

Comparative Mechanisms of Cold Adaptation

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Preface

The idea of conducting a symposium on the mechanisms of cold adaptation in the Arctic grew out of a series of informal conversations among the editors at the Naval Arctic Research Laboratory, Barrow, Alaska in 1975 and 1976. Each was involved in some phase of conducting, funding, or coordinating cold adaptation research, and each was experiencing some degree of frustration. We recognized that these studies play a significant role in man's understanding of the adaptation phenomenon in general, thus indicating a bright future for this field of inquiry. However, as interest blossomed and studies multiplied, communication among widely disparate researchers floundered. How could we best ensure adequate communication among colleagues in Florida, Alaska, and Canada? How could we cross disciplinary lines and learn what endocrinologists and biochemists, botanists and zoologists, laboratory scientists and arctic field scientists, and those interested in humans and those working with other species are discovering about cold adaptation? Our goal, therefore, was to stimulate such communication. We felt that a good start would be to bring together experts in the various areas of cold adaptation mechanisms research to discuss their work and to explore the best ways to continue information exchange in the future.

A symposium was planned under the joint sponsorship of the Office of Naval Research, the American Institute of Biological Sciences, and the Ecological Society of America, which was held at the 28th Annual Meeting of the AIBS in East Lansing, Michigan on August 24, 1977. Ten major papers and several shorter ones were presented that day, and a second day was devoted to a workshop on the question of where similar research should go in the future. A series of recommendations was presented to the cosponsors at the close of the symposium.

Participants were encouraged by what they heard from their colleagues and by the audience's response. The large lecture hall was consistently filled, and discussions were stimulating and often spirited. The idea for this book grew from the realization that interest in the subject of cold adaptation was obviously high; however, the amount of information presented could not be instantly digested. We hope this book will not only summarize our current knowledge, but will also be useful to scientists conducting research in this area, to students and others beginning their careers, and to funding agencies considering support for such research.

Investigators who want to do field research in the Arctic often have difficulty in locating where such work is being conducted. Thus, a chapter describing research opportunities for arctic field work has been included in this publication. The last

chapter summarizes the symposium's recommendations for future research directions.

The editors wish to thank the Office of Naval Research, the American Institute of Biological Sciences, and the Ecological Society of America for supporting the symposium. Special thanks go to the staff of AIBS in planning and conducting the symposium. We also gratefully acknowledge Mrs. Peggy Hood and Mrs. Linda Murray, who assisted in the typing of the manuscript, Ms. Judy Brogan who assisted in editing, and Mrs. Shirley A. Zimmerman, who coordinated correspondence between authors and editors and prepared the camera-ready copy for publication by Academic Press, Inc. Most of all, the editors wish to recognize the efforts of the authors and to thank them for their excellent presentations and for meeting most, if not all, of their deadlines.

Larry S. Underwood
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I. ENERGY ACQUISITION AND UTILIZATION

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Although many of the physiological adaptations among homeothermic residents of the Arctic are not unique, the following characteristics seem to be more unique to arctic species than to those of the temperate or tropical regions: 1) white plumage or pelage, which may be important in absorbing radiant heat in the spring, summer, and fall; 2) thick insulation in the form of fat, feathers, and/or fur; 3) thermolability of young, active growing sandpipers; and 4) high fat content of caribou and polar bear milk. These and other adaptations are discussed.

ENERGY ACQUISITION

Biochemical Energy

Energy Content of the Diet. The adaptive value of an energy-rich diet for birds and mammals living in the Arctic is quite clear. In winter the energy cost of thermoregulation may be high, and some animals have only a few hours in which to feed each day since their foraging is restricted to daylight hours. Along the arctic coast in summer, air temperatures usually average below 5°C. The cost of thermoregulation may be especially high for a young homeotherm before the insulative layer of their fur or feathers develops.

Birch seeds (Brooks 1968) make up 80 percent of the diet of redpolls (*Acanthis flammea*) in northern Finland, and birch and alder seeds make up 88 percent of their diet in the vicinity of Fairbanks, Alaska. The seeds of birch are substantially higher in caloric value than most seed types which have been measured.

In summer polar bears (*Ursus maritimus*) living on land along the Hudson Bay are omnivorous, feeding on a variety of grasses, berries, flightless birds, small mammals, and carrion. In winter these same bears move onto the ice pack of the bay and may feed exclusively on ringed seals (*Phoca hispida*). They often preferentially eat the blubber (Stirling and McEwan 1975) which has the highest energy content of any tissue of their prey.

In the Arctic young homeotherms must cope with the high energy demands of growth plus those of thermoregulation before their insulative layer of fur or feathers is fully developed. The diet of young precocial rock ptarmigan (*Lagopus lagopus*) reflects their greater-than-adult rate of energy utilization. The chicks' diet consists of twenty-six percent by weight of invertebrates (Theberge and West 1973), with the remainder composed of birch and willow catkins. In contrast, their parents' diet approximates 86 percent birch and 6 percent willow, with the remainder made up of other plant species. The energy per unit weight of the invertebrates is greater than that of birch and willow.

Young caribou exist exclusively on energy-rich milk until the rumen becomes inoculated with bacteria and protozoa so they can digest lower-in-energy plant material. Caribou calves in Alaska are born during a two- to three-week period from late April to early May, a time when environmental factors can severely stress the early postpartum calf. These factors include snow-covered calving grounds, low ambient temperatures, scarcity of food (especially when vegetation is encased in hard-crusting snow), and harassment by predators. Newborn caribou calves are almost entirely dependent upon an adequate supply of maternal milk during this period. Caribou milk contains more total solids and fat than does the milk of any other species of wild or domesticated ungulates that has been studied. Mean values for Alaskan caribou milk (Luick 1974) at mid-lactation are 31.6 percent dry matter and 15.5 percent fat. The concentration of these constituents increases markedly throughout the lactation cycle. During early lactation when the herds are migrating in search of adequate food and coping with predators, such a highly-concentrated milk could have considerable survival value for the young calves.

The high fat content of the milk of marine mammals is well known. In the Arctic for example, Alaskan fur seal milk is 52.2 percent fat (Ashworth, Romaiah, and Keyes 1966). The milk of polar bears also has a high energy content; 30.6 percent fats and 43.5 percent total solids (Baker, Harrington, and Symes 1963).

Quantity of the Diet. Redpolls, in comparison to non-arctic passerines, have a relatively higher rate and quantity of gross energy intake at low temperatures (Brooks 1968). To facilitate the process, the redpolls have a crop-like esophageal diverticulum that they filled with "extra" food just prior to the onset of darkness.

The quantity of food eaten daily by the Arctic fox (*Alopex lagopus*) and caribou (*Rangifer arcticus*) varies seasonally e.g., the Arctic fox consumes more in summer than winter (Underwood 1971) and the food intake of caribou (White 1974) increases with the availability of live green biomass, which peaks in July. In contrast, the daily food consumption of snowy owls (*Nyctea scandiaca*) caged outdoors at Barrow, Alaska was three lemmings (60 g each)/day in October and six lemmings/day in January (Gessaman 1972). A free-flying snowy owl, however, unlike the caribou and Arctic fox, will emigrate to the lower latitudes of southern Canada and northern United States when a maintenance diet is not available on the arctic tundra.

Digestive efficiency. The digestive efficiencies (i.e., energy assimilated/energy in food eaten x 100) of arctic homeotherms are no better than those of their temperate zone counterparts. Among herbivores, the lemming (Melchoir 1972) (*Lemmus trimucronatus*), willow ptarmigan (West 1968; Moss 1973) (*Lagopus leucurus*) and caribou (Luick and White 1971) have digestive efficiencies that average about 36 percent, 45 percent, and 56 percent, respectively. The increase in efficiency from lemming to ptarmigan to caribou may reflect the increasing complexity of the digestive systems. Cellulose and hemicellulose, which are only partially digested by gastric microflora in the lemmings, may be more fully processed by cecal fermentation in the ptarmigan. The reticulo-rumen fermentation of cellulose and hemicellulose by the caribou probably results in the most complete digestion among the three species.

The effect of low temperature on digestive efficiency has been reported for only one arctic homeotherm, the redpoll (Brooks 1968). The efficiency increased at temperatures below -30°C .

Absorption of Solar Radiation

In spring, summer, and fall, arctic homeotherms may gain enough energy from direct solar radiation to reduce the amount of metabolic heat they require to maintain homeothermy. The white winter pelage of the tundra hare, the varying lemming, weasels, the Arctic fox and the polar bears as well as the white winter plumage of the snowy owl and the rock and willow ptarmigans are well known. There is no evidence that such lack of color helps to balance heat loss with heat gain in the arctic winter when the natural photoperiod is so short and the sun's altitude so low. The whiteness, however, may be advantageous as a solar energy absorber in spring and fall when: 1) the length of the photoperiod exceeds 12 hours (e.g., at Barrow, Alaska--71° 20' N lat.) the photoperiod increases from nine to 20 hours from the first of March to the last of April), and 2) mean air temperatures are well below zero. It is generally assumed that heat gain from solar radiation is substantially greater in birds with dark-colored plumages than in birds with light-colored plumages. Recent studies of heat flux (Walsberg and King 1977) through black and white pigeon plumages showed, however, that this is true only under limited conditions. At very low wind speeds black plumages acquired a greater radiative heat load than did white plumages, but the heat loads of black and white plumages rapidly converged as wind speed increased. This phenomenon was most dramatically seen in erected plumages, in which (at wind speeds above 3m/s) the generally accepted relation of coat color to solar heat load reversed, i.e., white plumages acquired a greater heat load than did black plumages. The effect was caused by short-wave radiation penetrating further into light than dark plumages. The implication is that the white color of an arctic homeotherm may be energetically advantageous.

ENERGY UTILIZATION

Heat Production - Homeothermy

Basal Metabolic Rate (BMR). In 1950 Scholander, et. al. reported that the basal metabolic rate (per unit body weight) of arctic birds and mammals did not differ from that of temperate and tropical species. In recent years that contention has been disproved. For example, the

tundra hare (Wang 1973) (*Lepus arcticus*) has a BMR amounting to only 62–83 percent of the values predicted from its weight. Similarly, the BMR of the snowy owl (Gessaman 1972) is 42 percent lower than predicted for nonpasserines but only 6 percent less than that predicted for owls. On the other hand, the BMR's of the willow and rock ptarmigan (West 1972a) are 14 and 44 percent higher, respectively, than predicted, and that of the redpoll (West 1972b) also exceeds the predicted value. These data certainly discourage any generalizations about BMR levels of arctic species.

The BMR's of birds vary seasonally in a manner dependent upon body size. Analysis of data obtained on arctic and temperate species acclimatized out of doors demonstrated (Weathers 1977) that, with a mass less than 150 g, metabolism tends to be higher in winter than summer, while the reverse holds for larger forms.

Thermoregulatory Metabolism. A resting homeotherm (whether bird or mammal) produces heat above its basal level (BMR) by shivering. Mammals also accomplish this end through high rates of oxidative phosphorylation in brown fat (commonly called non-shivering thermogenesis). Non-shivering thermogenesis will be discussed in detail in later chapters of this symposium publication.

The maximum rate of heat production by a resting homeotherm is commonly called summit metabolism. Summit metabolism varies seasonally (higher in winter than summer) and varies from 3.0 to 6.0 times BMR among individuals. There is no evidence, however, that arctic species have a greater capacity to mobilize energy (i.e., a higher summit metabolism) than do inhabitants of lower latitudes. The summit metabolism of cold-acclimatized redpolls has been reported as 5.6 times their BMR. Rosenmann recently showed that the higher winter BMR of the red-backed vole (1975), an arctic inhabitant, is associated with a higher summit metabolism.

Wunder, et al. pointed out that microtines (1977) (which compose the major small mammal species in boreal and arctic regions) can combat problems of winter cold by increasing their weight-specific metabolic rates and therefore thermogenesis. They further suggested that a drop in body weight would compensate for the potentially higher total energy needs and would decrease an animal's need to accumulate calories while operating at higher metabolic turnover rates. A weight drop in winter has been demonstrated in red-backed voles (*Clethrionomys rutilus*) (Rosenmann, Morrison and Feist 1975).

Little is known about the energy cost of thermoregulation during exercise in arctic homeotherms. For example, does the heat produced by an animal during locomotory activity reduce the energy cost of thermoregulation? In other words, is energy metabolism during exercise at cold temperatures less than or equal to the sum of the energy cost of the activity and the cost of thermoregulation when the animal is resting under the same environmental conditions?

At air temperatures from 0 to -30°C , the energy cost of exercise in redpolls (Pohl and West 1973) equalled the sum of these two energy costs. From -30 to -42°C the metabolic rate during exercise remained the same and was therefore less than the sum of activity metabolism and thermoregulatory metabolism (at rest). Comparable information is not available on other arctic species.

Activity Metabolism. Within the past 10 years, physiologists have learned much about the energy cost of flight in birds (Tucker 1975) and bats and of running in bipedal and quadrupedal mammals (Taylor 1973). Almost none of this work, however, was done on arctic animals. Energy utilization associated with activity has been measured on two arctic species: the polar bear (Oritsland 1976) and the caribou (White and Yousef 1974).

Polar bears were trained to walk on a treadmill while their oxygen consumption was measured. Oritsland, et al. reported higher energy cost of walking (1976) in the polar bear than in other quadrupeds which had been studied. The values for caribou activity metabolism did not differ significantly from those reported for red deer (Brockway and Gessaman 1977) and similar-sized quadrupeds.

Heat Production - Hypothermy

Torpor. Hypothermy is a well-known strategy for conserving energy in a cold environment. However, it has neither been demonstrated in the laboratory nor in the wild in arctic birds that are either cold acclimated for winter or acclimatized, respectively. On the other hand, thermolability during the development of young sandpipers (Norton 1973) of the genus *Calidris* seems to be the most striking metabolic adaptation among breeding birds of the tundra. The free-living chicks consistently reduced the gradient between their core and ambient temperatures by allowing body temperatures to drop to $30-35^{\circ}\text{C}$ while remaining func-

tional, alert, and active. "This hypothermia differs from all other cases so far described among birds. First, it is characteristic of active birds. Second, in contrast to torpor, chick hypothermia coincides with the period of rapid growth and maximum rates of biosynthesis. Third, other studies of exothermy or thermolability in growing young birds have generally determined that endothermy develops gradually before fledging or independence from the nest is attained, but these sandpiper chicks showed no clear trend toward higher body temperatures during feeding periods as the fledgings approached 15-20 days of age (West and Norton 1975).

It has been shown that polar bears (Folk, Brewer and Sanders 1970) in captivity at Barrow, Alaska, entered torpor in January and February. Winter hypothermia has not been reported among free-roaming polar bears.

Hibernation. The Arctic ground squirrel (*Spermophilus undulatus*) is the only hibernator indigenous to the treeless Arctic. This paucity of hibernators in the Arctic probably reflects the scarcity of soils suitable for a hibernaculum (Hoffman 1974), i.e., where soil temperatures remain above freezing throughout the winter. Arctic ground squirrels stay within their hibernaculums for about 220 days per each year.

Reduction of Heat Loss

Fur and Feather Thickness. In a cold environment any mechanism that reduces heat loss is certainly adaptive. In 1950, Scholander, et al. showed that arctic species are better insulated than those in the tropics. Other investigators have shown that insulation among arctic species is greater in winter than in summer. For example, the lower critical temperature of willow ptarmigans is 7.7°C in summer but drops to -6.3°C in winter (West 1972a). The insulation (Frisch, Oritsland and Krog 1974; Hart 1956) of the polar bear is 30 percent greater in winter than summer. The layering of fur on the bear is not uniform; instead, the areas of the body surface that contact the substratum are especially well insulated. Wild redpolls (Brooks 1968) have 31 percent heavier plumage in November than in July.

Behavior. Behavioral thermoregulation may be divided into two categories: 1) the selection of a less thermally stressful environment and 2) changes in the surface area-to-volume relationship, which may be used simultaneously.

The ptarmigan, much like grouse in alpine habitats, finds shelter from severe storms and the heat sink of the arctic sky at night by burrowing under the snow mantle. When willow or birch are available within the cavity space the bird may remain covered for one to two days. Cade (1953) has observed redpolls entering and feeding in holes in the snow formed either by protruding vegetation or by birds themselves, and Irving reported that Eskimos at Anaktuvuk Pass have also seen this behavior (1960).

Polar bears confronted by a cold windy environment seek the lee of a natural wind break such as a pressure ridge as a resting place; if this is not available the animal will lie with its well-insulated rump oriented into the wind. The postures of a polar bear (Oritsland 1970) at different levels of thermal stress have been described by Oritsland (Figure 1).

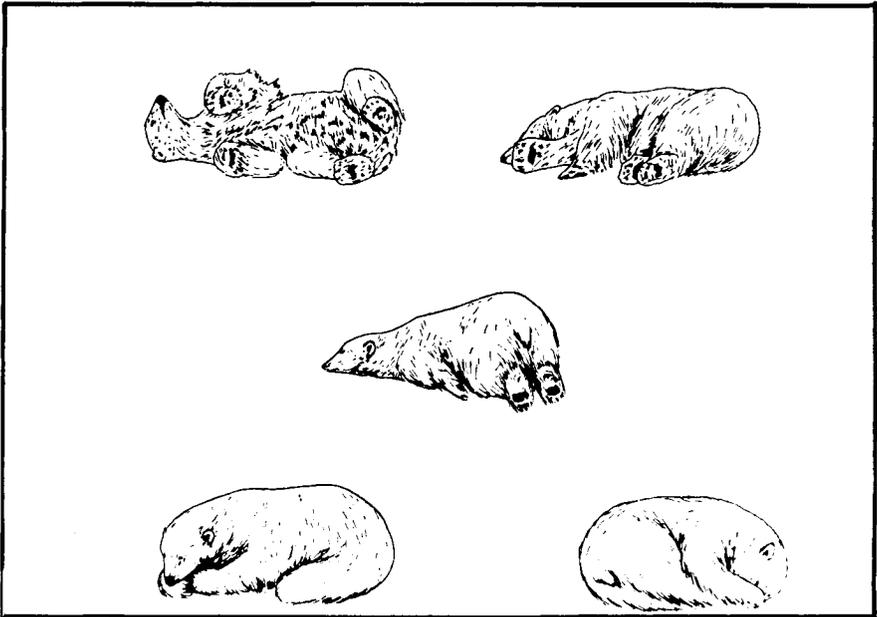


FIGURE 1. Polar bears' postures at mean windchills 830 W/m^2 (I), 1410 W/m^2 (II) and 1910 W/m^2 (III).

Control of Peripheral Circulation. Birds and mammals both have certain body surfaces that are poorly insulated. In mammals these include bare nostrils, toe pads of arctic foxes and wolves (*Canus lupus*), and palms and soles of polar bears. The feet and tarsi in many arctic birds are bare (e.g., raven, *Corvus corax*; redpoll). The tarsi and upper surface of the foot of ptarmigan and snowy owls are feathered but the undersurface of the toes is bare. Blood flow through these surface tissues is precisely regulated to maintain the temperature at or slightly above freezing and to minimize the heat loss from the extremities.

Tissue Production

In addition to the energy devoted to heat production, a significant amount of the energy acquired from the diet may be shunted into processes involving biosynthesis such as fat storage, growth, egg production, molt, fetal development, and lactation. The efficiency with which energy is used in these six productive processes has not been examined in any species of arctic homeotherm. But then, very few efficiencies have been measured on any non-domestic birds and mammals. This area has been neglected for too long by researchers.

In summary, most of the adaptations discussed in this chapter are not unique to homeothermic residents of the Arctic. The following characteristics, however, seem to be more unique to arctic species than to those of the temperate or tropical regions:

1. White plumage or pelage, which may be important in absorbing radiant heat in the spring, summer, and fall;
2. Thick insulation in the form of fat, feathers, and/or fur;
3. Thermolability of young, active, growing sandpipers; and
4. High fat content of caribou and polar bear milk.

REFERENCES

- Ashworth, V.S., G.D. Ramaiah, and M.C. Keyes. 1966. Species difference in the composition of milk with special reference to the northern fur seal. *J. Dairy Sci.* 49:1206.
- Baker, B.E., C.R. Harington, and A.L. Symes. 1963. Polar bear milk. I. Gross composition and fat constitution. *Can. J. Zool.* 41:1035.
- Brockway, J.M. and J.A. Gessaman. 1977. The energy cost of locomotion on the level and on gradients for the red deer (*Cervus elaphus*) *Quart. J. Exptl. Physiol.* 62:333.
- Brooks, W.S. 1968. Comparative adaptations of the Alaskan redpolls to the arctic environment. *Wilson Bull.* 80:253.
- Cade, T.J. 1953. Sub-nival feeding of the redpoll in interior Alaska: a possible adaptation to the northern winter. *Condor.* 55:43.
- Folk, G.E., M.C. Brewer, and D. Sanders. 1970. Cardiac physiology of polar bears in winter dens. *Arctic.* 23:130.
- Frisch, J., N.A. Oritsland, and J. Krog. 1974. Insulation of furs in water. *Comp. Biochem. Physiol.* 47A:403.
- Gessaman, J.A. 1972. Bioenergetics of the snowy owl (*Nyctea scandiaca*) *Arctic Alp. Res.* 4:223.
- Hart, J.S. 1956. Seasonal changes in insulation of fur. *Can. J. Zool.* 34:53.
- Hoffmann, R.S. 1974. Terrestrial vertebrates. Pages 475-568 in *Arctic and Alpine Environments*, Methuen, London.
- Irving, L. 1960. Birds of Anaktuvuk Pass, Kobuk, and Old Crow: A study in arctic adaptation. *U.S. Natl. Mus. Bull.* 217.
- Luick, J.R. 1974. Nutrition and metabolism of reindeer and caribou in Alaska. Progress Report 1973/1974, University of Alaska.
- Luick, J.R., and R.G. White. 1971. Food Intake and energy expenditure of grazing reindeer. In *The structure and function of the tundra ecosystem*. U.S. Tundra Biome Program.
- Melchior, H.R. 1972. Summer herbivory by the brown lemming at Barrow, Alaska. Page 136 in *Proceedings of 1972 U.S. Tundra Biome Symposium*, Lake Wilderness Center, University of Washington.
- Moss, R. 1973. The digestion and intake of winter foods by wild ptarmigan in Alaska. *Condor.* 75:293.

- Norton, D.W. 1973. Ecological energetics of calidridine sandpipers breeding in northern Alaska. Ph.D. Thesis. University of Alaska, Fairbanks.
- Oritsland, N.A. 1970. Temperature regulation of the polar bear (*Thalaxetos maritimus*). *Comp. Biochem. Physiol.* 37:225.
- Oritsland, N.A., et al. 1976. Physiological studies of polar bears at Churchill, Manitoba. In Proceedings of the 4th working meeting of the polar bear specialists group. Int. Union Conserv., Morges, Switzerland.
- Pohl, H., and G.C. West. 1973. Daily and seasonal variation in metabolic response to cold during rest and forced exercise in the common redpoll. *Comp. Biochem. Physiol.* 45A:851.
- Rosemann, M., P. Morrison, and D. Feist. 1975. Seasonal changes in the metabolic capacity of red-backed voles. *Physiol. Zool.* 48:303.
- Scholander, P.F., et al. 1950. Heat regulation in some arctic and tropical mammals and birds. *Biol. Bull.* 99:237.
- Stirling, I., and E.H. McEwan. 1975. The caloric value of whole ringed seals (*Phoca hispida*) in relation to polar bear (*Ursus maritimus*) ecology and hunting behavior. *Can. J. Zool.* 53:1021.
- Taylor, C.R. 1973. Energy cost of animal locomotion. Pages 23-42 in Comparative Physiology. North-Holland Publishing Co. London.
- Theberge, J.B., and G.C. West. 1973. Significance of brooding to the energy demands of Alaskan rock ptarmigan chicks. *Arctic.* 26:138.
- Tucker, V.A. 1975. The energetic cost of moving about. *Am. Sci.* 63:713.
- Underwood, L.S. 1971. The bioenergetics of the Arctic fox (*Alopex lagopus*), Ph.D. Thesis. Pennsylvania State University, University Park, PA.
- Walsberg, G.E., and J.R. King. 1977. Plumage color and solar heat gain: a dogma revisited. (Abstr.) 47th Annual Meeting of Cooper Ornithological Society.
- Wang, L.C.H., et al. 1973. Adaptation to cold: energy metabolism in an atypical lagomorph, the arctic hare (*Lepus arcticus*). *Can. J. Zool.* 51:841.
- Weathers, W.W. 1977. Climatic and seasonal correlations in avian basal metabolism. (Abstr.) 47th Annual Meeting of Cooper Ornithological Society.
- West, G.C. 1968. Bioenergetics of captive willow ptarmigan under natural conditions. *Ecology.* 49:1035.

- West, G.C. 1972a. Seasonal differences in resting metabolic rate of Alaskan ptarmigan. *Comp. Biochem. Physiol.* 42A:857.
- _____. 1972b. Effect of acclimation and acclimatization on the resting metabolic rate of the common redpoll. *Comp. Biochem. Physiol.* 43A:293.
- White, R.G., and M.K. Yousef. 1974. Energy cost of locomotion in reindeer in nutrition and metabolism of reindeer and caribou in Alaska. Progress Report 1973/1974. University of Alaska.
- White, R.G., et al. 1974. Caribou-reindeer ecology in selected areas in the Prudhoe Bay region. In The Prudhoe Bay region: selected environmental reports. U.S. Tundra Biome Program.
- Wunder, B.A., D.S. Dobkin, and R.D. Hettinger. 1977. Shifts of thermogenesis in the prairie vole (*Microtus ochrogaster*). *Oecologia.* 29:11.

II. NUTRIENT ACQUISITION AND UTILIZATION
IN ARCTIC HERBIVORES¹

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Processes of adaptation to cold in arctic herbivores are generally interpreted in relation to body size. Small mammals and birds must rely on adequate means of increasing thermogenesis to counter the effects of frequent exposure to temperatures below their thermo-neutral range. In large mammals, coat thickness results in a decrease in the lower critical temperature so that environmental temperature is rarely below the lower critical temperature. When body temperature is lower than environmental temperature larger mammals shiver. Nutrients and water are involved intimately in the mechanisms and control of thermogenesis. Further, nutrients are involved in structural components and hence morphological and insulative adaptations to cold. For example, many macronutrients are involved in shivering and non-shivering thermogenesis through their involvement in energy stores, as messengers, in pumps, in specific chemiosmotic energy transfers, and as cofactors and modulators of enzyme reaction. Most nutrients involved in cold thermogenesis are recycled as AMP, ATP, ADP, and ITPase regenerated (the irreversible phosphate loss is presumably small). Classical laboratory studies indicate food intake is determined by the nutritive value of the food. As nutritive value increases, food intake is regulated so that intake of the most important dietary component, generally energy, remains constant. Small birds and mammals generally employ different strategies of nutrient acquisition and conservation than larger mammals.

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INTRODUCTION

The objective of this chapter is to discuss the role of nutrients in comparative cold adaptation in northern herbivores and to deduce where nutrient acquisition and utilization processes may be specifically adapted for cold resistance.

The components of the ingesta which may be involved in such adaptations are:

1. Water,
2. Protein and N,
3. The macro-elements Ca, K, Mg, Na, P, S,
4. The trace elements, and
5. The vitamins and cofactors.

Discussions will be limited to the first three groups. The omission of the last two groups is partly due to space limitation but also reflects the general level of our knowledge of involvement of nutrients in cold adaptation.

The argument is developed that nutrient acquisition and utilization processes must provide a framework for the physiology and biochemistry of cold adaptation: at the very least they play a permissive role. This argument is based on the fact that nutrients and water are involved intimately in the mechanisms and the control of thermogenesis. This involvement is outlined in detail elsewhere in this volume, and is summarized briefly below.

Nutrients are also involved in structural components and hence morphological and insulative adaptations to cold. The involvement of some nutrients, mainly as cations, in thermogenic mechanisms leads to the hypothesis that the requirements of these nutrients may be linked to energy expenditure; and thus, also to body size.

Finally, nutrient acquisition and utilization processes are discussed and evidence for the specific adaptation of the acquisition or utilization processes in response to cold is outlined.

INVOLVEMENT OF NUTRIENTS IN THERMOGENIC PROCESSES

Many of the macronutrients, mainly as cations, are involved in shivering and non-shivering thermogenesis through their involvement in energy stores (the adenosine, guanosine, and inosine phosphates), as messengers (3'5'