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Energy intake of captive adult-sized arctic foxes *Alopex lagopus* in Svalbard, in relation to body weight, climate, and activity

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Abstract

Food intake, change in body weight, and rate of inactivity were studied in two groups of arctic foxes *Alopex lagopus*, caged at Ny-Ålesund on the western coast of Svalbard (79° N). One group consisted of five "tame" foxes held in captivity for 9 to 28 months, and the other group consisted of 20 "wild" foxes held in captivity for 4 to 23 days. Daily energy intake varied between individuals, but no significant seasonal differences were found. Throughout the year mean energy consumption in tame foxes was $623.8 \text{ kcal} \cdot \text{day}^{-1}$ and in wild foxes $530.2 \text{ kcal} \cdot \text{day}^{-1}$. Maintenance requirement was about $120 \text{ kcal} \cdot \text{kg weight}^{-1} \cdot \text{day}^{-1}$, or $360 \text{ kcal} \cdot \text{day}^{-1}$ for a 3 kg fox. Yearly mean weight for tame foxes was 3.37 kg, and no seasonal differences in weight were detected. Change in body weight (g/day) was correlated with energy intake ($\text{kcal} \cdot \text{kg weight}^{-1} \cdot \text{day}^{-1}$) in wild foxes, and for a single tame fox that was caught as an adult. Foxes were generally inactive 60–90 % of the day, with no seasonal differences. Relationships between energy intake, inactivity, and weather (temperature and wind velocity) were weak or absent.

Introduction

The arctic fox *Alopex lagopus* is subject to a highly variable food supply, both within and between years. As a consequence, energy economizing and energy storage should be highly profitable. UNDERWOOD (1981) observed that captive foxes fed ad libitum voluntarily reduced their energy intake in winter by a factor of nearly 3 compared to the summer intake, but still maintained a constant body weight. Arctic foxes in captivity may sometimes refuse to eat for several days or weeks (UNDERWOOD 1981; PRESTRUD 1982).

KORHONEN (1988a, b) found a seasonal shift in body weight, food intake, and locomotor activity in farm foxes, with a decrease in locomotor activity and an increase in food intake and body weight in the autumn. This trend was reversed during summer. The foxes were most active during the mating period in spring (KORHONEN 1988b). TEMBROCK (1958) and HILMER and TEMBROCK (1972) also found that arctic foxes in captivity were most active in the mating period and least active during autumn. UNDERWOOD (1981) found no seasonal shifts in body weight of captive foxes in Alaska. The same was found for Svalbard foxes by PRESTRUD (1982).

Arctic foxes can withstand temperatures below -30°C without any increase in metabolism (SCHOLANDER et al. 1950a; UNDERWOOD 1981). This is accomplished by good insulation due to very dense and long winter fur, and possibly to some extent by subcutaneous fat; there is no evidence of an adaptive low body temperature (SCHOLANDER et al. 1950b). The growth of fur in arctic foxes parallels annual changes in ambient temperature and photoperiod (UNDERWOOD and REYNOLDS 1980).

In the present study of arctic fox energetics on Svalbard, foxes were held in captivity during the whole year and their body weight, food intake, and activity monitored. The objectives were to verify the seasonal changes in energetics, and to identify factors influencing them.

Material and methods

Animals

Captive foxes were studied during 1987–1989 at the Research Station of the Norwegian Polar Research Institute in Ny-Ålesund on the western coast of Svalbard (78°55'N, 11°56'E). Arctic foxes held in captivity were classified into two groups:

1. "Tame" foxes. Five foxes (3 ♂♂, 2 ♀♀) held in captivity for 9 to 28 months. Four of these were caught as pups 1–2 months old, while the fifth was caught when older than 1 year. The pups originated from three different litters, and two were littermates. They were tamed to some extent, and were included in this study from the age of about 5 months, when they were of adult size. One female died during the study (April 1988).
2. "Wild" foxes. Twenty foxes (11 ♂♂, 9 ♀♀) caught primarily in October and November in the vicinity of Ny-Ålesund and caged for 4 to 22 days. Foxes were classified as juveniles (4–12 months) or adults (≥ 1 year) based on the appearance and wear of the canines. The method of trapping is given in FRAJFJORD (1992). Wild foxes were included to examine the possibility that tame foxes may have behaved abnormally and adapted to a long-term and constant supply of food.

Housing

Foxes were held singly in outside cages measuring $2.5 \times 2 \times 2$ m with an earthen floor in summer and a snow floor during other seasons. One wild fox was held in cage measuring $3 \times 1 \times 1$ m elevated 1 m above ground, while another was held in one half of this cage. A wooden box measuring $1.0 \times 0.5 \times 0.5$ m was placed in each cage, and a smaller box was used in the smaller cage. The roof of these boxes was slightly angled, and was a popular resting place for most foxes. In summer, most foxes were also offered a wooden resting shelf, hung up in one corner of the cage. Cages and boxes were cleaned regularly; otherwise disturbances were minimized although the close proximity to Ny-Ålesund made it impossible to exclude all kinds of disturbances. Snow often had to be removed from the cages in winter.

During the second winter, 1988–1989 (mid-November until mid-April), three foxes were housed together inside a building, in a cage measuring $5 \times 2 \times 1$ m (FRAJFJORD 1991). The wall on one side of this building was made of transparent plastic material, and the room was penetrated by winds to a small extent.

Foxes kept outdoors were exposed to natural temperatures and light regime, but wind velocity inside cages was probably slightly lower than outside (as found by UNDERWOOD 1981). Foxes could protect themselves against the wind, either by finding shelter inside or behind the nest box, or in a snow cave dug out by themselves. Despite this, most foxes only sought refuge in very bad or rainy weather, and they rested in exposed positions even in strong winds. Foxes kept indoors were exposed to approximate natural light and temperatures, but protected from winds.

Feeding and weighing

Foxes were fed dry fox food (mainly "Ewofox 3", manufactured by Felleskjøpet, Norway) softened in water ad libitum. The daily ration of dry food, amount of water added, and leftovers were weighed to the nearest g (Mettler electronic scale). Since the foxes rarely cached any of this artificial food, all leftovers could be collected daily. The food was prevented from freezing by a small heating element (from September to May). From November 1988 to February 1989, foxes were fed by personnel at the Research Station with less accuracy in weighing, which may have led to a small overestimation of the food intake of the three foxes. Foxes were sometimes kept together in pairs, but these days were excluded from food analysis except for the winter 1988–1989 when mean food intake for the three foxes was calculated. Metabolizable energy content of the food was given by the manufacturer. Water in the form of liquid or snow was provided ad libitum.

Wild foxes were weighed before and after experiments, and otherwise only occasionally. Tame foxes were weighed regularly about each second week, except during January when no fox was weighed. All foxes were weighed before feeding. No drugs were used in the handling of foxes.

Free-living foxes captured and recaptured were weighed to give some information on natural shifts in body weight.

Observations on activity

From September to November 1987, the rate of inactivity (lie + sit + stand) of foxes was observed from a building. All animals were scanned every 5 minutes and their behaviour noted. Most observations were made during the day, but some foxes were observed for 24 hours. Tame foxes were observed for a minimum of 24 hours every second week.

From December 1987 a video camera and time lapse recorder were used to study the inactivity of foxes during 24 hours. Recordings were made about every 2 weeks, including the period when three foxes were kept inside a building, or for a minimum of two 24-hour periods for wild foxes. All recordings from January and most from February were from foxes inside the building. Behaviour was sampled each 5 minutes from the video tapes. A 500 W halogen lamp was used to illuminate the cages during recordings in darkness. The foxes never showed any aversive reactions towards this light, and it most likely did not affect their activity.

Food intake, excrementory, and excretory output

One tame and one wild fox were held in a small indoor cage ($1.5 \times 1 \times 1$ m) for about a week in winter and spring 1988 for an accurate sampling of food intake and excretory output (the tame fox was used twice). The small size of the cage restricted the activity of these foxes, which was video recorded during at least two 24 hour periods. Foxes were fed as usual, and the faeces produced collected daily. In winter time, the urine could also be collected since it froze instantly. Body weight was recorded daily before feeding without handling the animals, by weighing a small nest box with the fox inside. Also, the room temperature was recorded once daily. The wild fox was used at the end of her captivity, when she was adapted to the artificial food.

Climate

Data on temperature and wind velocity were obtained from the Norwegian Meteorological Institute for the weather station in Ny-Ålesund. Because precipitation is low, less than 400 mm annually (STEFFENSEN 1982), and because these data were incomplete, precipitation was not included in the analysis. To study the joint effect of temperature and wind velocity, a wind chill index (WCI) given by ROSENBERG *et al.* (1983) was calculated (kcal/m^2). Mean monthly temperatures in the region range from -14.0°C in February to 4.5°C in July. January and November are the most windy months. The sun is below the horizon from November to February.

Statistics

Results are presented as monthly or seasonal means \pm SD between individuals. Analysis of variance (ANOVA) is used to study variation in means. In every ANOVA the individual fox is the sampling unit. Least squares linear regressions are used to study the effect of weather variables on daily energy intake and inactivity. In regression analysis daily energy consumption, percent inactivity, mean temperature, wind speed, or WCI are the sampling units.

Results

Daily food or energy intake in tame foxes was variable, with a maximum range of 87–1390 kcal/day in a single fox, but all ate daily and in no periods refused to eat. Males consumed slightly more kcal/day, weighed more, and were more inactive than females in most months (Fig. 1), but sample size was too small for statistical analysis. Individual variability was great as exemplified by the large standard deviations in figure 1. Seasonal differences (Tab. 1) in energy consumed ($F = 0.05$), weight ($F = 0.21$), and inactivity ($F = 0.74$) were not significant ($p > 0.05$).

Yearly mean energy intake for tame foxes was 620.7 kcal/day. When housed inside during the winter 1988–1989 ($n = 3$), energy intake was comparable to the previous winter (Fig. 1), with a mean of 567.3 kcal/day. Mean weight for all foxes for the whole year was 3.37 kg. Tame foxes were generally inactive 60–90 % of the day (Fig. 1), with a yearly mean of 76.7 %. No consistent relationship between energy intake and body weight was detected for the tame foxes ($r^2 = 0.03$ – 0.19 , $p > 0.05$), except for the male that was caught when more than 1 year old (Fig. 2). The regression slope of this male was not significantly different from the regression slope of wild foxes ($t = 1.87$, $v = 32$, $p > 0.05$).

Most wild foxes adapted rapidly to captive conditions and started to eat at once (most arctic foxes are not very timid to humans), although a few ate only minor amounts of food

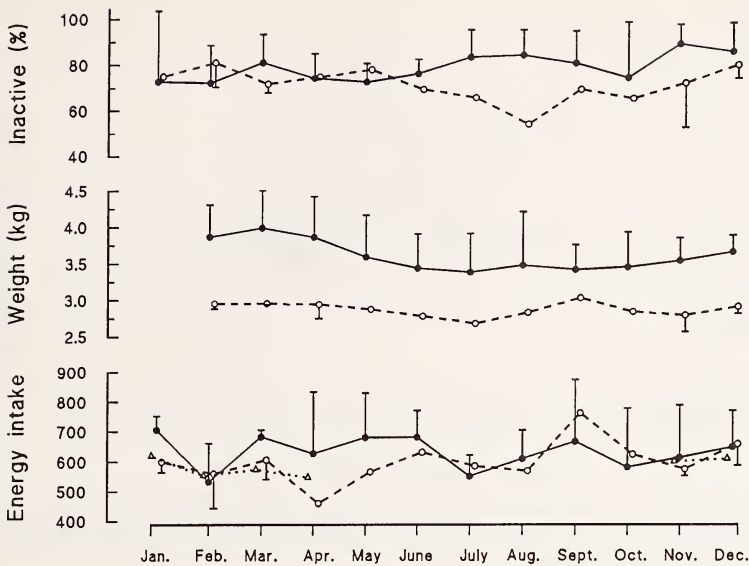


Fig. 1. Monthly mean energy intake (kcal/day), weight, and inactivity of male (●) and female (○) tame arctic foxes during November 1987 through April 1989. 2 males and 1 female were housed collectively during the winter 1988–1989 (△). Only one SD is shown for convenience

and one very fat female probably none at all. Ranges in weight, percent weight change (weight when released in percent of weight at capture), and energy intake were 2.30–4.75 kg, –16.8–37.0 %, and 0–1057 kcal/day, respectively. Several of these wild foxes had a higher energy intake than the tame foxes. Energy intake ($F = 0.81$), rate of inactivity ($F = 0.07$), and weight ($F = 2.68$) (Tab. 2) were not significantly different ($p > 0.05$) from tame foxes in the autumn and winter. Weight changes in wild foxes were significantly correlated

Table 1. Mean (\pm SD) daily energy intake (kcal/day), weight (kg), and inactivity (%) in five tame foxes by season

Spring = April–May, Summer = June–August, Autumn = September–October, Winter = November–March

Sex	Spring	Summer	Autumn	Winter
Energy intake				
Males	663.1 \pm 142.2	613.4 \pm 80.4	614.8 \pm 193.9	636.7 \pm 96.4
Females	556.0	598.5	685.2	600.4 \pm 61.5
Combined	636.3 \pm 127.9	609.7 \pm 66.1	632.4 \pm 162.1	622.2 \pm 77.4
Weight				
Males	3.69 \pm 0.54	3.40 \pm 0.55	3.43 \pm 0.40	3.79 \pm 0.35
Females	2.92	2.76	2.89	2.90 \pm 0.10
Combined	3.50 \pm 0.58	3.24 \pm 0.55	3.29 \pm 0.42	3.43 \pm 0.55
Inactive				
Males	74.9 \pm 8.8	80.2 \pm 9.2	75.7 \pm 18.8	86.6 \pm 9.0 (72.7 \pm 15.8) ^a
Females	72.5	62.8	67.2	77.9 \pm 2.5 (70.5) ^a
Combined	74.3 \pm 7.3	75.9 \pm 11.5	73.6 \pm 16.0	83.1 \pm 8.1

^a Second winter in captivity.

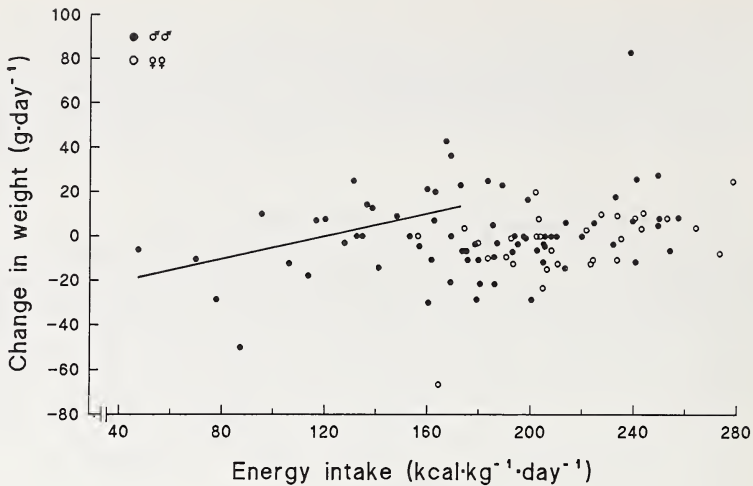


Fig. 2. Relationship between change in weight and energy consumption in five tame foxes during 1987–1988. Mean energy intake for periods between weighing. Regression was significant in one male: $Y = 0.26X - 30.78$, $r^2 = 0.29$, $p < 0.05$

with energy intake (Fig. 3). Minimum energy requirements to maintain weight was $117.9 \text{ kcal} \cdot \text{kg weight}^{-1} \cdot \text{day}^{-1}$ (Fig. 3). The female that did not eat anything lost about 73 g/day . Three wild foxes that were captive in mid-winter (February and March) did not reduce food intake. Mean energy intake of these three foxes (591.1 kcal/day) was not different from wild foxes during September to November ($F = 0.05$, $p > 0.05$). Likewise, their rate of inactivity was not different ($F = 1.17$, $p > 0.05$). Free-living foxes caught and recaptured during the autumn and winter (< 90 days between captures, $n = 16$) showed a change of 4 g/day in weight. This was only a quarter of the change observed in wild foxes in captivity (mean 15 g/day).

Inspections of scattergrams of energy intake with inactivity, temperature, wind speed, and WCI, and of inactivity with temperature, wind speed, and WCI did not indicate any curvilinear relationships. Thus, linear regressions were used to study these relationships. Regressions for every tame fox were calculated for energy intake with the three weather variables by season and by the whole year ($n = 20\text{--}328$), and for inactivity with energy intake and the three weather variables by the whole year ($n = 33\text{--}55$). Generally, the r^2 -values were low (range $0.00\text{--}0.15$) and no clear patterns (linear relationships) were observed. Two exceptions were found. In one female the relation between energy intake and WCI was high in spring ($r^2 = 0.29$, $p < 0.01$), i.e. 29% of the variation in energy intake

Table 2. Mean (\pm SD) of body weight at capture, number of days in captivity, weight change in % of weight at capture, food intake, and rate of inactivity ($n = 19$) in 20 wild arctic foxes

Foxes	n	Body weight (kg)	Days in captivity	Weight change (%)	Food intake (kcal/day)	Inactive (%)
Juvenile ♂♂	7	2.84 ± 0.48	11.0 ± 5.9	12.4 ± 13.1	589.4 ± 244.1	77.3 ± 7.4
Juvenile ♀♀	7	2.99 ± 0.48	9.3 ± 2.5	8.3 ± 15.7	579.5 ± 326.6	74.9 ± 17.7
Adult ♂♂	4	2.95 ± 0.40	10.3 ± 4.5	6.4 ± 8.4	533.4 ± 390.0	81.6 ± 7.3
Adult ♀♀	2	3.75 ± 1.41	9.0 ± 2.8	-13.9 ± 4.2	144.3 ± 204.0	68.3 ± 16.2
All combined	20	3.01 ± 0.59	10.1 ± 4.2	7.2 ± 14.2	530.2 ± 310.7	76.4 ± 12.0

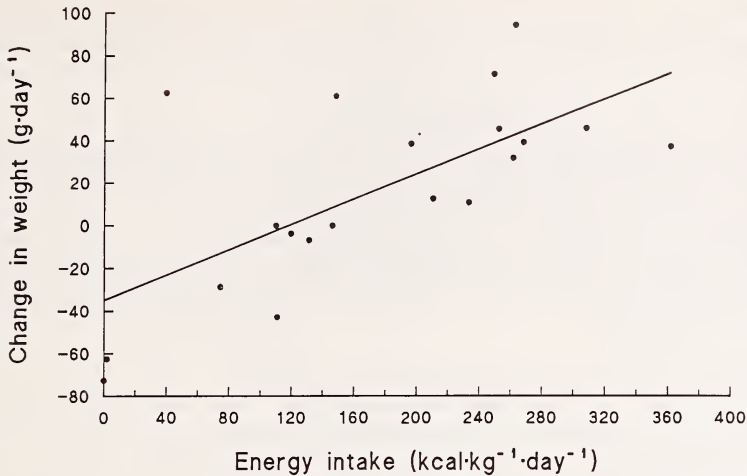


Fig. 3. Relationship between change in weight and energy consumption in 20 wild foxes in the years 1987–1989. Regression line: $Y = 0.30X - 34.9$, $r^2 = 0.46$, $p < 0.01$

was accounted for by variation in WCI. In the other female the relation between energy intake and wind speed was high in winter ($r^2 = 0.36$, $p < 0.05$). Linear regressions of base-10-logarithms of these 5 variables generally did not improve the r^2 -values. Among wild foxes energy intake was positively correlated with inactivity ($r^2 = 0.21$, $p < 0.05$), i.e. foxes that were most inactive consumed most food.

The two foxes that were kept in a smaller indoor cage for 3 short periods ate a variable amount of food (Tab. 3). In May, the male was eating more than twice as much as in March, but despite this still lost weight (Tab. 3). Since temperature also had increased significantly, the most likely explanation for “Dick” still losing weight was an increased level of activity by about 14 %. The female, “Susi”, gained only slightly in weight despite eating a fairly large amount of food and being highly inactive (Tab. 3). Mean production of waste (faeces and urine) was about 22 %, and about 78 % of the total energy consumed (energy ingested + fat metabolism) was used for respiration.

Discussion

UNDERWOOD’s (1981) conclusion that captive arctic foxes in Alaska voluntarily reduced their food intake from $240 \text{ kcal} \cdot \text{kg weight}^{-1} \cdot \text{day}^{-1}$ in summer to 85 kcal in winter was not

Table 3. Food intake, excrementary and excretory output and energy balance in two arctic foxes

Individual (month)	D	Wt	Wt ch	En in	Feces		Urine		Me	In- act.	Temp.
					kcal	%	kcal	%			
Susi ♀ (March)	7	2.95	14	216.5	50.6	23.4	4.8	2.2	74.4	99.3	-14.5
Dick ♂ (March)	7	3.75	-50	127.7	25.2	19.7	5.1	4.0	76.3	85.0	-18.8
Dick ♂ (May)	9	3.05	-14	279.1	71.7	25.7	—	—	<74.3	71.1	1.7

D = days on experiment, Wt = initial body weight (kg), Wt ch = change in body weight (g/day), En in = energy intake ($\text{kcal} \cdot \text{kg weight}^{-1} \cdot \text{day}^{-1}$), Me = metabolized energy (%), Inact. = % inactive, Temp. = room temperature ($^{\circ}\text{C}$). Kcal of faeces und urine means $\text{kcal} \cdot \text{kg}^{-1} \cdot \text{day}^{-1}$.

confirmed by the present study on foxes in Svalbard. In contrast, the Svalbard foxes ate a rather constant amount of food all year round. It is unlikely that this resulted from these foxes being more tame or better adapted to captive conditions than the Alaskan ones, because most wild foxes in captivity ate as much as and some even more than the tame foxes. The high food consumption of wild foxes in the autumn and winter indicated that these foxes had not reduced their metabolism or physiologically adjusted themselves to a reduced food availability. Rather, they apparently ate as much as possible and stored the excess energy as body fat, which makes sense for survival during winter time. UNDERWOOD (1971, 1981) gave no explanation of how his foxes could eat less in winter and still maintain body weight. It is unlikely that the large shift in food consumption in his foxes could be explained by foxes more often experiencing lower critical temperatures in the summer than in the winter.

Tame foxes (mean weight 3.37 kg) consumed on average 184.2 and wild foxes (weight 2.91 kg, excluding the single fox that did not eat anything at all) consumed 191.8 kcal·kg⁻¹·day⁻¹, which is slightly more than the Alaskan foxes (140.5 kcal·kg⁻¹·day⁻¹, weight 4.1 kg, UNDERWOOD 1981). This is approximately 3–3.5 times more than the basal metabolic needs (51.6 kcal·kg⁻¹·day⁻¹) (SCHOLANDER et al. 1950b; MCNAB 1989). Minimum energy requirements to maintain body weight were found to be about 120 kcal·kg⁻¹·day⁻¹, which is about twice a basal metabolic need of the fox. In addition to basal metabolism and thermoregulation, energy was used in activity, fat deposition, growth of fur, or increase in body size.

The lack of correlation between change in weight and energy consumption among most tame foxes is difficult to explain. Most likely, these foxes often ate more than was strictly needed for maintenance of body weight and utilized the energy less efficiently than what was optimal. In one "tame" fox that was caught as an adult, i.e. more resembling "wild" foxes, a relationship between energy consumption and weight change was found. In a study of red foxes, VOGTSBERGER and BARRETT (1973) calculated the energy loss in faeces to 9%. Energy loss in the present study was about twice as much, which indicates a less efficient utilization of the food, although quality of food would influence this. The correlation between inactivity and energy consumption in wild foxes probably resulted from the least anxious and most relaxed foxes eating most, i.e. foxes that did not adapt as well to captive conditions were more restless and consumed less food. The relations between food intake, inactivity, and weather variables were at best weak. Thus, energy consumption and inactivity were not greatly influenced by weather, probably due to a high insulation value of fox fur (UNDERWOOD 1971, 1981).

Seasonal variation in body weight of tame foxes was not as great as reported by UNDERWOOD (1981). This is in accordance with no seasonal differences in energy consumption and in rate of inactivity. A lowered activity in winter could be beneficial as it will save energy (TEMBROCK 1958; KORHONEN 1988b), but the fox still needs to search actively for food. In the present study, individual differences in yearly inactivity were quite large, as much as 20% in two foxes. Furthermore, one fox was 22% more inactive in his first winter than in the second. Thus, activity of captive foxes fed ad libitum is probably more dependent upon individual differences, housing conditions, and the development of stereotyped movements, than upon an inherent rate of seasonal activity.

The amount of fat in arctic fox carcasses varies seasonally and is highest in the early winter and lowest in spring (UNDERWOOD 1971; PRESTRUD 1982; HAMMILL 1983). Variations in weight during the autumn and winter probably mainly reflect fat deposition or fat catabolism. Fat layers are thickest on the back (UNDERWOOD 1971; PRESTRUD 1982), and may also have some insulative value, especially when the fox is lying in a curled position with its back against the wind. The amount of fat in a wild female that increased in weight from 2.9 to 4.5 kg was estimated as a minimum of 2 kg (44%), which is equivalent to about 19 000 kcal (PETERS 1983). If requirements are 120 kcal·kg⁻¹·day⁻¹ and mean

weight is set at 3.5 kg, this fat storage would last 45 days. Thus, a fox that is able to deposit a substantial layer of fat may survive 1–2 months without food even at low temperatures during the winter.

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Zusammenfassung

*Energieaufnahme bei gefangenen erwachsenen Polarfüchsen (Alopex lagopus) in Spitzbergen.
Beziehungen zum Körpergewicht, zum Klima und zur Aktivität*

Bestimmt wurden Nahrungsaufnahme, Änderungen des Körpergewichts sowie der Anteil an der Inaktivität bei Polarfüchsen, *Alopex lagopus*, die in Ny-Ålesund an der Westküste Spitzbergens (70°N) in Käfigen gehalten wurden. Eine der untersuchten Gruppen bestand aus fünf „zahmen“ Füchsen, die zwischen 9 und 28 Monate in Gefangenschaft gehalten wurden; die zweite Gruppe bestand aus 20 „wilden“ Füchsen, die 4 bis 23 Tage gefangen gehalten wurden. Zwischen den Individuen schwankte die tägliche Energieaufnahme, jedoch jahreszeitlich wurden keine signifikanten Unterschiede gefunden. Von den „zahmen“ Tieren wurden im Jahresdurchschnitt 623,8 kcal/Tag und von den „wilden“ Füchsen 530,2 kcal/Tag aufgenommen. Der Erhaltungsbedarf betrug etwa 129 kcal/kg Gewicht/Tag oder 360 kcal/Tag für einen 3 kg schweren Fuchs. Das mittlere Durchschnittsgewicht der „zahmen“ Füchse betrug 3,37 kg, jahreszeitliche Unterschiede gab es nicht. Gewichtsänderungen (g/Tag) konnten mit der Energieaufnahme (kcal/kg Gewicht/Tag) bei den „wilden“ Füchsen und für einen einzelnen „zahmen“ Fuchs, der als erwachsenes Tier gefangen worden war, bestimmt werden. Für etwa 60–90 % der Tageszeit waren die Tiere inaktiv, saisonale Unterschiede gab es dabei nicht. Beziehungen zwischen der Energieaufnahme, der Inaktivität und dem Wetter (Temperatur und Windgeschwindigkeit) waren entweder nur schwach ausgebildet oder existierten überhaupt nicht.

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