

ENERGY EXPENDITURE AND PREY REQUIREMENTS OF FREE-RANGING IBERIAN LYNX IN SOUTHWESTERN SPAIN

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Abstract: We developed an additive model to estimate seasonal energy expenditure of nonreproductive, free-ranging Iberian lynx (*Felis pardina*) at Doñana National Park in southwestern Spain. We considered only resting, locomotion, hunting, and eating costs. Data for the model were provided by radiomonitoring an adult male (15.4 kg) and an adult female (9.95 kg) in 24-hour samples ($n = 53$) between 1983 and 1985. Average daily energy expenditure was 912 kcal for the male and 673 kcal for the female, with greater seasonal variation in the male. Based on the energy content of the lynx's staple prey, the European rabbit (*Oryctolagus cuniculus*), we estimated the prey requirements of this endangered felid as about 1 rabbit per day.

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Knowledge of energetics of a species in the wild provides insights into the peculiarities of its life history strategy (Calder 1984, Nagy 1987) and is useful in understanding its ecological role (Calow 1987). However, few studies on energetics of free-ranging carnivores have been made; most papers deal with estimates of energy expenditure and consumption rates of captive animals (Golley et al. 1965, Litvaitis and Mautz 1980, Powers 1984).

Powell (1979) developed a general model to estimate the energy budget of free-ranging solitary carnivores. This model was used for fishers (*Martes pennanti*) (Powell 1979) and black-footed ferrets (*Mustela nigripes*) (Powell et al. 1985). From Powell's (1979) model, Gustafson (1984) estimated the energy expenditure and prey requirements of bobcats (*Felis rufus*).

Our paper is the first attempt to develop an energy model for nonreproductive, free-ranging Iberian lynx on a seasonal basis, including: (1) an estimate of energy expenditure due to activities such as locomotion, resting, hunting, and eating; and (2) an estimate of food requirements when preying on European rabbit, the lynx's staple prey in Doñana National Park (Delibes 1980). We did not consider reproductive costs because of the lack of information regarding field behavior of breeding females and growth rates of kittens.

The Iberian lynx is recognized as a distinct species (Honacki et al. 1982, Wozencraft 1989), phylogenetically more separated from the bobcat, the Canadian lynx (*Felis canadensis*), and the European lynx (*F. lynx*) than these species

are among themselves (Werdelin 1981). It is considered the most endangered carnivore in Europe (Mallinson 1978). Hence, learning its ecological requirements is an essential prerequisite to providing management recommendations.

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THE MODEL

The total energetic cost (C_T) for any mammal in a given time period can be expressed as the sum of the energetic expenditure caused by different activities (C_i), plus the cost of thermoregulation (C_{th}) (Powell 1979). For adult lynx, the main nonreproductive activities are resting (C_r), locomotion (C_l), hunting (C_h), and eating (C_e). Thus, the daily total cost should be represented as

$$C_T = C_r + C_l + C_h + C_e + C_{th}.$$

The energetic expenditure of resting (C_r) for a healthy mammal in its thermoneutral zone is roughly the same as its basal metabolic rate (BMR). Kleiber (1961) gave the following equation for estimating basal metabolic rate:

$$C_l = 70 W^{0.75} \text{ kcal/day,}$$

where W is the animal mass in kg.

The cost of locomotion (C_l) was estimated following the allometric equation of Taylor et al. (1970) in kcal/day:

$$C_l = 5.8 W^{0.75} t_2 + 2.6 W^{0.6} d, \quad (1)$$

where t_2 is the time spent while standing (walking and related activities, such as foraging and territorial marking), and d is the daily traveled distance in kilometers. Costs of searching for an approaching prey are also included in C_l .

The hunting energy expenditure (C_h) is related to the capture of prey, which usually occurs with an explosive attack and involves a large amount of energy cost in a short span of time. It has been estimated using the expression of Calder (1984) for the highest possible rate of energy expenditure:

$$C_h = 78.3 W^{0.84} t_3,$$

where t_3 is the time (hr) spent while attacking and subduing prey.

Many authors do not consider the cost of eating (C_e) as a significant energy expenditure in carnivores. However, lynxes observed in captivity spent considerable time eating and handling prey. Therefore, we arbitrarily assumed C_e to be equal to the cost of locomotion at mean travel speed ($S = 1.2$ km/hr; $\bar{x}$ distance run/hr from 24-hr monitoring periods) during the time (hr) spent eating (t_4). Also, Ackerman et al. (1986) considered feeding cost to be similar to walking in mountain lions. Because d in equation (1) can be replaced by the product of speed and time, the energy cost of eating (C_e) will be

$$C_e = (5.8 W^{0.75} + 3.12 W^{0.6}) t_4.$$

We considered thermoregulation costs to be insignificant in Doñana National Park because of climate and lynx patterns of daily activity and habitat use.

STUDY SITE AND METHODS

Field

The study was conducted from 1983 to 1985 in the Doñana National Park in southwestern Spain, a flat zone at sea level north of the mouth of the Guadalquivir River (approx 37°N, 6°30'W). Climate is Mediterranean, influenced by the Atlantic Ocean (Aguilar-Amat et al. 1979). Winters are mild and wet; the average winter temperature during the study period was 11.6

C. Summers are hot and dry, averaging 19 C.

We grouped field data in 3 seasons according to climate and biology of lynx in the study area: spring (Mar–Jun), summer (Jul–Oct), and autumn–winter (Nov–Feb).

To develop the model we used data from 1 adult male and 1 adult female Iberian lynx captured in cage traps baited with domestic rabbits. Individuals were immobilized with a mixture of ketamine hydrochloride and xylazine hydrochloride, weighed, and equipped with a 150-g radio transmitter with an activity sensor (151 MHz, Wildlife Materials, Inc.) (Delibes and Beltrán 1986).

Daily resting time (t_1) and daily traveled distance were estimated from 24-hour monitoring periods (M: $n = 38$, F: $n = 15$), with 1 radio location per hour. Resting was assumed when locomotor activity between consecutive fixes was not detected and the sensor did not indicate activity. We estimated system accuracy to be about 100 m, with a system error of 5° and mean observer–animal distance usually <1 km. To estimate daily traveled distance we added the straight-line distances between consecutive locations of each 24-hour monitoring period. The result was multiplied by 1.25. This multiplier was the average ratio between the actual distance traveled by sand-tracked lynxes (transects of >5 km) along different pathways ($n = 4$) and the linear distance between their outermost points.

We used 30 seconds as the usual time needed by a wild lynx to chase a rabbit, and a hunting success rate of 25%. This success rate is in the range of estimates from Brand et al. (1976) (9–36%) and Parker et al. (1983) (14–55%) in Canadian lynx. Therefore, daily time spent hunting (t_3) should average 120 seconds, because Delibes (1980) estimated the average daily needs of a captive lynx near 1 rabbit.

Laboratory

We used feeding trials with a captive 3-year-old male lynx weighing 11 kg to estimate the time spent eating a rabbit and the energy utilization of this prey. Wild adult European rabbits ($n = 10$) were captured at the study area, killed, and weighed ($\bar{x} = 870$ g, range = 800–1,080). Five were offered to the captive lynx, one per day, and we measured the time spent eating (t_4) each one. We estimated lynx digestion efficiency with the additive energy model of Grodzinski and Wunder (1975). After each

Table 1. Annual and seasonal variation of Iberian lynx resting time (hr) and traveling distance (km) for male and female lynx, respectively.

Season	M								F							
	Resting				Traveling				Resting				Traveling			
	n	$\bar{x}$	SD	Range	n	$\bar{x}$	SD	Range	n	$\bar{x}$	SD	Range	n	$\bar{x}$	SD	Range
Annual	38	10.3	3.8	6–18	38	9.0	2.9	4.4–20.4	15	10.1	3.5	4–16	15	6.7	2.1	2.4–10.9
Spring	12	9.7	2.6	2–14	12	8.9	2.0	5.6–12.5	5	10.4	4.9	4–15	5	6.0	2.4	2.8–8.6
Summer	16	12.9	2.4	9–18	12	7.0	1.7	4.4–9.7	5	10.4	4.2	5–16	5	7.0	3.6	2.4–10.9
Autumn–winter	10	8.3	2.3	5–12	10	11.1	4.2	5.1–20.4	5	9.6	3.2	7–14	5	7.0	1.5	4.6–8.6

daily trial, rabbit remains and lynx feces were collected, ground, and dried. We used a Parr calorimetric bomb to determine the energy content of 5 dried samples. To estimate rabbit energy content eaten by the lynx, we selected from remaining 5 rabbits the anatomical parts that were usually consumed. These were ground, frozen, dried, and we determined their energy content with standard methods (see Fraga et al. 1978 and Aldama and Delibes 1990). Based on urine production and urine energy content of a similar species, the bobcat, fed cottontail rabbits (*Sylvilagus floridanus*) (Golley et al. 1965) and snowshoe hares (*Lepus americanus*) (Powers 1984), we estimated the energy lost through urine.

RESULTS

Field and Laboratory Results

The male's mass was 15.4 kg (captured in Feb 1983), and the female mass from 2 captures averaged 9.95 kg (10 kg in Feb 1985 and 9.9 kg in Jan 1986). We could not measure seasonal mass fluctuations.

There were no sex-specific differences in annual resting time, about 10 hours/day, although it varied widely through the year (Table 1). Male daily traveled distance was significantly higher ($t = 2.25$, $P < 0.05$) than the female's.

Male resting time was higher in summer than in the other seasons, with significant differences between spring and summer ($t = 3.89$, $P < 0.001$), and summer and autumn–winter ($t = 4.76$, $P < 0.001$) (Fig. 1). Male daily traveled distance also was seasonally influenced, being greater in autumn–winter than in other seasons (Table 1). These differences are statistically significant between spring and summer ($t = 2.55$, $P < 0.05$) and summer and autumn–winter ($t = 3.5$, $P < 0.01$). Female data did not show significant statistical variation between seasons,

for either resting time or daily traveled distance ($P > 0.05$) (Fig. 1).

Average time the captive lynx spent eating a rabbit was 50 minutes, ranging from 30 to 72 minutes ($n = 5$).

Dry matter content of the ground rabbit samples was 29.7%, with an energy content of 4.7 kcal/g dry matter ($n = 50$, range = 4.3–4.9 kcal/g dry matter). Fecal biomass varied from 13.1 to 20% of the eaten biomass, averaging 18.6%. Water represented 56.6% of the fecal mass, with an energy content of 2.9 kcal/g dry matter ($n = 30$, range = 2.6–3.3 kcal/g dry matter). So, the digestibility (digested energy/energy intake) of the lynx on a rabbit diet was 83.5%. Taking into account energy lost through urine, metabolized energy was 72.7%. Thus, mean energy content of an average-sized rabbit from the study was estimated at 1,218 kcal, of which 885 kcal would be assimilated by the lynx.

Daily Energy Expenditure

The annual mean of daily resting energy costs for the male was estimated to be 234 kcal or 30 kcal/kg^{0.75} (seasonal range = 24–37 kcal/kg^{0.75}). For the female, the annual mean was 162 kcal (29 kcal/kg^{0.75}), with little variation through the year (seasonal range = 27–30 kcal/kg^{0.75}) (Table 2).

The annual mean daily energy involved in locomotion was estimated as 585 kcal for the male and 433 kcal for the female. When metabolic units of mass were considered, the locomotion costs were similar ($M = 75$ kcal/kg^{0.75}, $F = 77$ kcal/kg^{0.75}). Seasonal variation was more pronounced for the male, with a maximum in autumn–winter (Fig. 1).

Daily energetic costs of eating and hunting were considered constant through the year. For eating, $C_e = 8.9$ kcal/kg^{0.75} for both individuals, that is 69 kcal for the male and 49 for the female.

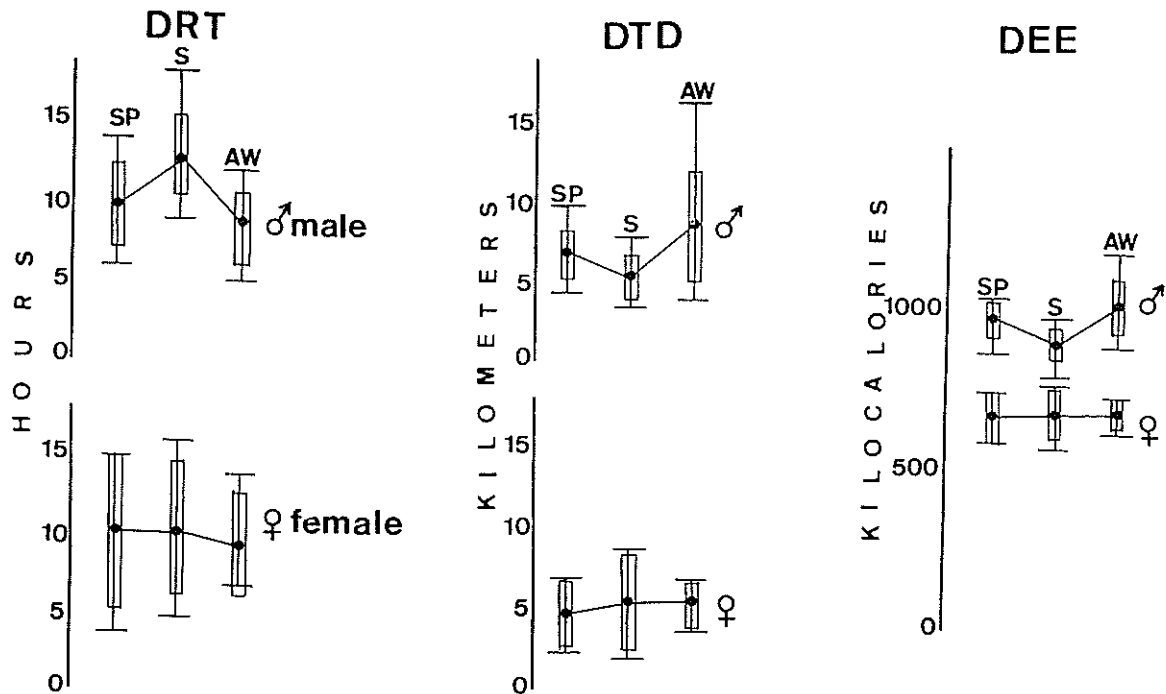


Fig. 1. Male and female seasonal variation in spring (SP), summer (S), and autumn–winter: (AW) daily resting time (DRT), daily traveled distance (DTD), and daily energy expenditure (DEE).

For hunting, $C_h = 3.4 \text{ kcal/kg}^{0.75}$ for 26 and 19 kcal, for the male and the female, respectively.

We substituted the above data in the energy model and found that the daily energy expenditure for male lynx (914 kcal) was significantly higher ($P < 0.001$) than the female's (673 kcal). However, when comparisons were referred to metabolic units of mass, the computed values were similar ($M = 117 \text{ kcal/kg}^{0.75}$, $F = 120 \text{ kcal/kg}^{0.75}$). The female did not show seasonal variation in daily energy expenditure, whereas the male's increased ($P < 0.001$) from spring to autumn–winter (Fig. 1).

Lynxes spent most of their energy in traveling, which accounted for 66 and 67% for the male and the female, respectively, of the total daily energy expenditure (Table 1). Hunting and eating costs had little influence in daily energy expenditure; together they amounted to

only 8%. In this sense, changes in hunting success probably would not produce significant variations in daily energy expenditure.

Prey Requirements

Based on daily energy expenditure values and metabolized energy from 1 rabbit, daily prey requirements for the adult male lynx to avoid an energy deficit would be 1.04 adult European rabbits per day (379 individuals/yr) or 898 g/day. Similarly, we estimated the female's prey requirements to be 0.76 adult rabbits per day (277 individuals/yr or 656 g/day).

Predictions of prey requirements for lynxes with different masses showed a wide range of food demands from 323 g/day for a 5-kg juvenile Iberian lynx resting 20 hours and traveling 2 km to 1,303 g/day for a 15-kg Iberian lynx resting 4 hours and traveling 20 km. An

Table 2. Annual energy costs (kcal/day) of resting (C_r), locomotion (C_l), hunting plus eating (C_{h+e}), and daily energy expenditure (DEE) for the radio-monitored male and female Iberian lynx.

	M (n = 38) ^a				F (n = 15)			
	$\bar{x}$	SD	Range	% DEE	$\bar{x}$	SD	Range	% DEE
C_r	234	70	178–401	26	162	61	12–256	25
C_l	585	160	251–979	66	443	134	220–618	67
C_{h+e}	95			8	68			8
DEE	914	91	724–1,163	100	673	69	527–750	100

^a Sample size (n) refers to the number of 24-hour radio-tracking periods.

average-sized adult Iberian lynx (12 kg) would expend 747 kcal/day when resting 10 hours and traveling 7 km, or 729 g/day and 308 rabbits per year (Fig. 2).

DISCUSSION

Four main assumptions must be discussed, because if they were violated, our results would be questionable. These are (1) lynxes in Doñana live in thermoneutrality, (2) Kleiber's equation gives a good estimate of basal metabolic rate, (3) Taylor's equation gives a good estimate of locomotory cost, and (4) lynxes only prey on rabbits.

Gustafson (1984) and Mautz and Pekins (1989), in areas with more severe climate than the Doñana region, found noticeable thermoregulation costs in bobcats. However, range of temperatures in Doñana and the patterns of activity and habitat use by lynxes (Beltran 1988), which allowed them to rest in favorable microhabitats when necessary, support our assumption that thermoregulation costs are negligible.

Mautz and Pekins' (1989) laboratory estimations of basal metabolic rate for the bobcat ($\bar{x} = 79 \text{ kcal/kg}^{0.75}/\text{day}$, range = 69–88) agree closely with results of Kleiber's (1961) equation. Also, laboratory experiments by Taylor et al. (1974) with cheetahs (*Acinonyx jubatus*) and Corts and Lindzey (1984) with mountain lions gave similar results to those expected from the allometric equation to estimate the costs of locomotion from Taylor et al. (1970).

Our model considered that lynxes only prey on rabbits because Delibes (1980) observed that rabbits constituted 85% of the biomass consumed by lynxes in the area. Ducks (7% of prey biomass) mainly during spring, and deer (5% of prey biomass) in autumn–winter were the main alternative prey. Further work on lynx energetics should consider such diversity in diet.

A more realistic estimate of energy expenditure than we have presented should include reproductive costs, at least for females (Powell and Leonard 1983, Oftedal and Gittleman 1989). Higher activity and longer distances traveled by the male in autumn–winter, and a concomitant increase in energetic costs, could be due to the search for receptive females.

Our results compared well with other studies. Resting time of the Iberian lynx represented 42% of daily time and was similar to inactivity rates of some other felids, such as tigers (*Panthera tigris*) (58.3% [Sunquist 1981]), and was greater than that of bobcats (22.9% [Hamilton 1982]).

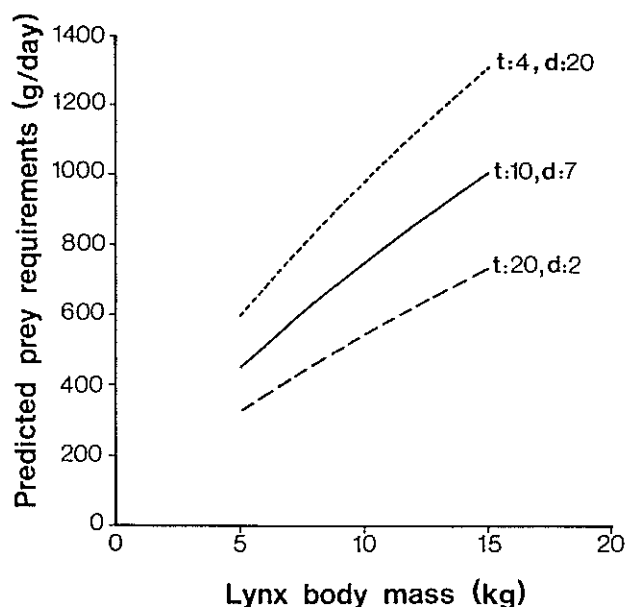


Fig. 2. Predicted prey requirements (g/day) for Iberian lynx of different masses (kg) at 3 different combinations of resting time (t) in hours and daily traveled distance (d) in kilometers; min. (t = 20 hr and d = 20 km), $\bar{x}$ (t = 10 hr and d = 7 km), and max. (t = 4 hr and d = 20 km).

Daily traveled distance was greater and highly variable (seasonally influenced) in the male and similar through the year in the female, which is like daily traveled distance of adult bobcats (Fendley and Buie 1986). Nevertheless, Parker et al. (1983) found that female Canadian lynxes traveled more distance than males.

Our estimates of dry matter and energy content of rabbits were similar to findings of Golley et al. (1965) for cottontails, Moors (1977) for European rabbits, and Litvaitis and Mautz (1980) and Powers (1984) for snowshoe hares. Obviously we must consider the possibility of seasonal and age-related changes in energy content and body composition of wild rabbits (see Fraga et al. 1978 for domestic rabbits).

Digestible energy of rabbits by the Spanish lynx (83.5%) is close to the range observed for the other medium-sized carnivores fed with mammalian prey, such as red fox (*Vulpes vulpes*) (85.4% [Litvaitis and Mautz 1976]) and bobcat (88–90% [Golley et al. 1965], 77.3% [Powers 1984]).

Delibes (1980) estimated prey requirements of a captive female Iberian lynx (8 kg) as 569 g/day (74 g food/kg lynx/day). We found similar values for free-ranging adult lynxes. These estimates were close to those obtained for Canadian lynx by Saunders (1963) and Brand et al. (1976).

Compared to allometric equations for general mammals (Nagy 1987) and carnivores (Gosz-

czynski 1986), the total energy requirements, and therefore feeding rates we measured were underestimated by up to 58.6% (Nagy 1987) and 25% (Goszczyński 1986), respectively. These could be explained, at least in part, by costs of reproduction and thermoregulation, which were not considered in our model.

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