

University of Nebraska - Lincoln

DigitalCommons@University of Nebraska - Lincoln

---

USDA National Wildlife Research Center - Staff  
Publications

U.S. Department of Agriculture: Animal and  
Plant Health Inspection Service

---

2012

## Estimates of Energy and Prey Requirements of Wolverines

Julie K. Young

*USDA/APHIS/WS National Wildlife Research Center*, [julie.k.young@aphis.usda.gov](mailto:julie.k.young@aphis.usda.gov)

Brian Hudgens

*Institute for Wildlife Studies*, [hudgens@iws.org](mailto:hudgens@iws.org)

David K. Garcelon

*Institute for Wildlife Studies*, [garcelon@iws.org](mailto:garcelon@iws.org)

Follow this and additional works at: [https://digitalcommons.unl.edu/icwdm\\_usdanwrc](https://digitalcommons.unl.edu/icwdm_usdanwrc)

---

Young, Julie K.; Hudgens, Brian; and Garcelon, David K., "Estimates of Energy and Prey Requirements of Wolverines" (2012). *USDA National Wildlife Research Center - Staff Publications*. 1219.  
[https://digitalcommons.unl.edu/icwdm\\_usdanwrc/1219](https://digitalcommons.unl.edu/icwdm_usdanwrc/1219)

This Article is brought to you for free and open access by the U.S. Department of Agriculture: Animal and Plant Health Inspection Service at DigitalCommons@University of Nebraska - Lincoln. It has been accepted for inclusion in USDA National Wildlife Research Center - Staff Publications by an authorized administrator of DigitalCommons@University of Nebraska - Lincoln.

## Estimates of Energy and Prey Requirements of Wolverines

### Abstract

Wolverine (*Gulo gulo*) populations have decreased throughout much of their North American range and there is interest in establishing recovery programs in the Sierra Nevada of California and the Rocky Mountains of Colorado. Determining the sufficiency of prey resources is an important consideration for initiating wolverine recovery, yet there are limited data on resource availability and needs. Our goal is to estimate prey requirements based on wolverine caloric needs and the caloric content of prey likely to be available. We achieve this goal by modifying existing models to account for wolverine biology. Models show a male wolverine requires 5096 kJ/day (2925-7462 kJ) and a female wolverine requires 3645 kJ/day (2158-5439 kJ). This translates to an annual energy budget for males of 1.9 million kJ/yr that could be met by consuming the equivalent of approximately 8 mule deer/yr (*Odocoileus hemionus*) and 1.4 million kJ/yr for females that could be met by consuming the equivalent of less than 6 mule deer/yr. In light of published records of prey availability, these results suggest populations of wolverines could be sustained where recovery programs are being considered in Colorado and California. We suggest incorporating energetic needs of focal species, such as those calculated here for wolverines, into the assessment of resource availability before implementing recovery programs. Further, these estimates can be applied to management and conservation of wolverines throughout their range.

**Keywords:** energetics, *Gulo gulo*, prey requirements, wolverine

### Introduction

Species recovery programs aim to establish viable, free-ranging populations. Because of range loss due to human persecution, recovery programs for mammalian carnivores often require reintroduction. Reintroduction programs, however, are costly to attempt and may fail (Griffith et al. 1989, Wolf et al. 1996). Before a reintroduction is attempted, therefore, it is prudent to ensure the factors responsible for a species' extirpation are no longer operating (IUCN 1998). Target reintroduction sites should be assessed to ensure habitat quality has not been degraded to the point where viable populations cannot be sustained in the area. Biological factors that must be considered for a

successful recovery program include whether there is enough suitable habitat to sustain a viable population, what type of conflict may occur with humans and other native species (e.g., disease), and if sufficient amounts of natural prey are available (Miller et al. 1999).

Assessing habitat availability and potential human conflicts for reintroduced carnivores is relatively straightforward if reintroductions are to be carried out on public lands offering legal protections. Likewise, potential conflicts with other native species may be assessed based on presence of potential competitors or predators, or mitigated through vaccinating released animals against common diseases (e.g., Hofmeyr et al. 2004). Assessing prey availability, however, may be challenging since the right prey species must be present and persist in sufficient abundance to meet the carnivore's dietary requirements.

Availability of prey is a key determinant of carnivore density (Carbone and Gittleman 2002), and was used to predict the potential size of

<sup>1</sup>Author to whom correspondence should be addressed.  
Email: julie.k.young@aphis.usda.gov

<sup>2</sup>Current address: USDA-Wildlife Services-National Wildlife Research Center, Predator Research Station and Department of Wildland Resources, Utah State University -BNR 163, Logan, UT 84322-5295 USA

recolonizing or reintroduced wolf (*Canis lupus*) populations in the United States (Mladenoff and Sickley 1998, Carroll et al. 2001). An adequate prey base can minimize carnivore exposure to areas where human conflicts typically occur (Graham et al. 2005, Stahl et al. 2007) and obviate the need for long-term intervention to prevent malnutrition and starvation (e.g., Hayward et al. 2007).

Ideally, assessing prey availability should be based on a comparison between the composition and abundance of the prey community in the target area and the relative abundance and biomass of prey species consumed there by the historical, healthy population of the focal carnivore. In the absence of local information, one could compare the biomass consumed and prey availability within healthy contemporary populations with the availability at the translocation site. For many carnivores, such information is not available. Even when the relative frequencies of prey in carnivore diets are known, quantities consumed are generally absent or not related to occurrence (O’Gara 1986, van Dijk et al. 2007). When consumption rates are unknown, prey requirements can be inferred from energy requirements determined from allometric energy models (e.g., West et al. 1997). Allometric energy models take advantage of the fact that basal metabolic rates and total daily energy needs scale with body size (Nagy 1987, 2005). This relationship differs among animal classes, feeding guilds (e.g., herbivores vs. carnivores), and biological state (e.g., Darveau et al. 2002; Glazier 2006). In this paper we demonstrate the application of allometric energy models to assess prey requirements for target reintroduction sites for wolverines (*Gulo gulo*) in North America.

Wolverines are decreasing in North America and viable populations no longer exist in parts of their historical range (Aubry et al. 2007). Interest in state recovery programs have developed in light of recent verified appearances of solitary wolverines in California and Colorado (Garcelon et al. 2009, Moriarty et al. 2009). The Sierra Nevada Mountain Range, California, and Rocky Mountain National Park, Colorado, have been identified as potential reintroduction sites, although the current suitability of these areas is unclear. Carroll et al. (2001) suggest the central and southern regions

of the Sierra Nevada Mountain Range include 22,000 km<sup>2</sup> of high quality habitat for wolverines.

Wolverines are capable of switching between scavenging and hunting (Haglund 1966) and exploiting a wide variety of prey (Rausch and Pearson 1972; Banci 1987, 1994; Landa et al. 1997; Lofroth et al. 2007; van Dijk et al. 2008). Home range size and density of wolverines are presumably related to food abundance (Fortin et al. 2005, Persson 2005). Wolverine reproductive rates are also a function of the abundance of select prey species (Landa et al. 1997, Persson 2005). Thus, to ensure a recovery program succeeds, it is important to assess dietary needs. Because of a paucity of information from historical wolverine populations in California and Colorado on which to base such an assessment, we used allometric models to estimate energetic needs based on published records of wolverine diet. We then used the caloric content of prey species likely to be available to estimate prey requirements.

## Methods

We calculated wolverine energetic requirements based on models for other mammalian carnivores that could be applied to wolverines (Table 1). We excluded papers on energetic models if they were essentially the same as those already represented. A daily energy requirement for wolverines was calculated from eight models which accounted for both basal metabolism and energy expenditure (Table 1). Energy expenditure, also called field metabolic rate (FMR; Nagy 1987), is the total daily energy costs. FMR typically includes basal metabolic rate, activity, thermoregulation, food assimilation, and production. It is often normalized to body mass (Nagy 2005).

To calculate rates based on allometric relationships, we used the midpoint of wolverine body mass and assumed that male wolverines weigh 15 kg and that females weigh 10 kg (Banci 1994). For models based on direct measures of basal metabolism, we used 699.4 kcal/day (Iverson 1972). We assumed that male and female wolverines were active 50% of the 24-hr day (Copeland and Yates 2008). Estimates from the different models were averaged to obtain the expected energy require-

TABLE 1. Energetic models applied to obtain daily requirements (kJ) of wolverines.

ID	Formula <sup>a</sup>	Taxonomic specificity	k(J) male	k(J) female	Sources
1	$\ln(E)=5.95+\ln(M)*0.75$	mustelids	2925	2158	Powell 1979
2	$\ln(E)=6.65+\ln(M)*0.58$	small carnivores	3717	2938	Carbone et al. 2007
3	$\ln(E)=6.62+0.53\ln(M)+\frac{1.22}{1+\exp(4.98/2.69-\ln(M))}$	mammalian carnivores	5959	2966	Carbone et al. 2007
4	$\ln(E)=7.1+\ln(M)*0.572$	mustelids	5705	4524	Carbone et al. 2007 <sup>b</sup>
5	$\ln(E)=6.76+\ln(M)*0.738$	mammals	6365	4719	Karasov 1992
6	$E=572.9(M^{0.738})+5.578(M^{0.6})*10.7(M^{0.316})$	multiple <sup>c</sup>	4940	3626	Karasov 1992
7	$E=2.55*354*M^{0.78}$	mammals/wolverine <sup>d</sup>	7462	5439	Karasov 1992; Iverson 1972
8	$E=32.8*M^{0.83}+536.2*M^{0.68}$	scavengers/mammals/ wolverines <sup>e</sup>	3692	2788	Ruxton & Houston 2003; Copeland & Yates 2006

<sup>a</sup>E equals energy requirement in kJ/day, and M is mass in kg. Mass is assumed to be equal to 15 for males and 10 for females.

<sup>b</sup>Regression from data presented in Carbone et al. 2007.

<sup>c</sup>Values for basal metabolism from carnivores, energy/km traveled from mammals (Taylor 1982), and daily travel distance from mustelids (Hayssen and Lacy 1985).

<sup>d</sup>Basal metabolism from wolverines (Iverson 1972), multiplier from mammals.

<sup>e</sup>Active foraging/traveling time = 75%/day, maximum sustained speed = 0.58 m/sec Copeland and Yates 2006); others based on mammals (Schmidt-Nielsen 1984).

ments of male and female wolverines. We used values from Powell (1979) of kcal/gm consumed (Table 2) to calculate how much a wolverine must consume to meet its energetic demands, assuming that yellow-bellied marmots (*Marmota flaviventris*) were similar to other sciurids, mountain beavers (*Aplodontia rufa*) were similar to marmots, and jackrabbits (*Lepus sp.*) were similar to snowshoe hares (*L. americanus*). For ungulates, we assessed values by Ruxton and Houston (2003) and Laundré (2005; Table 3). The values we report account for assimilation efficiency (~85%; Powell 1979, Laundré 2005).

We determined the minimum number of each type of prey (equivalent) a wolverine would consume under a mixed diet. For this, we calculated the average percent occurrence of four common prey items: ungulates, lagomorphs, small mammals, and sciurids. These categories were selected from several published records of wolverine diets (Table 2). Although percent occurrence data from food habitat analysis are not always as reliable as other measures (van Dijk et al. 2007), these are the best data available for wolverines. Because wolverine diet varies between seasons, the year was divided

into two 182-day seasons: winter and snow-free. Resulting prey requirements were calculated by season for male and female wolverines. We also calculated the number of ungulates a wolverine would need to consume to meet energetic demands because ungulate carrion has been shown to influence wolverine reproductive success (Persson 2005). To facilitate comparison to published records of ungulate population size in two areas targeted for wolverine reintroduction, the Sierra Nevada, California and Rocky Mountain National Park, Colorado, we use mule deer (*Odocoileus hemionus*) as the exemplary ungulate.

## Results

The highest value for daily energetic requirements of a 15-kg male wolverine was 2.5 times that of the lowest (Table 3). Using the average value (5095 kJ) and published records of seasonal wolverine diets (Table 2), a male requires 0.85 kg of prey/day in winter and 0.95 kg/day in snow-free seasons. In winter, the diet includes the equivalent of 1.8 ungulates, 70.7 sciurids, 20.6 lagomorphs, and 832.7 small mammals. During the snow-free season, the diet includes the equivalent of 0.9 ungulates, 122.9

TABLE 2. Frequency of occurrence, average dietary fraction, and caloric values of prey items consumed by wolverines.

Prey Item	% Freq Occurrence										Mean	Diet Fraction	Kg <sup>b</sup>	kJ/kg	kJ/prey	
	N. Boreal Forest*	N. Slope AK*	Central AK*	Northern Terts*	N.W. Rockies*	Norway**	Scandinavia	British Columbia								
<b>Winter</b>																
Lagomorphs	27		6	13	16	3,9		5.2				21.40	0.10	1.23	5476.0	6735
Porcupine	16		3	2	4			19				8.00	0.04	4.35	6783.0	29506
Sciuridae	14	40	9	2	11			23.8				15.20	0.07	0.38	5175.0	1967
Aves	12	11	11	12	6	6,6						9.67	0.04	*	*	*
Small mammals	10	30	20	2	6	14,5		3.4		5	15	12.56	0.06	0.03	4789.0	120
Beaver/muskkrat	1			4	2			4.3				2.50	0.01	12.00	5175.0	62100
<i>Carrion</i>			3													
Ungulate	29	37	45	86	83	73		61.5		94	74	65.22	0.30	46.00	6783.0	312018
unknown	23		6					42.1				14.50	0.07	*	*	*
fat/flesh	16			12								14.00	0.07	*	*	*
bone	32											32.00	0.15	*	*	*
Fish	5			14								8.33	0.04	*	*	*
Other	4	18	25	5	18			3.4				12.00	0.06	*	*	*
Empty	31		73	39								47.67	0.22		0	0
Reference	<i>a</i>	<i>b</i>	<i>c</i>	<i>d</i>	<i>e</i>	<i>f</i>				<i>i</i>	<i>j</i>					
<b>Snow-free Periods</b>																
Ungulate	37	12	33	37				33.3				30.46	0.15	46.00	6783.0	312018
Sciuridae	0	40	33	17								22.50	0.11	0.38	5175.0	1967
Aves	7	2	11	14								8.50	0.04	*	*	*
Mice & voles	93	12	11	57				43.7				43.34	0.22	0.03	4789.0	120
Beaver								20				15.50	0.08	12.00	5175.0	62100
Marmot	7		0					6.7				3.50	0.02	3.50	5175.0	18113
Porcupine								13.3				6.70	0.03	4.35	6783.0	29506
Other												13.30	0.07	*	*	*
Unknown								53.3				53.30	0.27	*	*	*
Reference	<i>h</i>	<i>b</i>	<i>c</i>							<i>i</i>	<i>j</i>					

a) Banci 1987; b) Magoun 1985; c) Gardner 1985; d) Rausch and Pearson 1972; e) Rausch and Hash 1981; h) Newell 1978; i) Myhre and Myrberget 1975; j) van Dijk et al. 2008; k) Lofroth et al. 2007

\*Obtained from Banci 1994

<sup>a</sup>annual diet

<sup>b</sup>from Powell 1979

TABLE 3. Equivalent number of mule deer needed to meet daily and annual energetic needs of a male (15 kg) and female (10 kg) wolverine.

Measure	Daily (kJ)	Annual (kJ)	Annual deer equivalent		
			Powell 1979	Laundré 2005	Ruxton & Houston 2003
<b>MALE</b>					
min	2925	1,067,625	4.3	4.3	4.9
mean	5096	1,859,862	7.5	7.5	8.5
max	7462	2,723,630	11.0	11.0	12.4
<b>FEMALE</b>					
min	2158	787,670	3.2	3.2	3.6
mean	3645	1,330,316	5.4	5.4	6.1
max	5439	1,985,162	8.1	8.0	9.1

sciurids, and 3362.1 small mammals. Minimum values (2925 kJ) would result in males requiring 0.49 kg of prey/day in winter and 0.54 kg/day in snow-free seasons. This would reduce the prey needed to approximately 57% of average, resulting in a diet equivalent to 1.0 ungulates, 40.6 sciurids, 11.9 lagomorphs, and 478.0 small mammals in winter and 0.5 ungulates, 70.6 sciurids, and 1929.9 small mammals in the snow-free season. If wolverines require the maximum values (7462 kJ), it would result in males requiring 1.24 kg of prey/day in winter and 1.39 kg/day in snow-free seasons, increasing the amount of prey needed to approximately 146% of average. In winter, the diet at maximum energetic values includes the equivalent of 2.6 ungulates, 103.6 sciurids, 30.2 lagomorphs, and 1219.4 small mammals. Summer diet would be equivalent to 1.3 ungulates, 0.7 sciurids, and 4923.5 small mammals.

A 10-kg female wolverine requires, on average, only 71.5% of a male's daily and annual energetic requirements (Table 3). The average female requires 3645 kJ of energy/day (Table 3) or 0.61 kg prey/day in winter and 0.68 kg prey/day in snow-free seasons. Females consume 2.1-2.4 fewer mule deer/yr than males to meet energetic requirements. Using average energetic requirements, a mixed diet in winter includes the equivalent of 1.3 ungulates, 50.6 sciurids, 14.8 lagomorphs, and 595.6 small mammals; whereas the snow-free season diet includes the equivalent of 0.6 ungulates, 87.9 sciurids, and 2404.8 small mammals. Minimum energetic requirements would reduce the diet to an equivalent of 0.7 ungulates, 29.9 sciurids, 8.7 lagomorphs, and

352.6 small mammals in winter and 0.4 ungulates, 52.1 sciurids, and 1423.9 small mammals in the snow-free season. Maximum energetic requirements would result in a dietary equivalent of 1.9 ungulates, 75.5 sciurids, 22.0 lagomorphs, and 888.8 small mammals in winter and 1.0 ungulates, 131.2 sciurids, and 3588.7 small mammals in the snow-free season.

## Discussion

Our estimates resulted in average expected energetic requirements of 5095 kJ/day for males and 3645 kJ/day for females. Wolverines have high energetic needs compared to other mammalian carnivores, such as Iberian lynx (*Lynx pardinus*; Almada et al. 1991), mountain lions (*Puma concolor*; Ackerman et al. 1986, Laundré 2005), and coyotes (*Canis latrans*; Laundré and Hernández 2003). Basal metabolism of mustelids weighing > 1 kg is approximately 20% higher than for other mammals (Iverson 1972), and our estimates suggest that wolverines had similarly high requirements.

Wolverines consume 0.1 kg of prey/day more in snow-free seasons than winters. Prey expected to be consumed in winter by wolverines has higher caloric content (Table 2), enabling mass requirements to be lower. For example, ungulates that make up a large portion of winter diet have 1.3 times more kJ/kg than sciurids. Despite differences by season in kg/day consumed, our calculations suggest wolverines may only require < 1 kg of prey/day annually.

We believe these estimates can be applied to management and conservation of wolverines

throughout their range. Although information is lacking to compare these calculations to wild wolverines, we believe our estimates reflect realistic energetic demands because we used a broad suite of models available for assessing carnivore energetic demands while focusing on models that fit wolverine biology. For example, we used the sigmoid function from Carbone et al. (2007), but not the linear regression model. The linear regression model uses a cutoff of 14.5 kg for categorizing carnivores as large or small. This cutoff categorizes male wolverines as large and females as small carnivores. Applying the large carnivore equation to a male wolverine results in extremely high (9000+ kJ/day) energy needs, a value greater than three times the energy needs calculated for females. Although sexually dimorphic, female and male wolverines are not inherently different as implied by this switch point. Thus, the sigmoid approach that did not include a weight-based switch point was more reasonable. While we elected to calculate diet based on average model values, maximum values increase caloric needs by only 0.5 kg/day.

#### Energetics and Prey in California and Colorado

Using a simplified assumption of a 1:1 sex ratio and a population of 50-100 wolverines, which Carroll et al. (2001) suggest could be sustained in the Sierra Nevada, a California population of wolverines would require the equivalent of 354-647 mule deer/yr. This equates to 1.3% or less of the 2.3-2.8 deer/km<sup>2</sup> estimated to inhabit 22,000 km<sup>2</sup> of suitable habitat (Loft et al. 1998, Carroll et al. 2001). Assuming the same density of wolverines that could be sustained as in the Sierra Nevada could also be sustained in the Colorado Rockies, wolverines within Rocky Mountain National Park would consume the equivalent of 13-33 deer/yr or persist solely on <2% of the park's most abundant source of biomass, the ~1000 elk (*Cervus elaphus*; Lubow et al. 2002).

Ungulate populations are predicted to increase in future years as global warming reduces the severity of winters that now limit park populations (Cole 1971, Boyce 1998, Wang et al. 2002). We expect

both areas will provide numerous opportunities for wolverines to exploit ungulate carcasses, as well as opportunities to hunt yellow-bellied marmots, lagomorphs, ground-nesting birds, insects, and small mammals. Nonetheless, further studies are needed in areas where reintroductions are being considered because the data are limited at best on the abundance of non-ungulate prey resources and how such resources may change in the future.

First, a study is needed to assess whether seasonal variation in wolverine prey use could result in a seasonal food deficit. For example, wolverines have been noted to switch from a prey base that relies primarily on carrion to the hunting of emergent ground squirrel and marmots in spring, and one study found the switches significant enough to stratify seasonal habitat analysis based on availability of different prey items within different seasons (Krebs et al. 2007). Thus, a comprehensive analysis of the seasonal availability of specific prey species would be a complimentary approach to understanding the likelihood of a successful translocation to our estimates of caloric needs. Second, wolverine recovery programs should consider public perceptions of the impacts of wolverines in light of current efforts to restore bighorn sheep (*Ovis canadensis*) populations in the Sierra Nevada (Wehausen et al. 2008) and programs to mitigate population decreases of mule deer in Colorado (Unsworth et al. 1999).

#### Model Caveats

We focused on independent, adult wolverines. Although energy expenditure during pregnancy is low for mustelids (Oftedal and Gittleman 1989), lactation costs could be >4-7 times basal metabolic rates (Allen and Ullrey 2004). Energetic requirements of reproduction are an important factor in explaining sexual dimorphism of mustelids (Erlinge 1979, Powell 1979, Moors 1980, Powell and Leonard 1983). Thus, our estimates may be too low to support reproductive activity (Magoun and Copeland 1998, Persson 2005). More information on wolverine energetic demands of growth and reproduction is needed to adjust our calculations.

Our estimates account for standard thermoregulation costs, yet species in extremely cold climates

may have higher thermoregulatory expenditures (e.g., Scholander et al. 1950). However, wolverines offset such costs by physical and behavioral characteristics (Aubry et al. 2007, Copeland et al. 2007). Morphological adaption to snow include moderate foot-load, thick winter pelage, a compact body (Telfer and Kelsall 1984), and a threshold of thermo neutrality as low as -40 °C (Iverson 1972). Wolverines behaviorally thermoregulate by using cavities and snow dens, a behavioral thermoregulation that reduces energetic demands for American martens (Taylor and Buskirk 1994).

Finally, energetic models have yet to be tested with movement and dietary information on free-ranging wolverines. Studies now using GPS collars to obtain spatial data on wolverines, allow for more fine-scale information on daily movement rates that could improve calculations. However, we were able to include information on activity based on detailed movement of GPS-collared wolverines (Copeland and Yates 2008), while the use of scat analysis and back-tracking surveys that are typically used to assess wolverine diet may not result in improvements to models because they are prone to biases (Cumberland et al. 2001, Lofroth et al. 2007, van Dijk et al. 2008).

## Literature Cited

- Ackerman, B. B., F. G. Lindzey, and T. P. Hemker. 1986. Predictive energetics model for cougars. *In* S. D. Miller, and D. D. Everett (editors), *Cats of the World: Biology, Conservation, and Management*, National Wildlife Federation, Washington DC. Pp. 333-352.
- Allen, M. E., and D. E. Ullrey. 2004. Relationships among nutrition and reproduction and relevance for wild animals. *Zoo Biology* 23:475-487.
- Almada, J. J., J. F. Beltran, and M. Delibes. 1991. Energetic expenditure and prey requirements of free-ranging Iberian lynx in southwest Spain. *Journal of Wildlife Management* 55:635-641.
- Aubry, K. B., K. S. McKelvey, and J. P. Copeland. 2007. Distribution and broad-scale habitat relations of the wolverine in the contiguous United States. *Journal of Wildlife Management* 71:2147-2158.
- Banci, V. A. 1987. Ecology and behavior of wolverine in Yukon. M.S. Thesis, University of British Columbia, Vancouver.
- Banci, V. A. 1994. Wolverine. *In* L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, L. J. Lyon, and W. J. Zielinski (editors), *The Scientific Basis for Conserving Forest Carnivores, American Marten, Fisher, Lynx and Wolverine in the western United States*, USDA Forest Service Rocky Mountain Forest and Range Experiment Station, General Technical Report RM-254, Fort Collins, Colorado. Pp. 99-127.
- Boyce, M. S. 1998. Ecological-process management and ungulates: Yellowstone's conservation paradigm. *Wildlife Society Bulletin* 26:391-398.
- Carbone, C., and J. L. Gittleman. 2002. A common rule for the scaling of carnivore density. *Science* 295:2273-2276.
- Carbone, C., A. Teacher, and J. M. Rowcliffe. 2007. The costs of carnivory. *PLoS Biology* 5:e22.
- Carroll, C., R. F. Noss, N. H. Schumaker, and P. C. Paquet. 2001. Is the return of wolf, wolverine, and grizzly bear to Oregon and California biologically feasible? *In* D. Maehr, R. F. Noss, and J. Larkin (editors), *Large Mammal Restoration: Ecological and Sociological Implications*, Island Press, Washington, D.C., USA.
- Cole, G. F. 1971. An ecological rationale for the nature or artificial regulation of native ungulates in parks. *North American Wildlife and Natural Resources Conference* 36:417-426.
- Copeland, J. P., J. M. Peek, C. R. Groves, W. E. Melquist, K. S. McKelvey, G. S. McDaniel, C. D. Long, and C. E. Harris. 2007. Seasonal habitat associations of the wolverine in central Idaho. *Journal of Wildlife Management* 71:2201-2212.

## Conclusions

We believe our values are a good first estimate of energetic requirements for free-ranging, adult wolverines. State agency records in areas of California and Colorado, where recovery programs would likely take place, suggest sufficient numbers of ungulates and alternative prey items are available to support viable populations of wolverines. Although we present these values in regard to recovery within these two states, our calculations can easily be adapted for other wolverine ranges or modified to fit other carnivore species. We suggest incorporating energetic needs of focal species, such as those calculated here for wolverines, into the assessment of resource availability before implementing recovery programs.

## Acknowledgements

We are grateful to J. Copeland for conceptual discussions. R. Powell, H. Weaver, and two anonymous *Northwest Science* reviewers provided editorial comments that improved the manuscript. The study was funded by the Institute for Wildlife Studies.

- Copeland, J. P., and R. E. Yates. 2008. Wolverine population assessment in Glacier National Park, comprehensive summary update. The Ecology and Management of Wildlife and Habitats, RWU 4201, USDA Forest Service, Rocky Mountain Research Station, Missoula, Montana.
- Copeland, J. P., and R. E. Yates. 2006. Wolverine Population Assessment in Glacier National Park: Spring 2006 Progress Report. U.S. Forest Service, Rocky Mountain Research Station, Missoula, Montana. [http://www.fs.fed.us/r1/clearwater/terra\\_org/wildlife\\_07/sensitive\\_species/wolverine/glacier05\\_06.pdf](http://www.fs.fed.us/r1/clearwater/terra_org/wildlife_07/sensitive_species/wolverine/glacier05_06.pdf).
- Cumberland, R. E., J. A. Dempsey, and G. J. Forbes. 2001. Should diet be based on biomass? Importance of larger prey to the American marten. *Wildlife Society Bulletin* 29:1125-1130.
- Darveau, C. A., R. K. Suarez, R. D. Andrews, P. W. Hochachka. 2002. Allometric cascade as a unifying principle of body mass effects on metabolism. *Nature* 417:166-170.
- Erlinge, S. 1979. Adaptive significance of sexual dimorphism in weasels. *Oikos* 33:233-245.
- Fortin, C., V. Banci, J. Brazil, M. Crête, J. Huot, M. Huot, R. Lafond, P. Paré, J. Shaefer, and D. Vandal. 2005. National recovery plan for the wolverine (*Gulo gulo*) [eastern population]. National Recovery Plan No. 26, Recovery of Endangered Wildlife (RENEW), Ottawa, Ontario, Canada. 33 pp.
- Garcelon, D. K., R. Rall, B. Hudgens, J. K. Young, R. Brown, and S. Kohlmann. 2009. Feasibility assessment and implementation plan for population augmentation of wolverines in California. Institute for Wildlife Studies Report, Arcata, CA, USA.
- Gardner, C. L. 1985. The ecology of wolverines in south-central Alaska. M.S. Thesis, University of Alaska, Fairbanks.
- Glazier, D. S. 2006. The 3/4-power law is not universal: evolution of isometric, ontogenetic metabolic scaling in pelagic animals. *BioScience* 56:325-332.
- Graham, K., A. P. Beckerman, and S. Thirgood. 2005. Human-predator-prey conflicts: ecological correlates, prey losses and patterns of management. *Biological Conservation* 122:159-171.
- Griffith, B., J. M. Scott, J. W. Carpenter, and C. Reed. 1989. Translocation as a species conservation tool: status and strategy. *Science* 245:477-480.
- Haglund, B. 1966. Winter habits of the lynx (*Lynx lynx* L.) and wolverine (*Gulo gulo* L.) as revealed by tracking in the snow. *Viltrevy* 4:84-299.
- Hayssen, V., and R. C. Lacy. 1985. A reexamination of basal metabolic rates in mammals: taxonomic differences in the allometry of BMR and body mass. *Comparative Biochemistry and Physiology* 81:741-754.
- Hayward, M. W., J. Adendorff, J. O'Brien, A. Sholto-Douglas, C. Bissett, L. C. Moolman, P. Bean, A. Fogarty, D. Howarth, R. Slater, and G. I. H. Kerley. 2007. The reintroduction of large carnivores to the Eastern Cape, South Africa: an assessment. *Oryx* 41:205-214.
- Hofmeyr, M., D. Hofmeyr, L. Nel, and J. Bingham. 2004. A second outbreak of rabies in African wild dogs (*Lycaon pictus*) in Madikwe Game Reserve, South Africa, demonstrating the efficacy of vaccination against natural rabies challenge. *Animal Conservation* 7:193-198.
- Hornocker, M. G., and H. S. Hash. 1981. Ecology of the wolverine (*Gulo gulo*) in northwestern Montana, USA. *Canadian Journal of Zoology* 59:1286-1301.
- IUCN. 1998. Guidelines for re-introductions. Prepared by the IUCN/SSC Re-introduction Specialist Group, IUCN, Gland, Switzerland and Cambridge, UK.
- Iverson, J. A. 1972. Basal energy metabolism of mustelids. *Journal of Comparative Physiology* 81:341-344.
- Karasov, W. H. 1992. Daily energy expenditure and the cost of activity in mammals. *American Zoology* 32:238-248.
- Krebs, J. E., C. Lofroth, and I. Parfitt. 2007. Multiscale habitat use by wolverines in British Columbia, Canada. *Journal of Wildlife Management* 71:2180-2192.
- Landa, A., O. Strand, J. D. C. Linnell, and T. Skogland. 1997. Wolverines and their prey in southern Norway. *Canadian Journal of Zoology* 75:1292-1299.
- Laundré, J. W. 2005. Puma energetics: a recalculation. *Journal of Wildlife Management* 69:723-732.
- Laundré, J. W., and L. Hernández. 2003. Total energy budget and prey requirements of free-ranging coyotes in the Great Basin desert of the western United States. *Journal of Arid Environments* 55:675-689.
- Lofroth, E. C., J. A. Krebs, W. L. Harrower, and D. Lewis. 2007. Food habits of wolverine *Gulo gulo* in montane ecosystems of British Columbia, Canada. *Wildlife Biology* 13:31-37.
- Loft, E. R., D. Armentrout, G. Smith, D. Craig, M. Chapel, J. Willoughby, C. Rountree, T. Mansfield, S. Mastrup, and F. Hall. 1998. An assessment of mule and black-tailed deer habitats and populations in California. Compilation of a workshop held April 29, 1997, at the Feather River Inn, Portola, California. 56 pp. Available online <http://www.dfg.ca.gov/wildlife/deer.habitatassessment.html> (viewed on 5/23/12).
- Lubow, B. C., F. J. Singer, T. L. Johnson, and D. C. Bowden. 2002. Dynamics of interacting elk populations within and adjacent to Rocky Mountain National Park. In F. J. Singer, and L. C. Zeigenfuss (editors), *Ecological Evaluation of the Abundance and Effects of Elk Herbivory in Rocky Mountain National Park, 1994-1999*, Chapter 1, U.S. Geological Survey Open Report 02-208, Ft. Collins, Colorado.
- Magoun, A. J. 1985. Population characteristics, ecology and management of wolverines in northwestern Alaska. Ph.D. dissertation, University of Alaska, Fairbanks.
- Magoun, A. J., and J. P. Copeland. 1998. Characteristics of wolverine reproductive den sites. *Journal of Wildlife Management* 62:1313-1320.
- Miller, B., K. Ralls, R. P. Reading, J. M. Scott, and J. Estes. 1999. Biological and technical considerations of

- carnivore translocation: a review. *Animal Conservation* 2:59-68.
- Mladenoff, D. J., and T. A. Sickley. 1998. Assessing potential gray wolf restoration in the northeastern United States: a spatial prediction of favorable habitat and potential population levels. *Journal of Wildlife Management* 62:1-10.
- Moors, P. J. 1980. Sexual dimorphism in the body size of mustelids (Carnivora): the roles of food habits and breeding systems. *Oikos* 34:147-158.
- Moriarty, K. M., W. J. Zielinski, A. G. Gonzales, T. E. Dawson, K. M. Boatner, C. A. Wilson, F. V. Schlexer, K. L. Pilgrim, and J. P. Copeland. 2009. Wolverine confirmation in California after nearly a century: native or long-distance immigrant? *Northwest Science* 83:154-162.
- Myhre, R., and S. Myrberget. 1975. Diet of wolverines in Norway. *Journal of Mammalogy* 56:752-757.
- Nagy, K. A., 1987. Field metabolic rate and food requirement scaling in mammals and birds. *Ecological Monographs* 57:111-128.
- Nagy, K. A., 2005. Field metabolic rate and body size. *Journal of Experimental Biology* 208:1621-1625.
- Newell, D. S. 1978. A Wolf, Wolverine, Fox and Bear Scat Study from Northern British Columbia. Fish and Wildlife Branch, Victoria, British Columbia.
- Oftedal, O. T., and J. L. Gittleman. 1989. Patterns of energy output during reproduction in carnivores. In J. L. Gittleman (editor), *Carnivore Behaviour, Ecology, and Evolution*, Volume 1, Cornell University Press, Ithaca, New York. Pp. 355-378.
- O'Gara, B. W. 1986. Reliability of scat analysis for determining coyote feeding on large mammals. *The Murrelet* 67:79-81.
- Persson, J. 2005. Female wolverine (*Gulo gulo*) reproduction: reproductive costs and winter food availability. *Canadian Journal of Zoology* 83:1453-1459.
- Poole, K. G. 1992. Wolverine Carcass Collections in the Western Northwest Territories. Unpublished report, Department of Renewable Resources, Yellowknife, North Western Territory.
- Powell, R. A. 1979. Ecological energetics and foraging strategies of the fisher (*Martes pennanti*). *Journal of Animal Ecology* 48:195-212.
- Powell, R. A., and R. D. Leonard. 1983. Sexual dimorphism and energy expenditure for reproduction in female fisher *Martes pennanti*. *Oikos* 40:166-174.
- Rausch, R.A. 1959. Studies on the helminth fauna of Alaska. XXXVI. Parasites of the wolverine, *Gulo gulo* L., with observations on the biology of *Taenia twitchelli* Schwartz, 1924. *Journal of Parasitology* 45:465-484.
- Rausch, R. A., and A. M. Pearson. 1972. Notes on the wolverine in Alaska and the Yukon Territory. *Journal of Wildlife Management* 36:249-268.
- Ruxton, G. D., and D. C. Houston. 2003. Could *Tyrannosaurus rex* have been a scavenger rather than a predator? *Proceedings of the Royal Society of London B* 270:731-733.
- Schmidt-Neilsen, K. 1984. *Scaling: Why is Animal Size so Important?* Cambridge University Press, Cambridge, UK.
- Scholander, P. F., R. Hock, H. Walters, and L. Irving. 1950. Adaptation to cold in arctic and tropical mammals and birds in relation to body temperature, insulation, and basal metabolic rate. *Biological Bulletin* 99:259-271.
- Stahl, P., J. M. Vandel, V. Herrenschildt, and P. Migot. 2007. Predation on livestock by an expanding reintroduced lynx population: long-term trend and spatial variability. *Journal of Applied Ecology* 38:674-687.
- Taylor, S. L., and S. W. Buskirk. 1994. Forest microenvironments and resting energetics of the American marten *Martes americana*. *Ecography* 17:249-256.
- Telfer, E. S., and J. P. Kelsall. 1984. Adaptation of some large North American mammals for survival in snow. *Ecology* 65:1828-1834.
- Unsworth, J. W., D. F. Pac, G. C. White, and R. M. Bartmann. 1999. Mule deer survival in Colorado, Idaho, and Montana. *Journal of Wildlife Management* 63:315-326.
- van Dijk, J., K. Hauge, A. Landa, R. Andersen, and R. May. 2007. Evaluating scat analysis methods to assess wolverine *Gulo gulo* diet. *Wildlife Biology* 13(sp2):62-67.
- van Dijk, J., L. Gustavsen, A. Mysterud, R. May, Ø. Flagstad, H. Brøseth, R. Andersen, R. Andersen, H. Steen, and A. Landa. 2008. Diet shift of a facultative scavenger, the wolverine, following recolonization of wolves. *Journal of Animal Ecology* 77:1183-1190.
- Wang, G., N. Thompson Hobbs, F. J. Singer, D. S. Ojima, and B. C. Lubow. 2002. Impacts of climate changes on elk population dynamics in Rocky Mountain National Park, Colorado, U.S.A. *Climate Change* 54:205-223.
- Wehausen, J. D., H. E. Johnson, D. W. German, D. F. Jensen, and T. R. Stephenson. 2008. Sierra Nevada Bighorn Sheep: 2007-08 Status. Annual Report, Sierra Nevada Bighorn Sheep Recovery Program, California Department of Fish and Game. 16 p. Available online at <http://www.nrm.dfg.ca.gov/FileHandler.ashx?DocumentID=27650> (viewed on 5/23/12).
- West, G. B., J. H. Brown, and B. J. Enquist. 1997. A general model for the origin of allometric scaling laws in biology. *Science* 276:122-126.
- Wolf, C. M., B. Griffith, C. Reed, and S. A. Temple. 1996. Avian and mammalian translocations: update and reanalysis of the 1987 survey data. *Conservation Biology* 10:1142-1154.

Received 13 July 2011

Accepted for publication 2 April 2012