and a dual-element detector (both commercially available), or with a scanner that can accommodate two infrared-detector packages, can use this method for the discrimination of relative rock types in the two-channel mode. It is possible that the ratioing now done by an analog computer could be simulated by the simple overlaying of positive and negative transparency images; however, the compositional information in regions of lower temperature (shadows, primarily) may be lost or diminished with such a procedure.

ROBERT K. VINCENT
FREDERICK J. THOMSON
Institute of Science and Technology, University of Michigan, Ann Arbor

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Peripheral Thermoregulation: Foot Temperature in Two Arctic Canines

Abstract. *Arctic foxes and gray wolves maintain their foot temperature just above the tissue freezing point (about −1°C) when standing on extremely cold snow, or when the foot is immersed in a −35°C bath in the laboratory. Proportional thermoregulation stabilized the subcutaneous temperature of the foot pad to a precision of ± 0.7°C (largest deviations). Selective shunting of blood-borne body heat through a cutaneous vascular plexus in the foot pad accounted for more than 99 percent of measured heat loss from the pad surface. Maximum energetic efficiency is achieved because the unit of heat exchange is located in the pad surface which contacts the cold substrate rather than throughout the pad.*

Terrestrial mammals survive in the arctic because of morphological and physiological adaptations to cold (*1*). Thick, closely spaced fur, for example, protects the trunk from excessive heat loss, although the legs which are relatively more exposed due to thin fur and high surface area to mass ratio may be predominantly protected by physiological mechanisms (*2*).

Previously attention had focused on countercurrent heat exchange in the legs wherein heat of the descending arterial blood is cooled as it warms returning venous blood. Heat flow to the feet is minimized, resulting in low foot temperature and lower heat loss to cold surfaces (*3*). How the foot temperature is maintained near 0°C even when animals are standing on substrates 50°C or more colder has not been accounted for. This study demonstrates that in the arctic fox and gray wolf the mechanism of this important physiological adaptation is increased blood flow to the foot pad surface during exposure to cold.

A colony of adult arctic foxes (*Alopex lagopus*) and gray wolves (*Canis lupus*) at the Naval Arctic Research Laboratory, Barrow, Alaska, was maintained year around in welded steel enclosures exposed to prevailing weather, typically 5°C in summer and −30°C in winter. During experiments the animals were lightly anesthetized with α-chloralose (50 mg/kg, intraperitoneal) which rendered them unconscious but capable of myoclonic responses to loud sounds. Vascular and thermoregulatory autonomic reflexes appeared to be intact, and normothermia was maintained (*4*). A net hammock suspended the animals in the laboratory in a normal standing posture. One hind foot was submerged to the ankle in a well-stirred mixture of ethanol, ethylene glycol, and water (1 : 1 : 1) cooled to −38°C with Dry Ice while temperatures of the foot were recorded continuously during immersion for up to 7½ hours.

A disk surface thermistor (*5*) taped under a hemisphere of polystyrene foam (10 mm in diameter) measured skin surface temperature. Because of incomplete insulation from the cold bath, temperature occasionally registered several degrees too low in this thermistor, but the instrument accurately followed shifts in skin temperature with a resolution of 0.05°C. Three 0.25-mm-diameter thermistor beads (*6*), embedded in a Teflon capillary tube (1.2 mm outside diameter) and inserted into the center of the foot through a 15-gauge needle from the ventral pad surface, sensed temperatures about 2 mm, 8 mm, and 12 mm inside the pad skin surface. Rectal, contralateral foot pad surface, bath, and room air temperatures were simultaneously monitored with an accuracy of ± 0.1°C. Rate of heat flux from the foot pad to the bath was measured with a heat flow transducer (*7*) taped against the pad. Thirty-nine experiments were conducted on 3 adult foxes and on 21 wolves varying in age from 3 weeks to 7 years.

In both species immersion of the foot in the cold bath caused an immediate drop in foot temperature (Fig. 1), albeit not to, or below, the tissue freezing point (*8*). One of two response patterns ensued: (i) either the pad surface temperature plateaued at a mean 12.8° ± 1.4°C ($\bar{X}$ ± standard error) for a period of about 45 minutes and then dropped to 1.5° ± 0.9°C for an indefinite period; or (ii) the pad temperature initially fell to 3.9° ± 0.9°C and then remained constant throughout the immersion. In 1-year-old wolves the first response with its apparent poor economy of heat was most common (Fig. 2), while wolves older than 3 years exhibited the second response exclusively. In all three of the adult arctic foxes studied, food pad temperature followed the second pattern but with much less temperature variability (Fig. 3). In the experiment illustrated the subcutaneous temperature of the pad after 10 minutes varied no more than ± 0.7°C.

In neither species was there any apparent cyclic rewarming ("hunting reaction"). Likewise, in no case did blood circulation to the immersed foot pad shut down ("cold pressor response") and permit freezing. The contralateral hind foot pad displayed a temperature pattern similar to the immersed foot but with an amplitude of about 5°C, while the front foot exhibited temperature dynamics independent of the immersed hind foot. Application of a tourniquet at mid-thigh caused an immediate rapid drop in pad temperature of the immersed foot. Pad temperature rose even more rapidly when the tourniquet was released.

When the surface temperature of the pad was about 15°C or higher, rate of heat loss to the bath was 1.8 ± 0.5 kw m^{-2} which was ten times the heat flux rate to room air of 18°C. This high rate of heat loss caused rectal temperature to decline an average 1.4° ± 0.2°C even though the rest of the animal was exposed to room air (Figs. 1 and 2). However, when the foot pad temperature abruptly fell to the low plateau near 2°C, heat flux dropped to 1.2 ± 0.1 kw m^{-2}, and rectal temperature slowly rose again. Although foot temperature patterns differed slightly among animals, it was clear in at least eight wolves and one arctic fox that the foot pad surface was thermally independent of central temperature (for instance as in Fig. 3). Because body core temperature fell throughout these experiments, temperature of the blood entering the leg and in the deep metatarsal arteries at the center of the foot also dropped. Despite this varying heat content of the

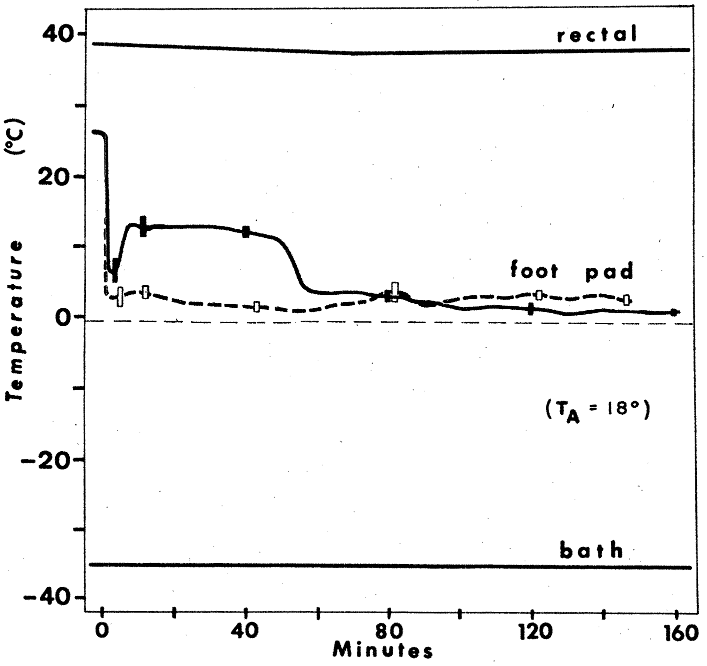

Fig. 1 (top left). Effect of cold bath (— 35°C) on mean foot pad surface temperature in 21 arctic gray wolves. Two patterns of temperature dynamics were averaged separately. Higher temperature response (solid line) produced by young wolves; flat, low response (dashed line) produced by adult wolves and by arctic foxes. The rectal temperature (top curve) is associated with higher temperature response; little or no change occurred during low flat response. Boxes indicate ± 1 standard error; for rectal temperature, the standard error was ± 0.2°C.

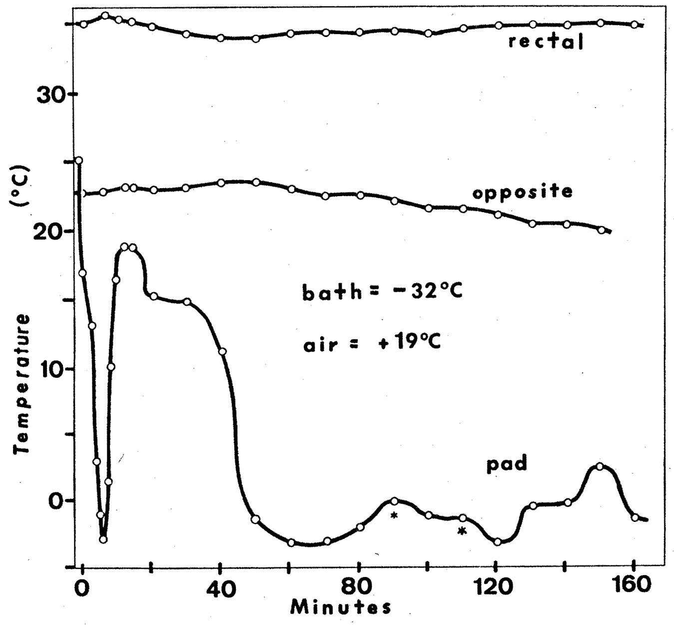

Fig. 2 (bottom left). Temperature changes when one hind foot of a 1-year-old wolf was immersed to the ankle in a —32°C bath. Initial period of vasodilatation with heat dissipation to bath caused rectal temperature to decline 1.4°C. Subsequent sustained regulated partial vasoconstriction offered relative insulation value indicated by a rising rectal temperature. Asterisks indicate movement when toes were being checked for freezing.

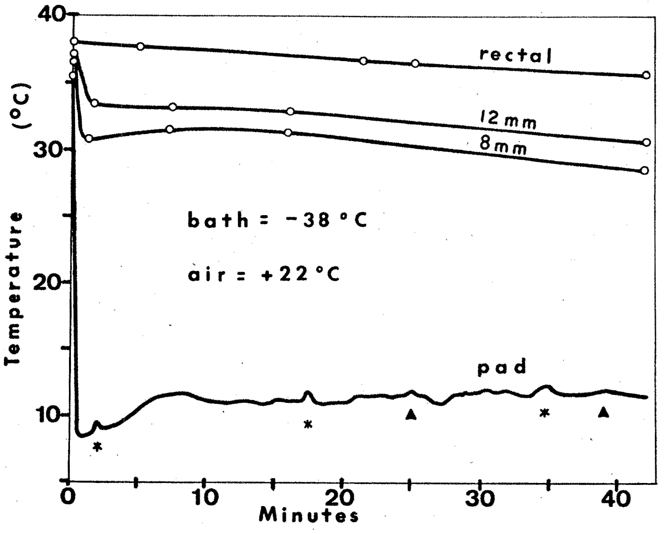

Fig. 3 (bottom right). Temperature changes when one hind foot of an adult arctic fox was immersed to the ankle in a —38°C bath. Temperatures were recorded just under pad surface and at two depths inside foot. Note constant pad surface temperature which was independent of a declining rectal temperature. Asterisks are as in Fig. 2.

blood, foot pad temperature was maintained constant. The subcutaneous thermistor (Fig. 3) registered 11.4° ± 0.7°C ($\bar{X}$ ± range).

Natural selection apparently produced in animals inhabiting cold regions the ability to regulate foot surface temperature at approximately 0°C. Irving and others (*9*) have found all species of arctic birds and mammals examined had a foot skin temperature near 0°C and full sensory and motor control without pain while standing on a cold substrate. Unacclimatized temperature zone and arctic species, however, seem unable to tolerate cold feet. For example, domestic dogs maintained indoors appear to find standing on ice painful. In one case, after a few weeks of acclimation to −40°C, they were able to walk without difficulty or pain when the foot temperature was near 0°C (*10*). In contrast, man and some tropical species may register pain and impairment of sensory and motor function if the hand temperature drops much below 15°C (*11*).

The ability of these cold-acclimatized wolves and arctic foxes to maintain their feet in excess of 35°C above the bath temperature must be accounted for in increased blood-borne heat input to the foot pads. Estimated tissue metabolism in the feet would account for less than 1 percent of the measured heat loss. Interruption of blood flow to the feet demonstrated that blood-borne heat must augment tissue metabolism to maintain foot temperature.

Vasoconstriction (cold pressor reflex) found in tropical and unacclimated temperate zone species in the cold conveys no adaptive advantage in continuously very cold regions; rather it acts as a positive feedback mechanism by permitting cooling and further reducing ability to prevent frostbite. Some animals inhabiting tropical and temperate regions, man included, exhibit phasic rewarming of cooled appendages by pulsatile increases in blood flow (*12*). These temperature cycles, with amplitude of only a few degrees and periodicity of several minutes, serve only to retard, not prevent, freezing of tissues in extreme cold. Pulsatile heat input ("on/off regulation") of sufficient amplitude, however, could prevent freezing but would be imprecise. It would be likely to provide less selective advantage under the stringent environmental demands faced by arctic species than would heat input matched continuously to heat output ("proportional regulation"). These arctic canines exhibited no phasic rewarming in their foot pads, but rather a continuous proportional control requiring vasodilation great enough to overcome a tenfold increase in heat loss upon immersion while the pad temperature was near 12°C and a sixfold increase while at 2°C.

The lack of correlation between temperature dynamics in the foot pad surface and the deep plantar metatarsal arteries at the center of the foot indicates that separate mechanisms control circulation to these regions. The deep arteries, on the other hand, are not independent of central arterial regulation since they reflect the trunk temperature dynamics. We found a presumptive morphological basis for proposing thermal independence in the foot pad surface in a separate series of experiments. In plastic castings of the blood vessels in the wolf front foot (*13*) we found that four unbranched arteries carry blood directly through the pad to a cutaneous plexus in the pad surface. No major vessels supply the core of the pads. The thermoregulatory surface, then, appears to be specialized for maximum efficiency by virtue of its location in the tissues that come in contact with the cold substrate. Since freezing would begin in these tissues only these tissues need be selectively perfused. Foot pad surface temperature is regulated by differential pumping of blood-borne heat even at added energy cost to the animal. Such selective perfusion of these small areas minimizes the additional cost, however. The same mechanism probably shunts excessive heat generated during exercise to the snow surface.

Countercurrent heat exchange does occur in the legs of terrestrial species, but without concomitant specialization of such other mechanisms as regulated vasodilation in the foot pad; countercurrent heat exchange must be considered maladaptive in arctic animals exposed to extreme cold. When an animal is exposed to an ambient temperature well below tissue-freezing temperature, countercurrent exclusion of heat from the appendages is tantamount to sacrificing the distal portion to freezing injury. No freezing of tissues has been reported in animals living in the arctic. A dynamic balance must be struck between heat loss to the environment and heat input from the body core. Regulation of heat balance in the foot pads of arctic-adapted terrestrial species therefore would be of prime adaptive significance.

ROBERT E. HENSHAW
LARRY S. UNDERWOOD
TIMOTHY M. CASEY

Department of Biology,
Pennsylvania State University,
University Park 16802

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