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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

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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^2 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[a]	Taxanomic 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	$\ln(E)=6.62+0.53\ln(M)+\dfrac{1.22}{1+\exp(4.98(2.69-\ln(M)))}$	mammalian carnivores	5959	2966	Carbone et al. 2007
4	$\ln(E)=7.1+\ln(M)*0.572$	mustelids	5705	4524	Carbone et al. 2007[b]
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[c]	4940	3626	Karasov 1992
7	$E=2.55*354*M^{0.78}$	mammals/wolverine[d]	7462	5439	Karasov 1992; Iverson 1972
8	$E=32.8*M\verb|^|0.83+536.2*M\verb|^|0.68$	scavengers/mammals/ wolverines[e]	3692	2788	Ruxton & Houston 2003; Copeland & Yates 2006

[a]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.

[b]Regression from data presented in Carbone et al. 2007.

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

[d]Basal metabolism from wolverines (Iverson 1972), multiplier from mammals.

[e]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	N. Boreal Forest*	N. Slope AK*	Central AK*	Northern Terrs*	N.W. Rockies*	Norway[a]*	Scandinavia	British Columbia	Mean	Diet Fraction	Kg[b]	kJ/kg	kJ/prey
Winter													
Lagomorphs	27		6 45	13	16	3.9		5.2	21.40	0.10	1.23	5476.0	6735
Porcupine	16		3 15	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	6	12	6	6.6			9.67	0.04	0.03	*	*
Small mammals	10	30	20 16	2	6	14.5	5 15 9	3.4	12.56	0.06	0.03	4789.0	120
Beaver/ muskrat	1		3	4	2			4.3	2.50	0.01	12.00	5175.0	62100
Carrion													
Ungulate	29	37	45 60	86	83	73	94 74 79	61.5	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		6	14					8.33	0.04		*	*
Other	4	18	2	5	18			3.4	12.00	0.06		*	*
Empty	31		73	39					47.67	0.22	0	0	0
Reference	a	b	c d e	f	g								
Snow-free Periods													
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			11					20	15.50	0.08	12.00	5175.0	62100
Marmot	7		0						3.50	0.02	3.50	5175.0	18113
Porcupine								6.7	6.70	0.03	4.35	6783.0	29506
Other								13.3	13.30	0.07		*	*
Unknown								53.3	53.30	0.27		*	*
Reference	h	b	c			i	j j j	k					

a) Banci 1987; b) Magoun 1985; c) Gardner 1985; d) Rausch 1959; e) Rausch and Pearson 1972; f) Poole 1992; g) Hornocker 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

[a]annual diet

[b]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
MALE					
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
FEMALE					
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^2 estimated to inhabit 22,000 km^2 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 asses 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).

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

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