

Journal of APPLIED PHYSIOLOGY

VOLUME 6

May 1954

NUMBER 11

Body Temperatures of Arctic and Subarctic Birds and Mammals

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IN TEMPERATE REGIONS the activity of men and animals is curtailed to avoid exposure to the annoyance and suffering caused by cold weather. In most climates a considerable amount of human effort is expended to obtain protection from cold, and for wild and domestic animals the search for warmth is a vital concern. With this experience in mind it seems strange to observe that warm-blooded animals live in the arctic climate with only their natural faculties for preserving the essential heat of their bodies.

In arctic Alaska there are about 30 species of land mammals, most of which are circumpolar in distribution (1). On the Tundra areas of arctic interior Alaska, 12 species of birds are regularly present in winter. Among them Gyrfalcons, Snowy Owls, Ravens, Willow and Rock Ptarmigan represent species which are widely distributed through the arctic part of the world (2). In North America, Europe and Asia several species of birds as well as some mammals are residents of the boreal forests and also range northward over the arctic tundra. In boreal forests there are many other species which do not extend over the tundra. Their northern range is not restricted by low temperature alone, for the coldest recorded weather is reported from continental subarctic Siberia (-68°C) and northwestern interior Canada (-65°C) (3, 4). The arctic region near sea level does not have such extreme cold as is frequent in continental subarctic lands.

A polar bear has been reported at 87°C on the Arctic Sea (5). Drifting between Wrangell Island and the New Siberian Islands the 'Maud' saw polar bears and seals, but they were uncommon far from land (6). In his travels over the ice of Beaufort Sea, Stefansson (7) found seals and bears enough to support his party. Many thousand Eskimo and arctic Siberian people have lived on arctic coasts by hunting the warm-blooded animals which alone are accessible to them in winter. Part of the prey of aboriginal arctic hunters consisted of land animals and their hunting parties went far inland from the coasts. In many places in interior arctic Alaska artefacts have been discovered which show that men lived there who used hunting implements attributable to the most ancient types of human culture (8, 9). It is apparent that man

and other warm-blooded animals have been inhabitants of arctic coasts and lands in widely distributed places and for long periods of time.

It has been assumed that these arctic inhabitants have the warm temperature appropriate to birds and mammals, but reported measurements are rare. From Parry's voyages between 1819 and 1825 (10), body temperatures of foxes, a wolf, polar bears and ptarmigan were reported which are about normal for animals of temperate regions. In the report of Back's expedition northward over the Barren Ground of Canada (11) the surgeon-naturalist, Mr. King, reported body temperatures in several birds and mammals which were similar to those in temperate regions. In arctic temperatures of -45°C , Alaskan reindeer and dogs have body temperatures normal for mammals (12).

It is of interest that the few records of animal temperatures in arctic cold weather were extracted from the narrative accounts of the explorations and published separately in France (13-15), where physicists and biologists were then joined in their sequence of historic researches aimed to settle by observation that heat exchange in animals could be described in the terms of physics.

Records of the temperature of arctic animals in their natural environment are so few that during the last three years we have taken advantage of every opportunity for measurement of body temperatures in wild and captive arctic and subarctic birds and mammals in Alaska. Because we could examine a good representation of the small number of species resident there in winter the evidence is now sufficiently complete to warrant generalization upon the temperature of all but the mammals as small as mice and shrews. The mammals and birds examined are listed in table 1.

METHODS OF TEMPERATURE MEASUREMENT

The instruments used for temperature measurement were *a*) mercury thermometers of glass, which were, however, too large in mass for birds weighing only 10 gm, but suitable for those of 30 gm; *b*) dial thermometers requiring at least 5 cm immersion for measurement and consequently unsuitable for small animals; *c*) Leeds and Northrup potentiometer indicators of the type requiring no reference junction. The iron-constantan thermocouples were prepared in a variety of sizes suitable for any animal.

Mercury thermometers were calibrated in the laboratory to within 0.1° . Before use all thermometers were compared with a standard in snow, water or air and used only if agreeing within 0.2° . In the extreme cold and strong winds where many measurements were made and in dim arctic daylight the accuracy of reading was less, but frequent repetitions and series of measurements showed agreement within $\pm 0.2^{\circ}$. Examination of discordant measurements usually revealed technical errors which could be corrected.

TEMPERATURE MEASUREMENT OF ANIMALS KILLED IN THEIR NATURAL STATE

Animals were stalked or ambushed until within certain range and shot. Most trials resulted in immediate death of the animals, which had been standing or moving in leisurely fashion. None were taken after prolonged running or flight. A few which were not killed instantly were despatched promptly by a second shot, and a few were killed during short runs or flights.

Temperature measurements were made by thermometers or thermocouples inserted through the rectum, or in the case of small birds, through the mouth. Occa-

TABLE I

A. Mammals

<i>Ursus arctos middendorffi</i>	<i>Eumetopias jubata</i>	<i>Ondatra zibethica zalophus</i>
Kodiak brown bear	Steller's sea lion	Muskrat
<i>Ursus americanus</i>	<i>Erignathus barbatus</i>	<i>Erethizon dorsatum myops</i>
Black bear	Bearded seal	Porcupine
<i>Thalarcos maritimus</i>	<i>Lepus americanus dalli</i>	<i>Ochotona collaris</i>
Polar bear	Snowshoe hare	Pika
<i>Vulpes vulpes alascensis</i>	<i>Lepus timidus othus</i>	<i>Ovibos moschatus</i>
Alaska red fox	Arctic hare	Muskox
<i>Alopex lagopus</i>	<i>Marmota marmota caligata</i>	<i>Oreammus americanus</i>
Arctic white fox	Hoary marmot	Mountain goat
<i>Canis lupus</i>	<i>Citellus undulatus barrowensis</i>	<i>Rangifer tarandus stonei</i>
Wolf	Parry's ground squirrel	Stone caribou
<i>Canis familiaris</i>	<i>Tamasciurus hudsonicus preblei</i>	<i>Rangifer tarandus</i>
Eskimo dog	Alaskan red squirrel	Reindeer
<i>Enhydra lutris</i>		
Sea otter		

B. Birds

<i>Gavia arctica pacifica</i>	<i>Lagopus mutus nelsoni</i>	<i>Picoides arcticus</i>
Pacific loon	Nelson's rock ptarmigan	Arctic three-toed wood-pecker
<i>Phalacrocorax pelagicus resplendens</i>	<i>Lagopus leucurus leucurus</i>	<i>Picoides tridactylus fasciatus</i>
Baird's cormorant	White-tailed ptarmigan	Alaska three-toed wood-pecker
<i>Branta bernicla nigricans</i>	<i>Larus hyperboreus barrovianus</i>	<i>Perisoreus canadensis pacificus</i>
Black brant	Glaucous gull	Alaska jay
<i>Mareca americana</i>	<i>Larus glaucescens</i>	<i>Pica pica hudsonia</i>
Baldpate	Glaucous-winged gull	American magpie
<i>Anas crecca nimia</i>	<i>Larus canus brachyrhynchus</i>	<i>Corvus corax principalis</i>
Aleutian teal	Short-billed gull	Northern raven
<i>Bucephala clangula americana</i>	<i>Aethia cristatella</i>	<i>Parus atricapillus turneri</i>
American goldeneye	Crested auklet	Yukon chickadee
<i>Lophodytes cucullatus</i>	<i>Lunda cirrhata</i>	<i>Pinicola enucleator alascensis</i>
Hooded merganser	Tufted puffin	Alaska pine grosbeak
<i>Haliaeetus leucocephalus washingtonii</i>	<i>Nyctea scandiaca</i>	<i>Acanthis hornemanni exilipes</i>
Northern bald eagle	Snowy owl	Hoary redpoll
<i>Canachites canadensis canadensis</i>	<i>Asio flammeus flammeus</i>	<i>Loxia leucoptera leucoptera</i>
Spruce grouse	Short-eared owl	White-winged crossbill
<i>Lagopus lagopus alascensis</i>	<i>Dendrocopus villosus septentrionalis</i>	<i>Plectrophenax nivalis nivalis</i>
Alaska ptarmigan	Northern hairy woodpecker	Eastern snow bunting

sionally thermometers were inserted through an incision in the body wall of large animals at the level of the liver. The temperatures recorded are accordingly those from deep in the body among the viscera.

Under these conditions it was possible to introduce thermometers into the wild animals within a minute of death except in the case of some of the large animals. The black bear which we shot rolled down the mountainside where it could not be reached for 10 min. The caribou were shot by resident Eskimos and we often had to wait for several minutes in hiding until they had killed the quota deemed necessary to meet their requirements for food. To determine the influence of these delays we were able to observe the rate of cooling of domesticated reindeer killed so that ther-

mocouples could be inserted among the viscera immediately after death. The deep body temperature did not change significantly in an hour after death in animals lying on the snow in strong wind at air temperatures around -45° . In wild caribou we did not observe significant change in deep body temperature for an hour after death. Accordingly we think that the temperatures reported in large animals are those existing during life.

Several wild porcupines (weight 6–12 kg) were killed and their deep body temperatures measured during the postmortal period. No significant change occurred while they were lying on the snow in air around -20° for a half hour. We concluded that our measurements on animals of this size correctly signified the temperatures existing during life. Even in the small mammals like red squirrels, postmortal changes were so slow that they could not affect our measurements.

TABLE 2. TEMPERATURE OF ARCTIC AND SUBARCTIC MAMMALS

Individuals	Observations	Mammal and Ref.	Arctic or Subarctic	Weight, Kg.	Condition	Air Temp., °C	Body Temp., °C*
3	3	Brown bear†	S-A	34–195	Shot	9	38.0 (38.0–38.0)
1	1	Black bear	S-A	70‡	Shot	7	38.3
4	4	Polar bear (14)	A		Shot	2–18	37.6 (37.2–37.8)
2	2	Polar bear†	A	212–265	Shot	5	37.3 (37.1–37.4)
1	1	Alaska red fox	A	4.7	Captive	7	40.1
1	9	White fox (20)	A	4	Captive	22–80	37.9 (37.6–39.0)
10	10	White fox (14)	A		Shot	–7–36	39.3 (36.6–41.5)
1	1	Wolf (14)	A	40	Shot	–33	40.5
1	9	Eskimo dog	A	40	Domesticated	22–55	38.4 (37.2–38.7)
5	5	Eskimo dog (20)	A	20–30	Domesticated	–3–19	38.6 (38.2–40.0)
1	1	Sea otter	S	15‡	Captive	7	38.5
2	2	Steller's sea lion	S	1000	Shot	6	38.5 (38.5–38.5)
5	5	Bearded seal§	A		Shot	1	37.2 (36.8–37.3)
2	2	Snowshoe hare	A	2‡	Shot	–19	38.5 (38.0–39.0)
1	1	Arctic hare (14)	A	2.5‡	Shot	–29	38.3
1	1	Marmot	S-A	1	Captive	11	38.3
18	61	Ground squirrel (19)	A	0.6–1.3	Captive	30–30	38.0 (36.6–39.4)
4	4	Alaska red squirrel	A	0.18	Shot	–10	39.4 (39.0–40.7)
2	2	Red squirrel (13)	A		Shot	–3–7	38.9 (38.9–38.9)
1	12	Muskrat	S-A	0.9	Captive	24–4	38.0 (37.0–39.1)
28	29	Porcupine	S-A	4–13	Shot-Captive	20–43	37.5 (36.0–38.2)
1	1	Pika	S	0.06‡	Shot	2	39.0
1	1	Musk ox (13)	A			5	40.0
3	3	Mountain goat	S	40–140‡	1 Shot 2 Captive	10–20	38.6 (37.8–39.0)
8	8	Caribou	A	42–120‡	Shot	–12–26	39.0 (38.5–40.0)
11	11	Reindeer	A	35–110‡	Shot-Captive	15–46	38.8 (37.5–39.8)

* Values are means and ranges, °C; mean of 22 species = 38.6° ; range of means = 37.2 – 40.5° .

† Record by Dr. Robert Rausch.

‡ Estimate by observer.

§ Record by Dr. Ira Wiggin

for Dr. Robert Rausch.

Birds as small as redpolls and chickadees (10–14 gm) cooled rapidly in cold air. When mercury thermometers were used they were carried in a warm pocket or warmed in the mouth before insertion in the bird. Even with the greatest speed, we cannot be sure that some cooling of the smallest birds did not occur in the coldest air. For larger birds there is no question that the temperatures recorded are characteristic of those in life.

The records quoted from other observers in table 2 were made by methods allowing comparison with our results.

TEMPERATURE MEASUREMENTS OF LIVING ANIMALS

A series of rectal temperature measurements was made upon living animals as soon as they had steadied down after capture or after they had been kept in outdoor cages. These animals were seized and held for measurements with varying degrees of struggling, but results with intractable animals were discarded.

Wild porcupines could be closely approached on the snow in the Talkeetna Mountains above tree line and firmly seized for rectal temperature measurements before their efforts to escape became violent.

Good arctic sled dogs when gently but firmly handled are extremely stable. Realizing that a dog's career is to obey and that his pleasure is to receive human attention, many dogs would lie or stand quietly for rectal and subcutaneous measurements to be made even in toe pads and nose tips. To these experimental processes they returned eager for the attention. Captive porcupines, ground squirrels and some foxes accepted these examinations without excitement. Herd reindeer, while commonly mild mannered, are not accustomed to being handled and struggled vigorously against isolation from the herd. Some castrated deer, trained to work alone as sled deer, could be separated and examined with little disturbance. Birds which could be securely grasped usually relaxed at once.

MEAN BODY TEMPERATURE OF ARCTIC AND SUBARCTIC MAMMALS

The mean body temperatures of 22 arctic and subarctic species shown in table 2 ranged from 37.2 to 40.5, with the average 38.6. Thirteen of these species were from arctic localities and their average temperature was 38.8°.

The average of nine species from subarctic localities was 38.3°. Five of the forms captured in subarctic Alaska also occur north of the arctic circle. There are only about 30 species of land mammals in arctic Alaska (1) and we have examined a large part of the Alaskan arctic mammalian fauna, which in turn is systematically close to (or the same as) the common arctic fauna of the world.

Although we excluded from consideration measurements made on animals which had struggled violently or which had been running, few of our alert wild animals were as placid as domesticated animals or those which are usually examined in the laboratory. This is perhaps one reason why the average temperature of our list of Alaskan mammals is 0.8° higher than Morrison and Ryser (16) reported for 56 species of mammals of temperate and tropical regions.

BODY TEMPERATURE OF ALASKAN BIRDS

Among 30 species of adult birds examined in Alaska (table 3) the single record of the Arctic Three-toed Woodpecker is so discordant from the other woodpeckers and from the mean of all birds that it is not used in making comparisons. The mean of the temperatures of the remaining 29 species is 41.1°C and the temperatures of the

TABLE 3. TEMPERATURE OF ARCTIC AND SUBARCTIC BIRDS

Individuals	Observations		Arctic or Subarctic	Weight, Kg	Condition	Air Temp., °C	Body Temp., °C*
1	1	Pacific loon	S	1.4	Captive	0.2	39.0
1	1	Baird's cormorant	S	2.0	Shot	8	40.5
2	4	Black brant	S	1.4	Captive	-23-24	40.5 (39.0-42.0)
1	1	Bald pate	S	0.8	Shot	14	41.5
4	4	Aleutian teal	S	0.3	3 Shot 1 Captive	4-20	40.4 (39.5-41.6)
1	1	American goldeneye	S	0.9	Shot	10	41.5
1	1	Hooded merganser	S	0.6	Shot	14	42.2
1	1	Bald eagle—downy	S	0.1	Nestling	5	41.0
8	8	Spruce grouse	SR	0.6	Shot	-11-15	42.0 (41.0-43.0)
30	30	Willow ptarmigan	AR	0.61	Shot	-37- -15	41.3 (41.0-41.5)
2	2	Willow ptarmigan	AR	0.6	Captive	-19	41.0 (41.0-41.0)
23	23	Willow ptarmigan	SR	0.53	Shot	-16- -4	42.0 (41.0-43.0)
2	2	Rock ptarmigan	SR	0.48	Captive	-10	42.3 (41.8-42.8)
13	13	White-tailed ptarmigan	SR	0.38	Captive	-10- -8	41.5 (40.5-42.5)
1	3	Glaucous gull	S	1.8	Captive	-23- -9	42.1 (41.2-42.5)
7	11	Glaucous-winged gull	S	1.6	Captive	-23-23	41.7 (39.0-42.7)
2	2	Glaucous-winged gull	S	1.6	Shot	5	41.0 (41.0-41.0)
4	4	Short-billed gull	A	0.43	Shot	12-13	40.7 (40.2-41.3)
1	1	Crested auklet	S	0.10	Captive	14	41.6
1	1	Tufted puffin	S	0.7	Captive	25	41.3
1	4	Snowy owl	AR	2.0	Captive	-23-11	40.9 (40.6-41.5)
7	13	Short-eared owl	A	0.3	Captive	-23-11	41.2 (39.2-42.2)
1	1	Hairy woodpecker	SR	0.09	Shot	-8	43.0
1	1	Arctic three-toed woodpecker	SR	0.06	Shot	-10	39.0
3	3	Alaska three-toed woodpecker	SR	0.06	Shot	-3-8	42.2 (42.0-42.5)
3	3	Alaska jay	AR	0.08	Shot	-12	41.0 (41.0-41.0)
1	3	American magpie	SR	0.15	Captive	-23-7	41.5 (41.0-42.6)
1	3	Northern raven	SR	1.2	Captive	-23-5	41.3 (40.5-42.0)
5	5	Black-capped chickadee	SR	0.01	Shot	-11- -2	40.0 (39.5-40.0)
5	5	Alaska pine grosbeak	SR	0.07	Shot	-15- -2	41.6 (40.0-42.7)
2	2	Hoary redpoll	SR	0.012	Shot	-12- -8	40.5 (40.0-41.0)
4	4	White-winged crossbill	AR	0.04	Shot	-12- -10	41.0 (40.5-41.0)
6	8	Eastern snow bunting	AR		Captive	-20-22	40.0 (39.5-41.0)
1	1	Eastern snow bunting	SR	0.035	Shot	-2	41.0

* Values are means and ranges, °C; mean of 30 species of adults = 41.1; range of means = 39.0°-42.3°.

species range between 39.0° and 42.3°C. From measurements by Wetmore (17) of the temperatures of 327 species of birds, we have calculated the average to be 41.6°C in the 50 families for which he has reported averages.

Among 78 species of captive birds examined at Quebec, the temperatures observed were commonly a little higher than Wetmore found in related species (18). These measurements were all made at about the same room temperature.

STABILITY OF BODY TEMPERATURE IN DIFFERENT DEGREES OF COLD

Caribou and Reindeer. Caribou feed on slopes where winter wind exposes the vegetation and as they travel they avoid stopping in sheltered areas where the snow drifts. Herders must keep reindeer on open ground where feed is accessible and the herd can be controlled. Neither herds nor individuals show that cold affects their behavior in winter, although in summer they seek cool places and avoid travelling through valleys in windless, warm weather.

Eight caribou were examined at Anaktuvuk Pass after they had been shot while walking. Although some ran for 50 yd before they dropped, they were scarcely at the start of the rapid pace which they can keep up for long times. We could remark no relation between their body temperature and various amounts of activity before death.

Measurements of body temperatures of caribou (table 2 and fig. 1) were made with mercury or dial thermometers. Usually several thermometers were placed at as many locations deep among the viscera. From one deep part to another readings did not differ significantly.

Somewhat higher temperatures were recorded in living reindeer which struggled than in reindeer which were shot for food while inactive. Quiet castrated males, accustomed to harness, were also noticeably cooler than active animals. The measurements of living reindeer were made in winter at Topagoruk, about 60 miles south of Barrow, and near Kotzebue in winter and summer. Thermocouples and thermometers were used in the animals which had been shot. Thermocouples were also inserted into some of the reindeer and caribou which had been shot for comparison of their indications with those of nearby thermometers. Not more than 0.3° distinguished measurements made with all instruments. Only a small part of the difference in temperature observed in various individual animals can be attributed to methodical errors. Since higher temperatures were observed in more active reindeer, we suspect that the mean temperature observed in reindeer and caribou may be a degree higher than would prevail under stricter conditions of rest. But the measurements of 19 individuals vary from 37.5° to 40.0°C and the body temperatures of caribou and reindeer were not affected by natural arctic temperatures between 15° and -46°C .

Ground Squirrels. (*Citellus undulatus barrowensis*). The abundance of arctic ground squirrels enabled Erikson (19) to make the following experimental observations upon 18 captive squirrels at Point Barrow in September before hibernation had

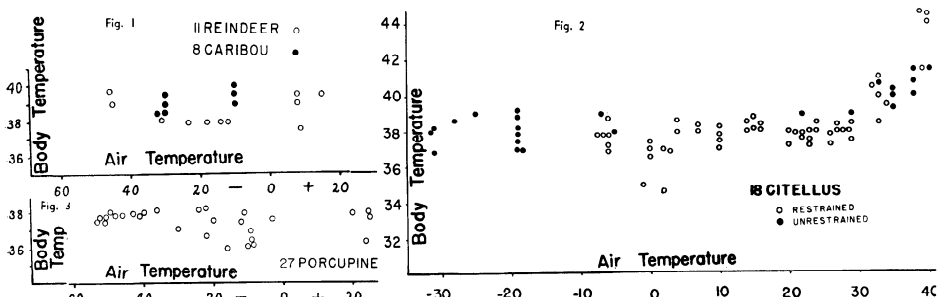


FIG. 1. Body temperature of reindeer and caribou in arctic Alaska.

FIG. 2. Body temperature of arctic ground squirrels (*Citellus undulatus barrowensis*) at Point Barrow in experimentally controlled temperatures. From Erikson (19).

FIG. 3. Body temperature of porcupines in natural subarctic and experimentally controlled temperatures.

begun. The squirrels weighed between 565 and 1300 gm. Six of them had been repeatedly used for measurement of their respiratory exchange and 12 were freshly captured. Squirrels thrive in captivity. Although they did not become tame they showed no apprehension or residual disturbance of their cheerful nature during repeated handling.

Body temperatures were measured by means of thermocouples inserted 60 mm past the anus and held in place by adhesive tape applied to the base of the animal's tail. In order to prevent the couple from being bitten off or pulled out the animals were strapped to a board. When first exposed to the temperature selected, struggling elevated their body temperature, but it usually became stabilized after about $1\frac{1}{2}$ hr. Body temperatures were then recorded for 1 hr. at 10 min. intervals. Between 30° and -10° , 47 measurements are recorded in figure 2 showing the stability of their body temperature.

At -20°C the restrained squirrels could not preserve their body temperature. Inasmuch as unrestrained squirrels had passed uninjured by cold through 24 hr. at -30°C thermocouples were inserted as before and the squirrels were placed inside a small wire cage not much larger than their bodies. In many cases the squirrels bit off the thermocouple leads, but 12 successful sets of observations showed their body temperature in extreme cold (fig. 2). Unrestrained and restrained squirrels showed similar body temperatures in air temperatures above -6°C . In air warmer than 30°C the body temperature rose, but because humidity was not controlled these observations do not define heat tolerance.

We have discarded two low and aberrant records in calculating the mean body temperature to be 38.0°C . In 61 measurements body temperatures were found distributed over a range of 2.8° . Single measurements did not deviate consistently from their mean value between 30° and -35°C . Measurements of the respiratory exchange of these squirrels had shown that below 10°C their resting metabolic rate was increased (20, p. 242). It is apparent that the body temperature of arctic ground squirrels is stable even at temperatures 40° lower than their critical temperature.

In September and when not hibernating these ground squirrels were competent homeotherms. Their body temperature was more stable than Gelineo (21) reported in exposing *Citellus citellus* in Yugoslavia for metabolic measurements in air between 32° and 18°C . Their body temperature varied over a range of 3.4° . Johnson (22) observed marked fluctuations in the body temperature of *Citellus tridecemlineatus* and *Citellus l. pallidus* at all times of the year. These fluctuations lead Johnson (23) to comment that hibernating animals have an established lack of temperature regulation even in their waking condition. If laxity of temperature regulation is possible for hibernating animals in temperate regions, it is certainly not visible in the arctic *Citellus*. Faulty temperature regulation would not be expected in animals which encounter temperatures varying between 20° and -5°C during the summer months when they are commonly outside of their burrows. In spring and autumn, they are occasionally outside in colder weather.

Porcupines. Above tree line in the Talkeetna Mountains porcupines feed during winter days on willow and alder bushes protruding through the deep snow. Their tracks can be seen for long distances on the mountain slopes, establishing that they are commonly abroad in winter and facilitating their capture. We know that they are sometimes active in weather colder than -30°C , but by night and in severe weather we believe that they resort to the dens which we have occasionally found under the snow at the base of alder bushes.

Wild porcupines were not evasive. Most of them were tractable when caught and some became quite tame in captivity. Temperature measurements made upon wild and captive porcupines are recorded in figure 3. These measurements were made with thermocouples and thermometers introduced rectally or among the viscera of animals which had been shot. Measurements were made by all methods on some freshly caught animals in the field, on a few captive animals out of doors and in a few of the porcupines exposed in the cold chamber in the laboratory. We could see no influence of the experimental procedure or method of measurement upon the body temperature. Neither did small difference in their slow activity appear to affect their temperature significantly. In 29 observations their body temperature varied only within the range from 36.0° to 38.2°C .

Arctic White Fox. White foxes and polar bears are the most northerly ranging mammals on the land and frozen surfaces of the Arctic Sea. Their natural habitat is ordinarily confined to arctic regions, but it is interesting that both animals are often exhibited in zoological gardens where they endure the hot summers of temperate climates.

An arctic white fox transported from Point Barrow to Washington, D. C., was able to preserve its usual body temperature after 1-hr. exposure to -80°C (20, p. 254). Our colleague, Dr. R. J. Hock, has permitted us to show the temperature record of this fox in figure 4.

Arctic Sled Dogs. These dogs show characters of many breeds according to the nature of their work and the taste of their owners. They commonly weigh from 20 to 40 kg. Dogs which are well covered with hair and which grow thick woolly undercoats in winter can meet any arctic weather. Those which have thinner coats by nature or through wear from harness are disturbed by cold wind. Some dogs appear to be as well adapted to the arctic climate as wolves.

A dog was selected as a pup of parents highly regarded by the Eskimos at Anaktuvuk Pass for vigor and docility. When it was a year old it was brought to Anchorage and during the next year it became well accustomed to the low temperature chamber and temperature measurements. A series of measurements are recorded in figure 4. When exposed to various temperatures between 20° and -80°C the white fox varied in body temperature by 2.6° . In air from 22° to -55°C the body temperature of the well-trained dog varied by only 1.5° . The variations in body temperature were not related to the temperature of the air.

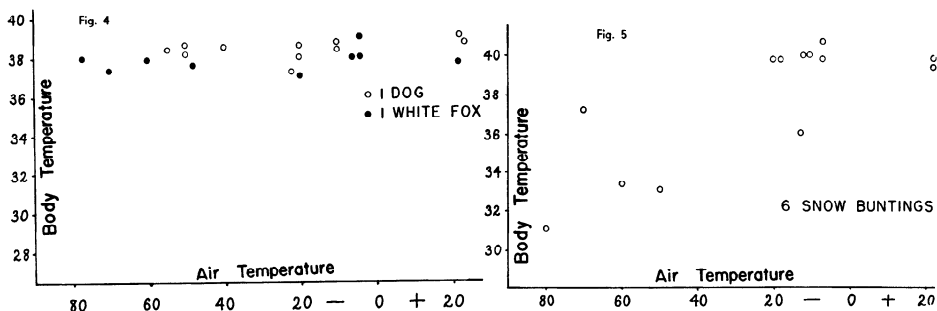


FIG. 4. Body temperature of an Eskimo sled dog and of an arctic white fox (from Hock, 20) in experimentally controlled temperatures.

FIG. 5. Body temperatures of snow buntings in experimentally controlled temperatures. From Hock (20).

Snow Buntings. These birds were examined in a cold chamber at Washington after they had been transported from Point Barrow by Dr. Hock, who kindly provided for us the results of his measurements. In air warmer than -20°C the recorded body temperatures showed little variation except in one aberrant case. Below -50°C the recorded body temperatures were low. Considering the technical difficulties for these small birds and for their observer, it is considered that the figures indicate excellent ability of snow buntings to regulate their body temperature.

While at Barrow these snow buntings had lived in an outdoor cage exposed to air which was occasionally as cold as -40° . Figures for their metabolism in air at temperatures from 40° to -40°C indicate that they preserved their body temperature well under those conditions (20).

Willow Ptarmigan. Among 30 birds examined at Anaktuvuk Pass the mean body temperature (41.3°C) was 0.9° lower than it was for 23 birds examined in the subarctic Chugach and Talkeetna Mountains (table 3). The arctic birds were examined in cold and often windy weather and in the dim light of arctic winter, circumstances unfavorable for accuracy. However, two willow ptarmigan which had been caught apparently uninjured in snares indicated near the same temperature. The latter were loosely held by hand out doors while the temperature was read by means of rectal thermocouples during about 2 hr. The arctic ptarmigan were killed instantly by rifle shots as they stood in the snow. The more wary subarctic willow ptarmigan had to be hunted and shot in flight. White-tailed ptarmigan were less wary, flew less and were frequently shot on the ground. It is likely that the mean temperatures of the three species of ptarmigan are similar and, when at rest, between 41.0° and 41.5° . The individual birds did not vary in temperatures more than has been observed in mammalian species.

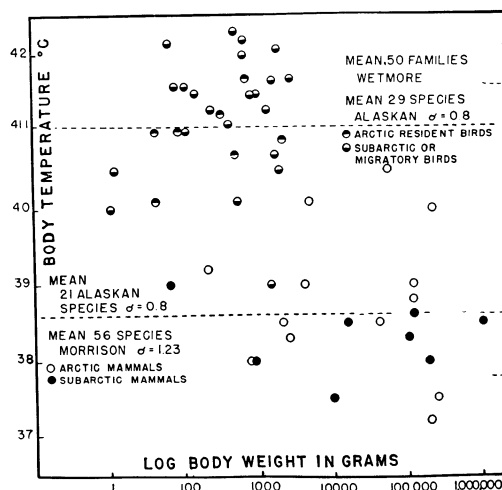
Giaja and Gelineo (24) reported that several domesticated birds withstood experimental exposure to surprisingly low temperatures for several hours without change in body temperatures. Their records were geese, -100° ; duck, near -100° ; turkey, near -40°C .

The greatest variation in body temperature recorded in a series of measurements of individuals of one species occurred among the 10 white foxes which Parry and Lyon (14) reported. Their range in temperature over 4.9° is so much larger than we have recorded that it seems likely that they have included measurements of some very active animals, for the resting state was not mentioned as a condition for measurement. In general we did not observe large variations in the body temperature of birds or mammals. It appears that the individuals of a species preserve their body temperature within a range which at rest is commonly less than two degrees.

BODY TEMPERATURES OF MAMMALIAN SPECIES

When the mammalian body temperatures of table 3 are plotted three species appear discordantly warm (fig. 6). These are Parry and Lyon's (14) measurement of a wolf (40.5°) and a muskox (40.0°) and our measurement of one red fox (40.1°). Our red fox was a temperamental animal which struggled when measured in air at 7° . We consider that measurement was elevated by struggling and we surmise that Parry and Lyon's wolf and muskox were active before they were shot. Disregarding these three, the average of the body temperatures of 19 species of mammals is 38.3° . Among them red squirrels were 0.9° warmer than average. Bearded seals, porcupines and polar bears, on the other hand, were more than 1° cooler than the average of all northern mammals.

FIG. 6. Mean body temperature of arctic and subarctic birds and mammals.



The differences among the body temperatures of arctic and subarctic mammals indicate that specific body temperatures vary a little ($\sigma 0.8^\circ$). Morrison and Ryser (16) found a larger dispersion ($\sigma 1.23^\circ$) among the body temperatures reported for 56 mammalian species of temperate and tropical zones, and a range of body temperatures from 35.8° to 40.3°C .

The mean of the body temperatures of 19 arctic and subarctic species of mammals (38.3°) is 0.5° higher than the mean reported for the 56 mammals of temperate and tropical regions. The mammals from temperate regions include 11 species weighing less than 100 gm, while our list has only one of that small size. In Morrison and Ryser's opinion no relation is evident between the weight of animals and their temperature in spite of Rodbard's (25) statement that such a relation exists. We can see no relation between body weight and temperature in the graph which Morrison and Ryser present, nor is such a relation visible in the arctic and subarctic mammals. When superimposed upon Morrison and Ryser's graph our animals occupy a band near the center of distribution of theirs. It appears that few of the cooler species of mammals occur in the arctic, but we cannot read any adaptive significance into the comment.

BODY TEMPERATURE OF AVIAN SPECIES

In his extended study of body temperature of birds in the central United States, Wetmore (17) shows that the temperature of some species falls at night and rises by day. During the day strenuous activity may elevate body temperatures several degrees above the level prevailing when they are at rest. In this sense the body temperature of birds is labile. We have excluded from our records measurements made after vigorous activity in order to examine the situation during the least activity which is consistent with an alert condition during the day. In this condition of rest we find that the body temperature of northern birds, and of mammals as well, is maintained close to a level characteristic for each species. Some of the northern species differ so much from each other in resting body temperature that they are distinct beyond the possibility of error (fig. 6).

Among the 78 species, most of North American birds, examined by Bernard, Cayouette and Brassard (18) there were evident mean temperature levels from 39.9°

to 43.3°C . As Wetmore showed, taxonomically related species were often similar in body temperature, but in this respect ducks deviated considerably from each other. The only study of arctic birds that we have found was made in summer on Spitzbergen by Martins in 1838 and 1840 (26). The mean temperature of 10 webfooted and hence migratory birds was 40.6°C . These various studies show us little about the regularity of body temperature in cold. They show clearly that the body temperature of many birds in mild climates has been found slightly different according to the conditions of measurement. The body temperature appears to be a characteristic of each species, and there is evidence that in some families of birds the body temperatures of the component species are similar.

Wetmore (17, p. 4) made few records below -4° but had numerous observations upon birds in the intense heat of summer continental climates. He was also familiar with birds in winter and with maritime birds living in proximity to the influence of cold water. He observes (p. 13) “. . . . I am, in light of the records available at present, unable to recognize any constant difference between body temperatures made in the same species at seasons of marked heat or marked cold.” Among the records of mammals reported by Morrison and Ryser (16) the influence of environmental temperature is not considered.

COMPARISON OF MEAN OF BODY TEMPERATURE OF BIRDS WITH THAT OF MAMMALS

The mean temperature of our northern birds is 0.5° lower than Wetmore's mean for a much larger number of species in a temperate climate. The mean temperature of northern mammals was found to be 0.6° higher than Morrison and Ryser (16) found among a list of 56 mammals of temperate and tropical regions. Fifteen of our birds are resident throughout the year in arctic or subarctic localities. The average of their body temperatures is 41.3°C , so they are not significantly different from the temperatures of the other birds which had migrated to arctic and subarctic Alaska. The arctic mammals which we examined were not significantly different in body temperature from those of subarctic Alaska. Birds and mammals in Alaska reveal no difference in body temperature which may be ascribed to the locality of residence.

Since our birds were on the average cooler than Wetmore's, while our mammals were warmer than Morrison's, it is not possible to assign the opposite differences to a climatic influence. Arctic birds cannot be adapted to cold by an average cooler temperature while arctic mammals are about equally warmer than their relatives in temperate regions. It seems likely that the difference between the mean temperature of the species of birds and mammals in the north and those in milder climates is the result of two assortments of species differing slightly in their levels of temperature regulation. The two classes of warm-blooded animals are clearly distinct from each other in respect to the levels at which their member species regulate body temperature.

Wetmore (17) considered that among the 327 species of birds which he examined those of lower body temperature were mainly in the families assigned to lower position in the systematic order. Wislocki's (27) report shows that the body temperature of monotremes, marsupials, the xenarthra and bats may be low and is often variable. That these animals with low and variable body temperature occupy a low systematic position has brought out the view that body temperature has evolved by rising and by improvement of regulation. All of the arctic mammals belong to system-

atic groups with established heat regulation and the level of regulation is not affected by environmental temperatures so different as those of arctic winter and the hot summer of temperate regions. In the past geographical variations and perhaps local changes in the temperature of the air have been as great as the present geographical differences in the earth's surface temperature. No record appears in the body temperature of animals to show that its level was ever influenced by the temperature of the environment.

SUMMARY

The resting body temperature has been measured in 22 species of arctic and subarctic mammals and in 30 species of birds in arctic and subarctic Alaska. Many measurements were made in the field in arctic winter temperatures and some have been made under even colder experimental conditions.

Resting body temperature is taken as that which prevails by day when animals are alert and not in strenuous activity. Series of observations show that from 20° to -30°C , and in some cases below -50° the individuals of a species maintain the same body temperature within a range of about 2° . Measurements of birds were not as extensive as those made on mammals, but no greater variation appeared among individuals of avian species.

The mean temperatures of all of the arctic and subarctic species of mammals which were examined differed within a range of 2.2° . Among avian species the difference was only slightly greater. The average of the mean body temperatures in 19 mammalian species which were observed in good resting condition was 38.3°C . The average of all observations of the mean body temperature of 30 avian species was 41.1°C . The distribution of mean temperatures of the various species of birds and mammals about the means of their respective classes bore no relation to the weight of the animals. The birds weighed between 10 and 2000 gm; the mammals weighed from 0.1 to 1000 kg. It is apparent that each species has its own temperature and that the species of each class are in separate groups in regard to level of temperature regulation. The mean of body temperatures of the northern mammals was 0.5° higher than has been summarized by Morrison and Ryser from records of 56 species of mammals of temperate regions. The mean of the species of birds examined in Alaska was 0.5° lower than was summarized from Wetmore's report on the temperature of birds in temperate United States. These small opposite differences cannot be ascribed to climate or method and may be the result of sampling from the limited number of arctic and subarctic species.

Arctic and subarctic birds and mammals keep their resting body temperatures stable in the great variety of arctic temperatures which require extreme flexibility in the variable physiological functions concerned with the regulation of animal heat.

We are indebted to Miss Mildred C. Wagner for very effective help in temperature measurements made at Anchorage.

Mr. Simon Paneak and his family at Anaktuvuk Pass gave us the kind hospitality of their home on many occasions and enabled us to study their well-trained dogs. They skillfully arranged their hunting so that we could obtain reliable temperature measurements of animals killed for food.

Mr. Thomas Brower extended his genial hospitality to us while we were working at Barrow. Mr. Arnold Brower conducted us to Topaguruk by dog team during a week of unusual cold so that we successfully obtained temperature measurements of reindeer and dogs.

Mr. Chester Seevuk kindly entertained one of us during two visits for observations upon the reindeer herd of the Alaska Native Service near Kotzebue.

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