

# Energy Cost of Running in an Arctic Fox, *Alopex lagopus*

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This work was conducted to determine effect of season and starvation on metabolic rate during running in the Arctic Fox (*Alopex lagopus*) on Svalbard (78°55'N, 11°56'E), Norway. Indirect calorimetry was used to measure metabolic rate of foxes running on a treadmill and heart rate was monitored using implanted radio transmitters. The relationship between heart rate and metabolic rate was also examined. Metabolic rate increased with running speed. In July the metabolic rate during running almost fitted general equations predicted for mammals, while it was up to 20% lower in January, indicating seasonal variation in metabolic rate. There was a significant positive linear relationship between heart rate and weight specific metabolic rate, suggesting that heart rate can be used as an indicator of metabolic rate. Starvation for 11 days decreased the net cost of running by 13% in January and 17% in July, suggesting that a starved fox runs more energetically efficient than when fed. Heart rate measured in July decreased by 27% during starvation. Re-feeding reversed the starvation-induced reduction in metabolic rate and heart rate during running almost up to post-absorptive levels. The present results are from one fox, and must be considered as preliminary data until further studies are conducted.

Key Words: Arctic Fox, *Alopex lagopus*, heart rate, metabolic rate, net cost of running, starvation, Svalbard.

The Arctic Fox (*Alopex lagopus*) is the only resident terrestrial carnivorous mammal in the high Arctic Svalbard archipelago (74° N–81° N). Here, they experience extreme contrasts in light and temperature, and periodic limitations of food availability (Fuglei 2000). Therefore, physiological adaptations to seasonal variations in ambient conditions and to periods of reduced food supplies must be important for the survival of this small-sized species. The Arctic Fox moves great distances, up to 2300 km, during seasonal migrations and in search for food, and also across the pack ice (Pulliainen 1965). Fox tracks have even been observed close to the North Pole (Nansen 1897). One Arctic Fox, live trapped and ear tagged in Ny-Ålesund, Svalbard (78° 55' N, 11° 56' E), was shot on the island of Novaya Zemlya (ca. 75° N, 55° E; personal communication K. Frafjord and P. Prestrud), a direct line distance of about 1200 km, and the real distance traveled must have been considerably longer.

Food items are scarce during the dark winter season, and during such periods the Arctic Fox faces a conflict between the need to conserve energy and the need to actively search for food. Studies on the effect of starvation on the energy cost of running have not been carried out for the Arctic Fox and a consistent pattern of such effects has not emerged from studies of other homeotherms. For the resting state, starvation-induced reduction of basal metabolic rate (BMR), also called metabolic depression, has been found in humans (Keys et al. 1950), laboratory Wistar rats (Fuglei and Øritsland 1999a; Kleiber 1975) and also in wild species such as the Emperor Penguin (*Aptenodytes forsteri*; Dewasmes et al. 1980) and the Arctic Fox (Fuglei and

Øritsland 1999b; Prestrud 1982). This adaptation is of importance because it acts to reduce the rate of body weight loss and therefore increase the chances for surviving periods of starvation. Compared to post-absorptive conditions, the net costs of running were unchanged in semi-starved humans (Joffe et al. 1919), starved dogs (Lusk 1916–17), Emperor Penguins (Dewasmes et al. 1980) and laboratory Wistar rats (Fuglei and Øritsland 1999a). The net cost of running is a measure of efficiency and is conventionally expressed as the energy needed for moving 1 kg a distance of 1 m (Dewasmes et al. 1980; Taylor et al. 1970). Thus, an unchanged net cost of running indicates no changes in energetic efficiency during exercise. In contrast, the net cost of walking decreased with semi-starvation in humans (Keys et al. 1950). Heart rate (HR) has been proposed as an indicator of metabolic rate in mammals (Lund and Folk 1976; Nilssen et al. 1984), and in birds (Bevan et al. 1994), but such data are not available for the Arctic Fox.

This work was conducted to determine the effect of season and starvation on metabolic rate and HR during running in the Arctic Fox. Additionally we wanted to examine whether HR can be used as an index of metabolic rate in the Arctic Fox.

## Methods

### Animals

This work was performed on Svalbard, Norway, in Ny-Ålesund (78° 55' N, 11° 56' E), at the Norwegian Polar Institute's Research Station. One male Arctic Fox was caught and held year round in an outdoor wire mesh-netting cage (2.5 m long × 2 m wide × 2 m

high), equipped with a wooden sleeping box (0.5 m long  $\times$  0.5 m wide  $\times$  1 m high). The fox was fed *ad libitum* with commercial dry fox food (FK-Revepellets, manufactured by Felleskjøpet, Norway) softened in water. Water was always provided *ad libitum*. Freezing of the food and water was prevented during the winter by use of thermostatically controlled heating elements in the feeding cup.

#### Metabolic rate

Detailed descriptions of the apparatus and methods used to measure oxygen consumption and carbon dioxide production, and the calculation of metabolic rate are described elsewhere (Fuglei and Øritsland 1999a, b). Briefly, metabolic rate during running was measured in an open-circuit system, composed of a treadmill located inside a plexiglas respiratory chamber (101 cm long  $\times$  38 cm wide  $\times$  50 cm high) in a climate chamber. BMR (IUPS Thermal Commission, 2001) was measured in the same system using a plexiglas respiratory chamber (41 cm long  $\times$  41 cm wide  $\times$  41 cm high; for details see Fuglei and Øritsland 1999b). Oxygen concentration was determined using an oxygen analyzer (S-3A, R-1 and N-22M, Applied Electrochemistry Inc., Sunnyvale, California). A carbon dioxide analyzer (Binos-100, Rosemount GmbH & Co, Hanau, Germany) was used to determine carbon dioxide. Chamber airflow, which was maintained at  $33.0 \text{ l} \cdot \text{min}^{-1}$  when measuring metabolic rate during running and at  $10.0 \text{ l} \cdot \text{min}^{-1}$  when measuring BMR using a Charles Austen Pump (B100 DEC, England), was monitored using a mass flow meter (Bronkhorst Hi-tec, Vorde, Holland) with a control valve (F 113-EA-55-V) and a readout system (E-5514-FA). Values for oxygen consumption and carbon dioxide production were determined from the difference in the concentration of the air entering and leaving the chamber, and from the rate of airflow through the chamber. Metabolic rate was expressed as watts per kg body weight.

BMR was subtracted from metabolic rate during running in order to focus exclusively on the net cost of running (Dewasmes et al. 1980; Fuglei and Øritsland 1999a). Thus the net cost of running was calculated from the equation:

$$[1] \quad M_N = (M_{\text{run}} - \text{BMR}) \cdot v^{-1}$$

where  $M_N$  is the net cost of moving 1 kg a distance of 1 m ( $\text{J} \cdot \text{m}^{-1} \cdot \text{kg}^{-1}$ ),  $M_{\text{run}}$  is metabolic rate during running ( $\text{J} \cdot \text{s}^{-1} \cdot \text{kg}^{-1}$ ), BMR is basal metabolic rate ( $\text{J} \cdot \text{s}^{-1} \cdot \text{kg}^{-1}$ ), and  $v$  is speed ( $\text{m} \cdot \text{s}^{-1}$ ).

#### Heart rate

The HR transmitter was surgically implanted in April 1997. The fox was fasted for 12 h before surgery and then anaesthetized with a mixture of medetomidine (Domitor® Orion Corporation Animal Health, Turku, Finland; 0.05 mg/kg) and ketamine (Parke-Davis; 3 mg/kg). The HR transmitter (DataCol 5.0, Mini Mitter, Oregon, USA, model VHF-C-1) was 6.3 cm  $\times$  2.3 cm and weighed 44 g, approximately 1.5% of the

body weight. The HR transmitter was inserted in the abdominal cavity through a ventral midline incision. The two HR electrodes exited the abdominal cavity. One was placed under the skin above the sternum and the other was positioned on the inside of the left foreleg pit via a subdermal tunnel. A more detailed description of the operational procedure is presented elsewhere (Fuglei et al. 2002). The fox was kept indoors in a small cage for 1-2 days until recovery, and inspected regularly. All training and experiments were conducted at least 1-2 months after surgical implantation of the transmitter. Each HR value was the average of 10 heartbeats.

#### Experimental protocol

Experiments were conducted in the winter and summer season during 24-h darkness in January 1997, and 24-h daylight in July 1997. In January metabolic rate was measured in one post-absorptive, then starved and then re-fed fox, and the same was measured in July, but then simultaneously with HR. Mean air temperature in the metabolic chamber was  $-3 \pm 3 \text{ }^\circ\text{C}$  in January and  $9 \pm 1 \text{ }^\circ\text{C}$  in July. When not engaged in the experiments, the animal was exposed to ambient temperatures in the outdoor holding cage averaging  $-18 \text{ }^\circ\text{C}$  in January and  $3 \text{ }^\circ\text{C}$  in July. These temperatures are considered to be within the thermoneutral zone of winter and summer adapted Arctic Foxes (Casey et al. 1979; Underwood 1971). The fox was trained for the exercise experiment daily for three weeks, at three different running speeds:  $3.9 \text{ km} \cdot \text{h}^{-1}$ ,  $4.8 \text{ km} \cdot \text{h}^{-1}$  and  $5.8 \text{ km} \cdot \text{h}^{-1}$  ( $1.08 \text{ m} \cdot \text{s}^{-1}$ ,  $1.33 \text{ m} \cdot \text{s}^{-1}$  and  $1.61 \text{ m} \cdot \text{s}^{-1}$ ). Metabolic rate in the post-absorptive, starved and re-fed state were measured between 08:00-12:00 h both in January and July. To ensure post-absorptive, pre-starvation conditions, food was withdrawn 12-h prior to the experiments (day 1). Then, measurements were taken at each speed over several days in January ( $3.9 \text{ km} \cdot \text{h}^{-1}$ ,  $n = 3$ ;  $4.8 \text{ km} \cdot \text{h}^{-1}$ ,  $n = 4$ ;  $5.8 \text{ km} \cdot \text{h}^{-1}$ ,  $n = 2$ ) and in July ( $3.9 \text{ km} \cdot \text{h}^{-1}$ ,  $n = 8$ ;  $4.8 \text{ km} \cdot \text{h}^{-1}$ ,  $n = 6$ ;  $5.8 \text{ km} \cdot \text{h}^{-1}$ ,  $n = 6$ ). During the starvation experiments, only two speeds were used,  $3.9 \text{ km} \cdot \text{h}^{-1}$  and  $5.8 \text{ km} \cdot \text{h}^{-1}$ . The fox starved for 11 days, both in January and July. During re-feeding for four additional days, the fox was fed *ad libitum*. The fox was weighed using a spring scale (Pesola 0-10 kg) with an accuracy of  $\pm 0.1 \text{ kg}$ .

#### Statistics

Repeated measurements of post-absorptive metabolic rates and HR during running, 4-10 days before initiating starvation experiments, were expressed as means  $\pm$  SD. The relationship between post-absorptive metabolic rate and HR were tested with linear regression (PROCLIN, SAS).

#### Results

After 11 days of starvation, the body weight of the Arctic Fox held in captivity under ambient conditions decreased to 81% of its initial body weight of 4.05 kg in January, and to 75% of initial body weight of 3.66 kg

in July. After four days of re-feeding, the body weight increased to 93% of its initial level in January and to 89% in July.

Post-absorptive metabolic rate during running increased linearly with increasing speed. In July the metabolic rate while running almost fitted general equations predicted for mammals (Taylor et al. 1982; equation 2) relating metabolic rate at a constant speed to speed and body weight, while it was up to 20% lower in January (equations 3 and 4).

[2] Metabolic rate =  $10.7 \cdot BW^{-0.316} \cdot v + 6.03 \cdot BW^{-0.303}$ , where metabolic rate is  $W \cdot \text{kg}^{-1}$ ,  $BW$  is body weight in kg, and  $v$  is speed in  $\text{m} \cdot \text{s}^{-1}$ . The calculated metabolic rate during running gave the following formula for the fox when it weighed 4.05 kg in January:

[3] Metabolic rate =  $6.88 \cdot v + 3.95$ , and for the fox when it weighed 3.66 kg in July:

[4] Metabolic rate =  $7.10 \cdot v + 4.07$

The post-absorptive metabolic rate while running was up to 14% lower in January compared to July (equations 5 and 6, Figure 1).

[5]  $M_{\text{run}}$  in January =  $3.23 \cdot v + 6.97$  ( $n = 9$ ;  $r^2 = 0.80$ )

[6]  $M_{\text{run}}$  in July =  $2.63 \cdot v + 9.38$  ( $n = 20$ ;  $r^2 = 0.71$ ), where  $M_{\text{run}}$  is metabolic rate during running in  $W \cdot \text{kg}^{-1}$  and  $v$  is speed in  $\text{m} \cdot \text{s}^{-1}$ .

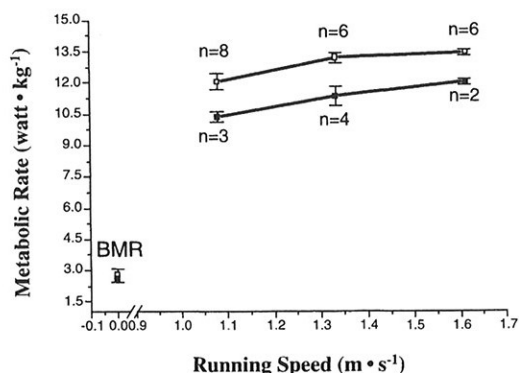


FIGURE 1. Post-absorptive basal metabolic rate (BMR;  $W \cdot \text{kg}^{-1}$ ) and metabolic rate in one Arctic Fox running on a treadmill at three different speeds in January (solid squares) and in July (open squares) ( $n$  = the number of experiments). The equations describing the relationships between metabolic rate and running speeds are: Metabolic rate in January =  $3.23 \cdot v + 6.97$  ( $n = 9$ ;  $r^2 = 0.80$ ); Metabolic rate in July =  $2.63 \cdot v + 9.38$  ( $n = 20$ ;  $r^2 = 0.71$ ).

Conventionally, the net cost of running is expressed as the energy needed for moving 1 kg a distance of 1 m, also referred to as the efficiency of locomotion (Dewasmes et al. 1980; Fuglei and Øritsland 1999a). In the post-absorptive Arctic Fox, the net cost of run-

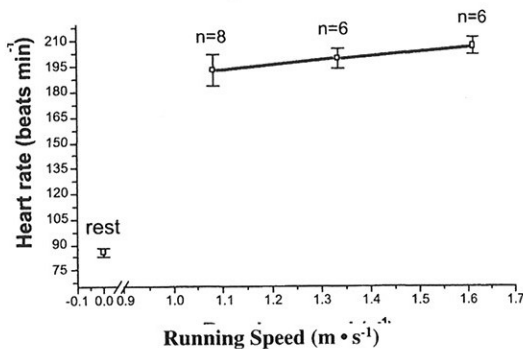


FIGURE 2. Post-absorptive mean heart rate (bpm) in one Arctic Fox running on a treadmill at three different speeds in July ( $n$  = the number of experiments).

ning was about 15% lower in January compared to July (Table 2). HR, which was measured only in July, increased with running speed (Figure 2). There was a significant positive linear relationship between HR and metabolic rate at increasing running speeds (Figure 3). The equation describing the relationship between the two variables is:

[7] Metabolic rate =  $-5.18 + 0.09 \cdot \text{HR}$  ( $n = 19$ ;  $r^2 = 0.98$ ;  $p < 0.0001$ ), where metabolic rate is in  $W \cdot \text{kg}^{-1}$  and HR is beats  $\cdot \text{min}^{-1}$ .

Starvation for 11 days induced a reduction in metabolic rate during running, with up to 11% lower values in January and 14% in July (Table 1a). Starvation for 11 days decreased the net cost of running from post-absorptive values by up to 13% in January, and 17% in July (Table 2). HR measured in July decreased after 11 days starvation by up to 27% at different running speeds (Table 1a).

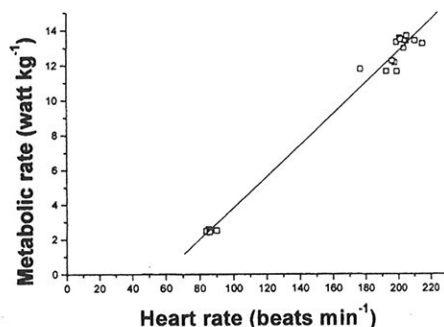


FIGURE 3. Basal metabolic rate and metabolic rate while running on a treadmill ( $W \cdot \text{kg}^{-1}$ ) at three different speeds as a function of heart rate (HR; bpm) in one Arctic Fox. The regression equation is: Metabolic rate =  $-5.18 + 0.09 \text{HR}$  ( $r^2 = 0.98$ ,  $p < 0.0001$ ).

TABLE 1a. Metabolic rates during running ( $M_{run}$ ;  $W \cdot kg^{-1}$ ) at two speeds 3.9 and 5.8  $km \cdot h^{-1}$  of one Arctic Fox when in a post-absorptive state (day 1) and during starvation (day 3-11) in January and July. Heart rate (HR) in beats per min (bpm) was monitored only in July. Several experiments were conducted on the post-absorptive fox (day 1), as indicated by SD values and the number of experiments in parenthesis.

Days	January		July			
	3.9 $km \cdot h^{-1}$ $M_{run}$ ( $W \cdot kg^{-1}$ )	5.8 $km \cdot h^{-1}$ $M_{run}$ ( $W \cdot kg^{-1}$ )	3.9 $km \cdot h^{-1}$ $M_{run}$ ( $W \cdot kg^{-1}$ )	HR (bpm)	5.8 $km \cdot h^{-1}$ $M_{run}$ ( $W \cdot kg^{-1}$ )	HR (bpm)
1	10.38 ± 0.27 (n = 3)	12.07 ± 0.13 (n = 2)	12.07 ± 0.41 (n = 8)	193 ± 9 (n = 8)	13.44 ± 0.14 (n = 6)	207 ± 5 (n = 6)
3	9.76	11.54	11.14	181	12.36	199
5	9.66	11.68	10.72	175	12.18	192
7	9.11	10.84	10.49	165	12.21	185
9	9.32	11.29	10.51	147	12.06	175
11	9.36	10.74	10.36	140	12.05	163

TABLE 1b. Metabolic rates during running ( $M_{run}$ ;  $W \cdot kg^{-1}$ ) at two speeds 3.9 and 5.8  $km \cdot h^{-1}$  of one Arctic Fox during 2 and 4 days of re-feeding in January and July. Heart rate (HR) was monitored in July only.

Days	January		July			
	3.9 $km \cdot h^{-1}$ $M_{run}$ ( $W \cdot kg^{-1}$ )	5.8 $km \cdot h^{-1}$ $M_{run}$ ( $W \cdot kg^{-1}$ )	3.9 $km \cdot h^{-1}$ $M_{run}$ ( $W \cdot kg^{-1}$ )	HR (bpm)	5.8 $km \cdot h^{-1}$ $M_{run}$ ( $W \cdot kg^{-1}$ )	HR (bpm)
2	10.98	11.80	10.30	149	12.20	169
4	9.84	11.53	10.75	176	12.00	189

TABLE 2. The net cost of running ( $M_N$ ;  $J \cdot m^{-1} \cdot kg^{-1}$ ) in one Arctic Fox in post-absorptive condition (PA) and after 11 days starvation (S) in January and July, when running at two speeds 3.9, and 5.8  $km \cdot h^{-1}$ .

Running speed	January		July		
	PA	S	PA	S	
$M_N$ ( $J \cdot m^{-1} \cdot kg^{-1}$ )	3.9 $km \cdot h^{-1}$	7.24	6.36	8.56	7.11
$M_N$ ( $J \cdot m^{-1} \cdot kg^{-1}$ )	5.8 $km \cdot h^{-1}$	5.90	5.12	6.58	5.81

*Ad libitum* re-feeding for four days reversed the starvation-induced reduction in metabolic rate during running to about 96% of post-absorptive values in January, and 89% in July, while HR increased to 92% of post-absorptive values (Table 1b).

## Discussion

Compared to the general formula for the metabolic cost of running in mammals (Taylor et al. 1982), the measured values in the Arctic Fox in January were as much as 20% lower, indicating that the Arctic Fox is an energetically efficient runner. Both the metabolic rate during running (Figure 1) and the net cost of running (Table 2) were lower in January compared to July. A seasonal trend in post-absorptive BMR in Arctic Foxes, with 11-15% lower values in winter than in summer, is suggested to be a physiological adaptation important for energy conservation during winter (Fugeli and Øritsland 1999b). Thus, the present study supports the indication of a physiological adaptation

aiding energy conservation during winter in Arctic Foxes. This may be important for food searching and therefore survival.

The metabolic cost of running in the herbivorous Svalbard Reindeer (*Rangifer tarandus platyrhynchus*) is reported to fit the values predicted by the equation of Taylor et al. (1982) within 3% (Nilssen et al. 1984). Another inhabitant of the Arctic, the carnivorous Polar Bear (*Ursus maritimus*), is in contrast to the Arctic Fox considered to be an inefficient runner (Hurst et al. 1982; Øritsland et al. 1976). The Arctic Fox and the Polar Bear have some similar behavior patterns; i.e. both species wander great distances in search for food during seasonal migrations. Humans excepted, they lack natural enemies, and Polar Bears break the snow cover over subnivean birth lairs of Ringed Seals (*Phoca hispida*) when hunting for pups (Lydersen and Gjertz 1986; Smith 1980). However, the Arctic Fox is much smaller, has an unfavorable higher surface-volume ratio, and is adapted to terrestrial life. Thus, its star-

vation survival capacity during rest is relatively poor, and the energetically efficient locomotion indicated by the present work may be important for still keeping active searching for food.

There was a clear linear relationship between HR and metabolic rate during increasing running speed (Figure 3). To develop a representative equation for the relationship between HR and metabolic rate that can be used to estimate metabolic rate in free-living Arctic Foxes, further studies must be conducted on several individuals running over a wider range of speeds.

The starvation-induced decrement of BMR previously found in Arctic Foxes (Fuglei and Øritsland 1999b; Prestrud 1982) appears to be maintained during running in that metabolic rates during running were 10-11% lower than those during the post-absorptive states in January and July (Table 1a). Furthermore, the net cost of running decreased during starvation (Table 2). Also HR was reduced by up to 27% (Table 1a), indicating an energetically increased efficiency in the starved Arctic Fox when running. This increased efficiency when running during starvation is consistent with earlier studies on humans (Keys et al. 1950), and in Emperor Penguins below a specific body weight (Dewasmes et al. 1980). It is interesting to note that the net cost of running decreased with increasing running speed (Table 2). In general, the cost of moving 1 kg a distance of 1 m is independent of speed (Fancy and White 1985). However, the relationship between increasing metabolic rate and running speed has been described as a series of curvilinear relationships (Fancy and White 1985). This means that the total cost per m declines curvilinearly with increasing speed until a minimal asymptotic cost per m is achieved (Fancy and White 1985; Taylor et al. 1970). Regarding the present study, the differences between the running speeds were low and may be within the curvilinearity mentioned above, and had not yet reached the minimal asymptotic cost at that gait.

The reversion of metabolic rate and heart rate during re-feeding (Table 1b) demonstrates that the starvation-induced decrease of the variables was not a training effect, and thus validates the present results.

Conclusions: Both post-absorptive metabolic rate during running and the net cost of running were lower in winter compared to summer, which implies that the Arctic Fox may be an energetically efficient runner during the season when food is least available. HR can be used as an indicator of metabolic rate in the Arctic Fox. Starvation for 11 days reduced metabolic rate during running and the net cost of running, suggesting that the Arctic Fox appears to run in a more energetically efficient manner when starved. This may be important for survival when the food is limited. The present results are from one fox, and must be considered as preliminary data until further studies are conducted.

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