Adaptations by the Arctic Fox *(Alopex lagopus)* to the Polar Winter

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ABSTRACT. In this article physiological, behavioural and morphological adaptations by the arctic fox to low temperatures and food scarcity in winter are discussed. The arctic fox *(Alopex lagopus)* adapts to the low polar winter temperatures as a result of the excellent insulative properties of its fur. Among mammals, the arctic fox has the best insulative fur of all. The lower critical temperature is below −40°C, and consequently increased metabolic rate to maintain homeothermy is not needed under natural temperature conditions.

Short muzzle, ears and legs, a short, rounded body and probably a counter-current vascular heat exchange in the legs contribute to reduce heat loss. A capillary rete in the skin of the pads prevents freezing when standing on a cold substratum. By seeking shelter in snow lairs or in dens below the snow cover and by curling up in a rounded position, exposing only the best-insulated parts of the body, the arctic fox reduces heat loss.

The arctic fox copes with seasonal fluctuations in food supply by storing fat and caching food items during summer and fall. Saving energy through decreased activity and decreased basal metabolic rate might also be an adaptation to food scarcity in winter.

Key words: arctic fox, basal metabolic rate, lower critical temperature, fat deposition, starvation

RÉSUMÉ. Dans cet article, on discute des adaptations physiologiques, comportementales et morphologiques du renard arctique aux températures basses et à la pénurie alimentaire en hiver. Le renard arctique *(Alopex lagopus)* s'adapte aux basses températures polaires hivernales grâce aux remarquables propriétés isolantes de sa fourrure. Parmi les mammifères, c'est lui qui possède la fourrure la plus isolante. La température critique inférieure se situe au-dessous de −40 °C et, dans des conditions de températures normales, le taux de métabolisme n'a donc pas besoin de s'élever pour maintenir l'homéothermie.

Un museau, des oreilles et des pattes courtes, un corps ramassé et arrondi, ainsi que probablement un échange calorique vasculaire à contre-courant dans les pattes contribuent à réduire la perte de chaleur. Un réseau capillaire dans la peau des coussins empêchent ceux-ci de geler lorsque l'animal se tient sur une surface glacée. En cherchant à s'abriter dans des tanières de neige ou des terriers sous la couverture de neige, et en se mettant en boule — position qui ne laisse exposées que les parties du corps les mieux isolées —, le renard arctique réduit sa perte de chaleur.

Le renard arctique affronte les fluctuations saisonnières de l'approvisionnement alimentaire en faisant des réserves de graisse et en mettant de la nourriture dans des caches durant l'été et l'automne. Le fait de sauver de l'énergie en réduisant l'activité et le taux de métabolisme basal peut aussi être une adaptation à la pénurie alimentaire en hiver.

Mots clés: renard arctique, taux de métabolisme basal, température critique inférieure, réserves de graisses, famine

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INTRODUCTION

The polar region supports relatively large populations of mammals and birds. The winter climate is characterized by low temperatures, snow fall, frequent strong winds and darkness during part of the winter. Despite these seemingly inhospitable conditions, polar animals live and reproduce successfully, and most of them are able to maintain their deep body temperature within the normal range of other homeotherms (Irving, 1972).

Homeothermic animals living in the polar environment require special adaptations to survive. Their main challenges are the possibility of extensive heat loss due to low temperatures and finding adequate food in an environment where food is often scarce.

Arctic foxes are mammals in which strategies of survival in the polar environment seem well developed. They are found in considerable numbers throughout the entire Arctic, inhabiting the arctic tundra of Eurasia and North America and the alpine tundra of Scandinavia. They are also present on the islands of Svalbard, Iceland and several smaller islands scattered throughout the North Atlantic and the Bering Sea. The sea ice also seems to be a suitable habitat for non-breeding foxes (Macpherson, 1969).

The arctic fox is relatively small, weighing only 3-4 kg. It has short legs, a short muzzle, small, rounded ears and a thick fur during winter (Macpherson, 1969). It is found in two genetically fixed colour phases, blue and white.

Macpherson (1969) states that arctic fox populations vitally affect the settlement and economy of the large, inhospitable areas of Canada and other northern countries. The arctic fox is the mainstay of the northern trapping industry in the Soviet Union (Bannikov, 1970). The annual harvest throughout its range is between 100 000 and 150 000 individuals.

This paper discusses adaptations of the arctic fox to the polar winter, emphasizing behavioural, morphological and physiological adaptations to low temperatures and food scarcity. Compared to other arctic animals such as reindeer *(Rangifer tarandus* ssp.), polar bear *(Ursus maritimus)* and ptarmigan *(Lagopus mutus* ssp.), relatively few reports on adaptations of the arctic fox to the polar winter are available. Therefore, adaptations of the arctic fox are discussed in light of adaptations of other species living under equivalent conditions.

GENERAL PHYSIOLOGICAL AND BEHAVIOURAL ADAPTATIONS TO LOW TEMPERATURES AND FOOD SCARCITY

The problems of surviving low temperatures and food scarcity is definitely not specific to polar animals. Many animals living in the Subarctic also experience low temperatures and shortage of food during winter. However, the extent to which these conditions are experienced is unique to polar regions. While the environment throughout the polar regions is not homogeneous, in this article "polar winter" means a severe winter characterized by long periods of temperatures below −20°C.

A terrestrial homeotherm living in this environment has to cope with potentially extensive heat loss due to a gradient

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of as much as 80-90°C between the interior of the body and the external environment, often in combination with strong winds increasing the chill factor, and to withstand long periods of food scarcity. In fact, non-migratory terrestrial homeothermic animals in the Arctic may experience negative energy balance during the winter due to starvation (Underwood, 1971; Reimers et al., 1982; Mortensen et al., 1983).

To maintain constant deep body temperature, the rate of heat loss from an animal must equal the rate of heat production. The relationship between heat production and heat loss in a homeotherm is approximated by the formula: $M = C(T_b - T_a)$, where M is the metabolic rate, C is the thermal conductance of the animal, T_b is the deep body temperature and T_a is the ambient temperature (Scholander et al., 1950a).

According to Scholander et al. (1950b), there are three ways an animal may adapt to low temperatures: by 1) increasing the heat production; 2) reducing thermal conductance; and 3) reducing the temperature gradient between the body and the environment. In general, homeothermic animals may adapt to periods of food scarcity by reducing the energy expenditure and/or by storing food/energy in advance. The energy expenditure may be reduced by (Kleiber, 1975) 1) reducing the basal metabolic rate (BMR); 2) avoiding increased heat production due to low temperatures; 3) reducing locomotor activity; and 4) avoiding energy-requiring processes such as reproduction and growth when food abundance is limited.

Neutral fat is stored in non-hydrated form and gives an animal approximately eight times as many calories per unit weight when compared to stored carbohydrate (Allen, 1976). Fat is consequently "chosen" as the energy substrate animals store to meet periods of food shortage. Recent data suggest that some animals may also have labile protein reserves. This is not yet shown in arctic animals and will not be considered here. Storage of energy/food may take place when there is a surplus of food by 1) fat storage in body tissue and 2) caching of food items.

ADAPTATIONS BY THE ARCTIC FOX

The following discussion will concentrate on the various strategies listed above except for "avoiding energy-requiring processes such as reproduction and growth when food abundance is limited," since there is little information on this issue.

Increasing Heat Production

The BMR of mammals is related to body size, according to the formula $M = 70 W^{3/4}$ (Kleiber, 1975), where W is the body weight (kg) and M is the metabolism (kcal/24 h). Elevated BMR by northern-living homeotherms during normal winter temperatures is not a common adaptation to low ambient temperatures (Scholander et al., 1950a,b). This formula also applies to the arctic fox. Scholander et al. (1950b) (winter), Casey et al. (1979) (summer), Underwood (1971) (summer and winter) and Prestrud (1982) (summer and winter) found that the BMR of the arctic fox could be predicted from Kleiber's formula during the summer as well as winter. Additionally, Segal et al. (1976) did not find any seasonal variation in the BMR of the arctic fox, but the BMR

in this study was twice that predicted from Kleiber's formula. They do not give any reasonable explanation for this deviation.

Increased activity, and thereby increased heat production as an adaptation to cold, are not found in polar homeotherms. On the contrary, polar homeotherms often reduce their activity as temperatures drop towards the T_{lc} (lower critical temperature) (Irving, 1972). This conclusion also seems to apply to the arctic fox (Underwood, pers. comm. 1989; own observations).

Reducing Thermal Conductance and Reducing the Temperature Gradient between the Body and the Environment

In the thermoneutral zone, the arctic fox either has to change the conductance of its fur or the temperature gradient between its interior and the environment to maintain a constant deep body temperature as the ambient temperature drops. This may be achieved by physiological and/or behavioural mechanisms. Scholander et al. (1950 a,b) concluded that animals living in a cold climate mainly adapt to low temperatures by regulating their thermal conductance (heat dissipation), notably by changing the insulative properties of the fur and skin. Several authors have later confirmed this conclusion with respect to the arctic fox (Irving et al., 1955; Underwood, 1971; Casey et al., 1979). Underwood (1971), in a detailed study of thermoregulation of the arctic fox, concluded that the rate of heat loss was seasonally constant due to an increase in the fur insulation and to a slight decrease in the skin temperatures during winter. This latter mechanism is probably a result of vasoconstriction of arterioles in the skin. A reduction in the blood flow will decrease the skin temperature, and thereby increase the overall insulation.

The seasonal change in fur depth was found by Underwood (1971) and Underwood and Reynolds (1980) to be nearly 200%. Considerable site specific variation exists in depth of fur both when making comparisons for a given month and seasonal comparisons for a given site. In general, the sites commonly in contact with the snow surface both when walking or lying down (foot pads, the posterior medial aspects of the lower legs and the lateral part of the trunk) show a substantial increase of fur depth in winter. The dorsal and lateral parts of the trunk exposed when lying down also have thick fur and show a substantial seasonal increase in fur depth. Those parts of the fox not in contact with the snow surface or exposed to the environment (distal portion of legs, head and ventral part of the trunk) have less fur than the previously defined areas in all seasons and show only minor seasonal changes.

From a thermoregulatory point of view, being small in a cold climate is a disadvantage. The fur depth (insulation) has to be relatively short, otherwise movement may be impeded. In addition, the body surface relative to the body volume increases as the animal size decreases, implying a relatively larger heat loss from small than from large animals. Scholander et al. (1950b) measured the insulative properties of several arctic animals. They found a direct linear relationship between the fur thickness and insulation up to the size of the arctic fox (Fig. 1). Larger animals all had about the same or slightly lower insulation in winter. The arctic fox is one of the smallest mammals living exposed to the
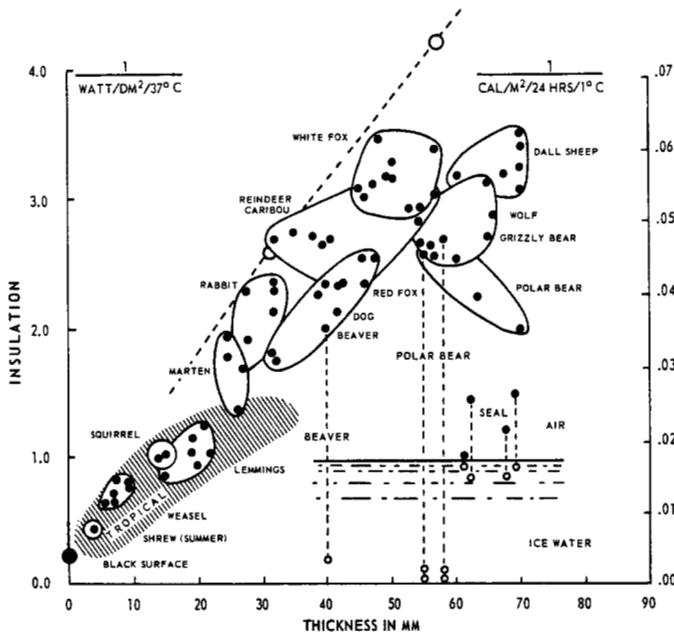
FIG. 1. Insulation in relation to winter fur thickness in a series of arctic animals. The insulation in tropical mammals is indicated by the shaded area. (From Scholander *et al.*, 1950c.)

severe High Arctic environment. Smaller mammals do not have the ability to grow an insulation sufficient to withstand the severe conditions and have to escape below the snow cover, leave the area or expend large amounts of energy for heat production.

The lower critical temperature and the rate of increase in metabolic rate below T_{lc} are indicators of insulation. Compared to tropical animals, polar animals have a low lower critical temperature and a slow rate of increase in metabolic rate below the lower critical temperature (Scholander *et al.*, 1950a,b).

The lower critical temperature of the arctic fox in winter fur has not been measured. Both Scholander *et al.* (1950a) and Underwood (1971) tried but did not succeed, because they did not have the necessary equipment available to reach sufficiently low ambient temperatures. They both state that the T_{lc} of the arctic fox is well below −40°C. Scholander and co-workers kept an arctic fox at −80°C (without measuring the metabolism) for one hour without any drop in rectal temperature. The animal was shivering and was probably below the lower critical temperature. These results suggest a very low thermal conductance. The Svalbard reindeer has a lower critical temperature, about −50°C, the lowest critical temperature measured in any homeotherm (Nilssen, 1984). It is supposed that the lower critical temperature of the arctic fox is below this temperature. In comparison, an Alaskan red fox (*Vulpes vulpes*) had a T_{lc} of −13°C and nearly doubled its metabolic rate at −50°C (Irving *et al.*, 1955). Scholander *et al.* (1950a:247) illustrate the very excellent insulative properties of arctic fox winter fur: "An arctic fox with body temperature of 40°C, and a lower critical temperature of −40°C, can merely by doubling its metabolism, go to −120°C, and it takes only a 37 per cent increase in heat production to sustain it in the coldest temperature recorded on earth, somewhere near −70°C."

To avoid freezing the pads when standing on a substratum of −30 to −40°C, there is increased blood flow to a capillary

rete in the skin of the pads (Henshaw *et al.*, 1972). There is also probably a "counter-current" mechanism in the legs to avoid heat loss when warm blood flows into the legs. Also, in contrast to other canids, the foot pads of arctic foxes are covered by fur.

The arctic fox also has the opportunity to regulate both the conductance and the temperature gradient by behavioural means. As snow is an excellent insulator, the arctic fox may avoid low air temperatures by seeking shelter in snow lairs or dens. Such behaviour enables the fox to decrease the temperature gradient considerably and to avoid wind during periods of extreme cold, thereby avoiding increased heat loss. Several polar animals live all or parts of the winter in or below the snow to escape low ambient temperatures (Remmert, 1980). It is not known to what extent the arctic fox uses the opportunity to escape low ambient temperatures and strong wind by seeking shelter in snow lairs or dens. My own observations from Svalbard indicate that the reproductive dens are in use throughout the whole winter and that the foxes dig lairs or hollows in the snow during bad weather conditions to seek shelter. Underwood (pers. comm. 1989) observed the same thing in Alaska.

When exposed to low ambient temperatures and/or wind, the arctic fox curls up like a ball, hiding its head in the tail and trunk (Fig. 2). To enter this curled posture, the fox lowers the lateral hip area onto the ground, drawing the hind legs forward and under the posterior trunk. The front legs are drawn back along the inner side of the curl formed by the ventral area of the torso. The head is laid onto the forepaws and the tail is positioned forward over the legs and muzzle, thus completing the curl (Follman, 1978). In this position, the heat loss is minimized because the "ball form" has the smallest surface-volume ratio and the exposed parts of the body have the thickest fur. The temperature gradient between the inside of this curl and the ambient temperature could be as much as 52.5°C (Follman, 1978).

The arctic fox has small ears, a short muzzle, relatively short legs and a small rounded body, which are considered morphological adaptations to cold temperatures (Macpherson, 1969).

FIG. 2. When the fox curls up in this position the areas exposed to the ambient temperatures are minimized, the best-insulated parts of the body are exposed, and consequently heat loss is minimized. When sleeping, the poorly insulated head is covered by the tail and trunk, as seen from marks in the snow covering the fox. (Photo, J. Angard.)

ADAPTATION TO FOOD SCARCITY

The arctic fox is the main terrestrial predator and scavenger throughout most of the Arctic, being an opportunistic and generalistic feeder utilizing any food source available. Ptarmigans, hares (*Lepus* sp.), lemmings (*Dicrostonyx* sp. and *Lemmus* sp.) and white pups of the ringed seal (*Phoca hispida*) are the main preys during winter. In addition, carcasses of muskoxen (*Ovibos moschatus*), reindeer, whales and seals are important food items at this time of the year. Compared to the summer, the abundance of food in winter is strongly limited. Several authors (Braestrup, 1941; Elton, 1942; Macpherson, 1969) have noted that starvation is an important cause of mortality during winter, particularly among young foxes during cyclic population declines. Underwood (1971) and Prestrud (1982) have both shown a decrease in the fat content of fox carcasses from winter to summer, supporting the conclusion that many arctic foxes experience negative energy balance during winter.

Reducing the Basal Metabolic Rate (BMR)

It is well known that several species living in cold climates reduce their BMR and deep body temperature to save energy through the winter. A wide spectrum of patterns of hypothermia ranges from daily torpor, usually with shallow cooling and minor reductions in BMR, to seasonal dormancy or hibernation, with significant reductions in deep body temperature and BMR. As noted earlier, seasonal variations in the BMR of the arctic fox have not been shown (Underwood, 1971; Casey et al., 1979; Prestrud, 1982). This also applies to the deep body temperature (Underwood, 1971).

Reductions in food intake, metabolic rate and body weight in winter are common among several northern-living cervid species (Silver et al., 1969; McEwan and Whitehead, 1970; Ryg and Jacobsen, 1982). A metabolic depression among these species in winter could be an adaptation to food shortage. Nilssen (1984) showed that the winter metabolic depression in the Svalbard reindeer (*R. t. plathyruncus*) was a result of decreased food intake. The component of the metabolic rate due to the digestion of food (SDA=specific dynamic action) is reduced when food intake is decreased. When Nilssen (1984:74) measured BMR in food-deprived animals there were no differences between summer and winter. His conclusion was: ". . . the apparent changes in resting metabolic rate do not reflect changes in basal metabolic rate, but rather changes in food intake, and can therefore not be defined as a physiological adaptation aimed at energy conservation during winter."

Underwood (1971) measured the food intake of captive arctic foxes, finding that the amount of food consumed averaged 275% higher in the summer than in the winter when the animals were fed *ad lib.* (220-240 kcal/kg body weight in summer and 70-80 kcal/kg body weight in winter). This observation was partly confirmed by Prestrud (1982), who remarked that the food intake was irregular during the winter, when periods of 10-14 days without food intake was common despite *ad lib.* feeding on natural prey. If these observations are correct, one should also have expected a winter decrease in basal metabolism due to the lack of SDA and a decrease in weight in the arctic fox as found in the northern cervids. This, however, has not been found.

The reason might be that the methods used to measure seasonal variation in metabolic rate of arctic foxes are not well suited to register a possible winter metabolic depression. Both Underwood (1971) and Scholander et al. (1950b) measured the metabolic rate during a short period in winter, as thermoregulatory response was the purpose of their studies. If the metabolic rate is reduced at irregular intervals during winter due to a variable intake of food or other causes, measurements would have to be conducted several times during the whole season in order to document a possible depression.

Underwood (1971) did not register the food intake before measuring the metabolic rate. His experimental foxes could therefore well have been experiencing the same specific dynamic action during the measurements. In that case a possible winter metabolic depression caused by low and irregular food intake would not have been recorded.

Prestrud (1982) measured the BMR in two foxes kept in Ny Ålesund, Svalbard (79°N), once each month during winter. The BMR ranged from 35 kcal/kg$^{3/4}$/24 h to 100-110 kcal/kg$^{3/4}$/24 h in the period November-February. The average BMR during winter was not different from the summer, but the standard deviation was predominantly larger during winter than during summer. The relatively high BMR of 100-110 kcal/kg$^{3/4}$/24 h is difficult to explain physiologically, as the foxes were resting within the thermoneutral zone during measurements.

Underwood (1971) could not demonstrate any seasonal variations in weight in his arctic foxes. He therefore concluded that the high food intake during summer was a result of increased energy expenditure due to a high level of locomotor activity compared to the winter and increased heat production necessary for thermoregulation as foxes in summer fur more often experience temperatures outside the thermoneutral zone than foxes in winter fur. Information on locomotor activity and ambient temperature was not given. A threefold increase in energy expenditure from summer to winter, as shown by Underwood (1971), implies a considerable increase in the level of locomotor activity. Furthermore, the temperature during the summer when Underwood (1971) conducted his studies (at Point Barrow, Alaska) should have been far below the summer average if the energy expenditure of the foxes increased due to thermoregulation. Riewe (1971) found that four arctic foxes maintained a stable body weight in the period October-November on a daily food intake of 125 kcal/kg body weight/day, which is not in accordance with Underwood's (1971) results. In conclusion, the observations by Underwood (1971) of a low food intake in winter and no seasonal variations in metabolic rate or body weight may have another explanation than that given by Underwood (1971)

Captive foxes fed *ad lib.* may not behave naturally. As noted, prolonged periods of starvation are most probably normal for the arctic fox in winter, particularly during heavy storms lasting for several days. This, together with complete darkness during most of the day in winter, makes the accessibility of food limited. Reduced BMR is common among mammals when they are starving (Keys et al., 1950; Kleiber, 1975; Harlow, 1981a). Prestrud (1982) measured the metabolism during forced and voluntary starvation in two foxes (Fig. 3) and found a reduction in BMR of as much as 40-50%. This is a remarkably large reduction compared to other species, which have shown a decrease of 20-30% in BMR during starvation (Harlow, 1981a; Keys et al., 1950). The results must be regarded as an indication of an unusual decrease in BMR of starving arctic foxes.
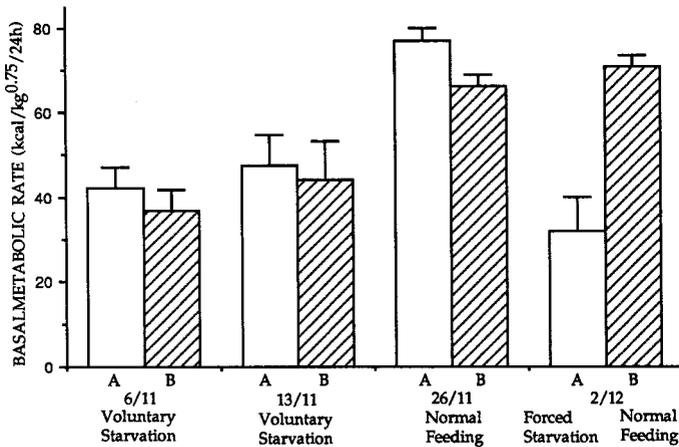
FIG. 3. Basal metabolic rate during voluntary starvation and during forced starvation in two arctic foxes (A and B) on 4 different days in November and December. (One bar represents the mean of three measurements in one fox taken the same day. The variation is given as S.E.). Fox A and B had a strongly reduced food intake for 4-5 days before 6 November. This reduced food intake continued until new measurements were taken on 13 November. The food intake was reduced despite *ad lib.* feeding. Fox A was starved for 6 days by removing all the food from the cage before the measurements on 2 December. The metabolic rate was measured in an open respiratory system (Prestrud, 1982).

In conclusion, the winter measurements of metabolic rates of arctic foxes (Scholander *et al.*, 1950b; Underwood, 1971; Prestrud, 1982) were conducted in such a way that one cannot disregard the possibility that the arctic fox periodically depresses the BMR for energy conservation under natural conditions. The observed low food intake during winter and low metabolic rate during starvation indicate that the arctic fox could have the same mechanism as the northern-living cervids with regard to a low food intake despite *ad lib.* feeding. This point should be a good topic for further studies.

Avoiding Increased Heat Production Due to Low Temperatures

It is evident from the above discussion that the insulative properties of arctic fox fur are sufficient to avoid increases in heat production and to maintain a constant deep body temperature. The arctic fox only occasionally experiences increased energy consumption in winter caused by the harsh climate.

Reducing Locomotor Activity

Seasonal variations in the locomotor activity of the arctic fox have not yet been studied. As already noted, Underwood (1971) has stated that foxes have a higher activity level during summer than winter, but he did not present data on this. Presumably the locomotor activity during winter is reduced to save energy in periods when food is not available.

Fat Storage

A number of polar animals use fat storage for energy conservation to meet periods of food shortage in winter (Reimers *et al.*, 1982; Mortensen *et al.*, 1983). Fat is the overall energy substrate during seasonal torpor and hibernation. Large fat stores have been found before onset of dormancy in these species (Pond, 1978).

The arctic fox also has a substantial seasonal variation in fat storage. Prestrud (1982) found the fat content of whole carcasses of foxes in Svalbard to be 22% (0.82 g fat/g fat-free dry weight) in November-December and 7% (0.32 g fat/g fat-free dry weight) in May-June (Fig. 4). The difference was significant ($p < 0.05$). Underwood (1971) used a subjective relative fat index (5 categories, where category 5 denoted extensive and category 1 denoted no fat deposits) to describe the amount of body and visceral fat observed on carcasses caught by local trappers in March and December. The fat index decreased from an average of 3.6 in December to 2.8 in March. However, Hammill (1983), using several fat indices on a large trapped arctic fox, found a slight increase in fat deposition between November and March.

The relative fat content of arctic foxes living in Svalbard in late autumn is similar to that found in the Svalbard reindeer (Reimers *et al.*, 1982) and the Svalbard ptarmigan (Mortensen *et al.*, 1983). The fat deposits are less than those of hibernating species (30-50%) (Mutch and Aleksiuk, 1976; Galster and Morrison, 1976; Harlow, 1981b).

The fat content of arctic fox carcasses in winter ranged from 3 to 38% (Prestrud, 1982). Of the 38 carcasses examined in the period November-February, 13 had a fat content less than 10% and 5 had a fat content higher than 30%. The fat content of an extremely fat fox caught in 1986 (Fig. 5) was estimated to be more than 50% by measuring the subcutaneous fat thickness and relating the measurement to a regression between subcutaneous fat thickness and total fat content in arctic fox carcasses developed by Prestrud (1982). Thus the fat content of arctic foxes in winter showed considerable variation, indicating a highly variable food supply either because the single individual's capacity of finding food is variable or because the food is highly dispersed spatially or both.

The adaptive significance of storing fat was examined by Prestrud (1982). A resting arctic fox having an average weight of 3.5 kg and an average fat content of 22% will survive on a basal metabolic level of 70 kcal/kg$^{3/4}$/24 h for about 30 days. It is therefore evident that the fat stores are important
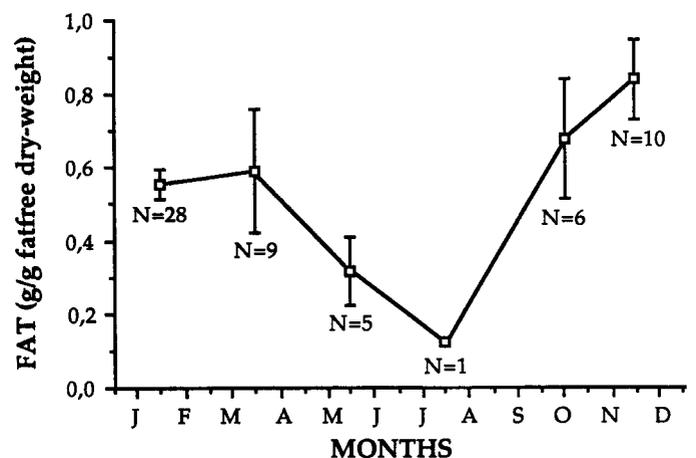
FIG. 4. Seasonal variation in fat content. Each point is the mean fat content in foxes caught in a two-month period, except for the mean in October, which is based on foxes caught only in that month. The sample is composed of 25 juvenile and 34 adult foxes, of which 25 are females and 34 are males. Juvenile foxes from June to September are not included in the sample. (N is the number of carcasses examined, and the variation is given as S.E.)

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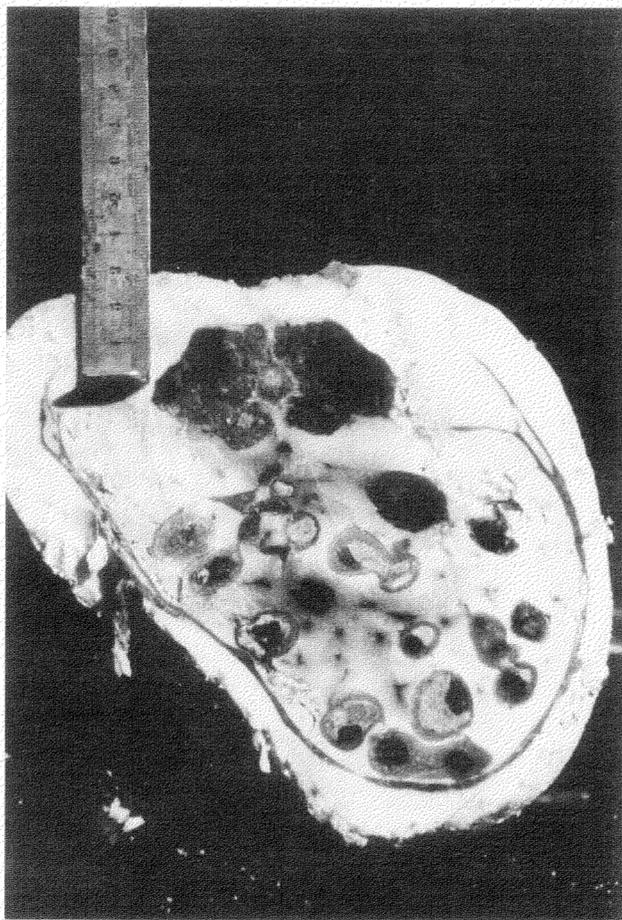
FIG. 5. Cross-section of an extremely fat fox carcass. The carcass is cut just in front of the hip. The spine is seen in the upper middle part of the photo. The diameter is about 15 cm and the intestine is seen imbedded in fat. The subcutaneous fat is about 3-4 cm thick. The carcass has been squeezed during freezing.

but not sufficient to last a whole winter. In comparison, the Svalbard reindeer can survive 54 days and the Svalbard ptarmigan about 18 days without food on a normal BMR, having about the same relative fat content as the arctic fox. These figures clearly show the advantage of being large for an arctic animal covering parts of the energy expenditure in winter on fat. The high weight-specific BMR of the arctic fox relative to larger arctic species such as the reindeer and polar bear is a drawback for survival in the arctic environment.

The late winter and spring depletion in fat content of the arctic fox (Fig. 4), which is also in compliance with Hammill's (1983) results, may be related to the reproductive season (March-July). A strong link between the reproductive and metabolic cycles is common in many mammals (e.g., Ryg et al., 1990). A certain amount of body fat as an energy reserve is probably a necessity for successful reproduction in the arctic fox. In winters when the conditions are especially severe, the fat content at the onset of the reproductive season might be too low for successful reproduction.

Subcutaneous fat is also commonly used as insulation in mammals, and Schultz and Ferguson (1974) found that subcutaneous fat in arctic foxes had a high degree of unsaturated fat acids, indicating that this fat also has an important function as insulation.

Caching Food Items

Everyone who has been in contact with arctic foxes for a long period of time will notice its remarkable ability to hide food in excess, either by digging it into the earth or by pulling it under a stone or into a scree/den. Several authors have reported on caches, some containing more than 100 seabirds (Murie, 1959). Both Stephenson (1970) and Burgess (1984) provided evidence that caching is important to meet periods of limited food abundance.

Gabrielsen (pers. comm. 1990) has analyzed the body composition of seabirds commonly found in the fox caches in Svalbard. He found the protein content and fat content of adult little auks (*Alle alle*) to be 27-28% and 6-12% of the body weight respectively and of adult Brunnich's guillemots (*Uria lomvia*) to be 20-22% and 6-20% of the body weight respectively. Litvaitis and Mautz (1976) estimated the assimilation efficiency of food items eaten by red foxes (*Vulpes vulpes*) to be above 75%. This is in accordance with results found by Karl Frafjord (pers. comm. 1990) for arctic foxes.

Given these figures, a cache of 10 adult little auks and 4 adult Brunnich's guillemots represents an energy storage comparable to the mean fat content of an arctic fox in late autumn weighing 3.5 kg. These calculations and the above-mentioned observations indicate that the adaptive significance of food caching by the arctic fox is high.

CONCLUSIONS AND HYPOTHESIS

The continuum of decreasing metabolic rate and body temperature from slow-wave sleep and daily torpor to seasonal torpor or hibernation seems to represent homologous processes as means of conserving energy reserves in several mammals and birds experiencing periods of low temperatures and food scarcity (Walker and Berger, 1980). In general, the arctic fox has some features in common with many of these animals; the food abundance is periodically greatly limited and there is a substantial storage of fat or caching in the autumn. Measurements indicate an unusually large reduction in the BMR of starving foxes, and the food intake seems to be voluntarily reduced periodically. Based on these facts, the following hypothesis regarding survival strategies of free-living arctic foxes in winter is suggested.

The fat stores are utilized during periods of limited food abundance. The fox "realizes" at an early stage of food shortage that further food searching is unprofitable. It seeks shelter in snow lairs or dens, thereby escaping low temperatures and strong wind. During such periods of starvation, the BMR is reduced considerably to save energy. Due to the excellent insulative properties of the fur and the relatively high ambient temperature in a lair or den in the snow, hypothermia may be avoided despite reductions in BMR. The advantage of avoiding hypothermia is that the fox may remain in a relatively alert state, being able to defend itself against predators and to react immediately and start food searching when the food availability becomes better. Unnecessary energy expenditure to maintain body temperature is avoided during normal winter conditions due to the excellent insulative properties of the fur. Carcasses of reindeer, seal and muskoxen and prey such as ptarmigan, lemmings and ringed seal pups are the main food items during winter, in addition to caches of food. The fat deposits may be replaced rapidly when the fox finds a rich food source — for instance, carcasses of large animals.

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