preference (Hayward *et al.*, 2007).

Because of the roles both porcupines and beavers (Gill & Cordes, 1972; Jones, Lawton & Shachak, 1994) play as ecosystem engineers, we believe the topic of predation on these species deserves further attention. Predators that specialize on porcupines and beavers could radically reduce their numbers (e.g. puma predation on porcupines; Sweitzer, Jenkins & Berger, 1997). In CO, for example, resident M06 killed 12 beavers in 4 months and disperser-turned-resident M01 killed 39 porcupines in 4 months. In WY, disperser F97 killed 20 porcupines in 2.5 months. Thus, puma predation on beavers and porcupines may influence ecosystem structure and function in localized areas, potentially increasing environmental heterogeneity at the landscape level (Jones *et al.*, 1994; Sweitzer, 1996).

Theory that suggests that carnivores select for primary prey regardless of their availability, and only select for secondary prey when they are abundant (Hayward, 2011), may fail to explain species with high levels of intraspecific variation in prey selection, or species in which younger age classes hunt different prey than adults (Hayward *et al.*, 2007; Pettorelli *et al.*, 2015). Small prey (e.g. non-ungulates) formed a large portion of dispersing puma diets of both sexes (Fig. 1). Knopff *et al.* (2010) also noted a higher proportion of small prey in young pumas, and this stage-dependent foraging pattern might be important in describing the ecology of the species, as well as in modeling potential dispersal habitat that could see their expansion east in North America (e.g. LaRue & Nielsen, 2016) or across hostile matrices where their primary prey has been reduced through anthropogenic effects (Stoner *et al.*, 2013).

## Acknowledgments

We thank the Summerlee Foundation, Charles Engelhard Foundation, Eugene V. & Clare E. Thaw Charitable Trust, National Geographic Society, Connemara Fund, BBC Natural History Unit, Community Foundation of Jackson Hole, Hogan Films, High Lonesome Ranch, the Robert and Patricia Switzer Foundation, the Institute on Ecosystems, Ecotour Adventures, Mr. and Mrs. Folger, L. Westbrook, Mr. and Mrs. Robertson, Mr. and Mrs. Gorst, Mr. and Mrs. Heskett, Mr. and Mrs. Habersfeld, Mr. and Mrs. Burgess, and Ms. Smith for financial support of the project. Also thanks to P. Lendrum, M. Peziol, C. O'Malley, A. Kusler, C. McFarland, N. Wight, M. Nelson, B. Lowrey, and J. Williams for fieldwork. No funders influenced our work in any way, and the authors have no conflicts of interest to declare.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Figure S1.** An anesthetized subadult female puma during dispersal, the day after she killed and consumed a porcupine.