Ecological Adaptations of Tundra Invertebrates

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Introduction

The existence of latitudinal gradients in species diversity is a basic observation of biogeography. The variety or diversity of most higher plant and animal taxa decreases as one nears the poles. Similar gradients in diversity are seen with increasing altitude, fewer species occur at higher elevations. The end points of these latitudinal and altitudinal gradients lie in the tundra communities of the high arctic, antarctic, and alpine regions of the world.

Much insight into the factors causing these gradients has come from broad comparisons of faunal or floral assemblages occurring at different latitudes or altitudes. Additional insight remains to be gleaned from careful examination of the physiological and ecological characteristics which adapt species for existence under the environmental conditions that prevail at particular places along major gradients. The tundra, as an end point, is ideally suited for such an analysis. This offers, of course, only one justification for the study of ecological and physiological characteristics of tundra organisms. Plant and animal life reaches the limits of its existence in extreme arctic, antarctic, and high alpine tundra. The species that occur under such circumstances probably demonstrate the lim-
its of physiological and evolutionary adaptability under extreme conditions.

This chapter outlines the patterns of diversity found in the invertebrate component of the tundra communities of the world. The characteristics of tundra environments, and the physiological and ecological responses of invertebrates to these, are then discussed. Thus, it is hoped, the role of the environment in determining the diversity, function, and importance of invertebrates in the tundra ecosystem will be revealed. Additional information, particularly on quantitative aspects of tundra invertebrate populations and their role in ecosystem function, will be forthcoming soon when the results of studies conducted under the International Biological Program are published.

The distribution and physiological and ecological attributes of most groups of tundra invertebrates is very poorly known. As in other areas, the Insecta have received the most study, and the reviews of Downes (1962, 1964, 1965) and Oliver (1963, 1968) dealing with arctic insects are particularly useful. Research on the Antarctic subcontinent and subantarctic islands has emphasized systematics and biogeography (Gressitt, 1967 and 1970), although valuable ecological observations appear in the volumes edited by Gressitt (1967, 1970), and Gressitt and Strandmann (1971). The most extensive survey of adaptations to alpine existence is that of Mani (1962, 1968) dealing with high-altitude insects.

### Composition of Tundra Invertebrate Faunas

The invertebrate fauna of arctic tundra is depauperate in number of species and higher taxa (Table 1). Of the approximately 27 orders of Insecta (depending upon taxonomic scheme) found worldwide, 24 occur in the British Isles and 18 have been collected in the vicinity of a single tropical forest site, the El Verde field station, Puerto Rico (Drewry, 1970). In contrast, 17 orders occur on Greenland (Henriksen, 1939), 12 near Point Barrow, Alaska (Hurd, 1958), 8 at Lake Hazen, Ellesmere Island, Canada, 6 on Bathurst, 7 on Devon Islands, Canada, and only 5 at Isachsen, Ellef Ringnes Island, Canada (McAlpine, 1964). The number of reported species shows a similar decline, over from 650 on Greenland to approximately 250 at Barrow and Lake Hazen and 37 at Isachsen. Figure 1 represents arctic areas of North America mentioned in text.

The reduction in species does not occur in all taxa equally. In the Annelida, Enchytraeidae are abundant and relatively diverse, while Lumbricidae are reduced or absent altogether. The Prostigmata make up

<table>
<thead>
<tr>
<th>Insect order</th>
<th>Barrow, Alaska</th>
<th>Greenland, Ny-Ålesund</th>
<th>Bathurst, Labrador</th>
<th>Devon Islands, Canada</th>
<th>Isachsen, Ellef Ringnes Island, Canada</th>
</tr>
</thead>
<tbody>
<tr>
<td>Coleoptera</td>
<td>3500</td>
<td>2000</td>
<td>1000</td>
<td>500</td>
<td>250</td>
</tr>
<tr>
<td>Dicaeidae</td>
<td>500</td>
<td>300</td>
<td>100</td>
<td>50</td>
<td>25</td>
</tr>
<tr>
<td>Diptera</td>
<td>3500</td>
<td>2000</td>
<td>1000</td>
<td>500</td>
<td>250</td>
</tr>
<tr>
<td>Hymenoptera</td>
<td>3500</td>
<td>2000</td>
<td>1000</td>
<td>500</td>
<td>250</td>
</tr>
</tbody>
</table>

| Total Orders| 21500          | 12500                 | 6250              | 3125                 | 1562                                 |

*Note: Numbers represent the number of specimens collected.*
Figure 1  The arctic areas of North America, showing locations of sites mentioned in text.

From that of other parts of the world. Herbivores are striking in their scarcity. Plant grazing groups such as Orthoptera are absent altogether, and plant sucking insects are few in numbers of species and individuals. A large proportion of tundra invertebrates belong to the broad category “saprovores”—animals that ingest dead plant and animal remains. Many of these actually assimilate the bacteria, fungi, yeasts, etc., that are responsible for decay, while others digest and assimilate the dead organic substrate. This is a heterogeneous assemblage about which we know very little. Among the saprovores of arctic tundra are many nematodes, Enchytraeidae, Acarina, Collembo, and larvae of Diptera.

The trophic structure of the tundra invertebrate fauna is clearly related to taxonomic structure. The causal sequence (trophic structure derives from the fact that certain invertebrate taxa are favored, or vice versa) remains to be explored. It is interesting to note that these same trends in faunal composition are seen in the tundra-like moor lands of Great Britain (Moor House; Table 1).

The geography of the antarctic region differs from the arctic, with important consequences. The north pole lies near the center of a polar sea, which greatly ameliorates the climate of surrounding land masses. The south polar region occupies a large continental land mass covered by an ice cap extending some 3000 m above sea level. The Antarctic peninsula extends to 63° S latitude, a latitude that is well within the boreal forest zone of the northern hemisphere; yet the terrestrial arthropod fauna of Antarctica consists of only 21 free-living insect species, 55 free-living mites, and 56 parasitic Acarina and Insecta (Gressitt, 1967). Only two free-living higher insects occur, both Diptera of the family Chironomidae. The Antarctic thus resembles the Arctic in that Acarina, Collembo, and Diptera are the persistent forms under the most severe climatic conditions.

Unlike the islands of the Canadian Arctic archipelago, the subantarctic islands are distant from the nearest land mass and surrounded by an unfrozen, turbulent sea. Endemism, rare in the arctic, is common in the invertebrates of the subantarctic islands, and accidents of biogeography play a significant role in shaping the fauna. The islands resemble the arctic in having few orders, with Acarina, Collembo, and Diptera among the most important. They differ from arctic regions in the greater abundance of Coleoptera.

The geography of alpine tundra is likewise important in shaping the invertebrate fauna. Alpine tundra generally exists as islands of habitat of various sizes, surrounded at lower elevations by forest, plans, and other ecosystem types. While certain species of alpine tundra invertebrates have obvious affinities with arctic forms, numerically the alpine fauna
may be derived, in large part, from the fauna of surrounding ecosystems. Schmoller (1971) found that all species of Carabidae and Arachnida from Colorado alpine tundra also occurred below tree line. Edwards (1972) recorded 10 insect orders and at least 141 species in the windborne "fallout" on snowfields in alpine tundra above taiga forest in interior Alaska. In view of this large and diverse input, it is difficult to separate the true, successful alpine species from species which breed but maintain a population only with input of individuals from below tree line, and species occurring only as accidentals (Alexander, 1964). Locally extinct populations may be quickly replaced by new colonizers in alpine tundra, while extinctions in arctic tundra may be of more lasting importance to faunal diversity. Thus, considering alpine tundra as "islands" of habitat, the equilibrium species composition would shift in the direction of greater diversity due to the high rate of colonization (MacArthur and Wilson, 1967).

Areas with steep topography provide nonalpine habitats in close proximity to alpine tundra and, in addition, generate the air currents that transport arthropods. Thus, the gently rolling tundralike moorlands of the northern Pennines in Great Britain support 19 insect orders (Nelson, 1971) while 17 orders have been collected from the alpine tundra of the steeper Hardangervidda area in Norway by workers in the Norwegian IBP tundra program. This is a greater diversity than occurs at any of the arctic tundra sites. Within the alpine zone diversity decreases with elevation, as both distance from source areas and climatic severity increase.

Characteristics of Tundra Environments

We may list several characteristics of the tundra environment that are important for invertebrate animals and may require particular physiological adaptations:

1. Low winter temperature. Air temperatures of -40°C and below are encountered during the winter in the tundra zone. Similar and even colder temperatures occur in the northern boreal forest zone, or taiga; however, ground surface temperatures differ in the two zones. Precipitation is greater in the forest zone, creating an insulating snow layer of greater depth. Tundra areas tend to be areas of little precipitation and shallow snow. In the absence of protection afforded by trees, the snow in the tundra region is heavily influenced by wind. Some areas are blown free of snow altogether, leaving the ground surface exposed to ambient air temperatures. Where the snow remains it may develop a platelike or lamellar structure of high density and poor insulating property. Further, at least in the arctic and antarctic regions, tundra invertebrates are confined to a layer of seasonally thawing ground (the "active layer") lying above perennially frozen ground, or permafrost. Near Barrow, Alaska, the equilibrium temperature of permafrost is -10.6°C (Brewer, 1958). Thus, during winter the ground surface is surrounded by cold above and below, and quickly drops to low temperatures. Kelley and Weaver (1969) reported that the ground surface temperature near Barrow averages below -8°C for 8 months, and below -15°C for 4 months. MacLean et al. (1974) found a mean of less than -20°C at the ground surface in January, February, March, and the first half of April in a year of lighter than average snowfall. In March, 25 measurements made on 6 days averaged -26.2°C under an average of 28.6 cm of snow. No measurements were made on windswept areas devoid of snow. Temperature there must follow air temperature, and reach minima of -40°C to -50°C.

2. Short growing seasons. The snow-free season may be 90 days or less, leaving only a short time for growth and reproduction. The frost-free season, the period between the last freezing temperature in spring and the first freezing temperature in fall, is of almost no meaning in a true polar or high altitude climate. At Barrow, Alaska, for example, the long-term average daily minimum temperature is below freezing for 324 days of the year, and freezing temperatures may occur even at the height of the summer season. It is important to note, however, that biologists frequently underestimate the length of the period of activity, particularly for soil dwelling organisms. Even after daily minimum and even mean temperatures fall below 0°C the soil may remain in an unfrozen state. Loss of energy from the soil is counteracted by latent heat of fusion released as water changes state to ice. As a result the soil column remains isothermal at or close to 0°C, although the surface layers may be frozen. This is the "zero curtain" phenomenon. Cold adapted organisms are able to remain active at 0°C, thus lengthening the period of activity by several weeks. After all water has changed to ice soil temperature drops rapidly to the winter values mentioned above, and all activity ceases.

3. Low temperature during the growing season. The long-term average daily mean air temperature at Barrow, and the temperatures recorded in two seasons, one warmer than average (1972) and one cooler than average (1973), are shown in Figure 2. The expected daily mean air temperature is below 5°C throughout the season. Temperature ex-

determining summer climate. Lake Hazen, at 81°49’ N, has a warmer climate (and greater invertebrate diversity) than does Bathurst Island (75°43’ N) or Ellef Ringnes Island (78°47’ N). In arctic Alaska the Point Barrow area (71°20’ N), at the convergence of the Beaufort and Chukchi seas, is exceptionally cool and foggy. Coastal localities in either direction (southwest or southeast) are significantly warmer, and exceptionally steep climatic gradients exist between coastal and inland tundra localities (Clebsch and Shank, 1968). This is reflected in floral (Clebsch and Shank, 1968) and faunal composition. For example, the number of recorded species of crane flies (Diptera, Tipulidae) increases from 4 at Barrow to 14 at Prudhoe Bay (70°16’ N). The number of recorded butterfly species is 5 at Barrow, 12 at Prudhoe Bay, and 23 at Kavik Camp, 90 km inland from Prudhoe Bay (Philip, personal communication).

The temperature regime of alpine tundra is quite different. During the day, with reduced atmospheric filtering, the radiation load may be quite high, resulting in very high temperatures, especially on the ground surface. In the evening, reradiation may be equally high and temperatures may fall precipitously. Thus, the daily temperature range is much greater than in the Arctic and becomes a factor in physiological adaptation to the environment (Remmert and Wunderling, 1969). Ballard (1972), investigating soil temperatures in subalpine British Columbia, found that at the time of the annual radiation maximum (21–22 June), the diurnal range in soil temperature 1 cm below bare ground was 35°C, and 5 cm below bare ground it was 20°C. At a depth of 5 cm below an herbaceous meadow, the diurnal range was nearly 17°C, and ground surface temperatures in the meadow probably exceeded 49°C. In contrast, on 21–22 June the diurnal temperature range 5 cm under arctic tundra at Barrow varied between 0.7° and 3.3°C (12 measurements). Even at the peak of the season, when maximum temperature gradients are developed, the diurnal temperature variation at 5 cm rarely exceeded 6°C. Thus, alpine organisms must be able to tolerate much wider variations in environmental temperature than arctic orantarctic tundra organisms.

4. Low primary productivity. All of these factors, plus others discussed by Tieszen and Wieland, Courtin and Mayo, and McGown (this volume) result in low annual primary production, hence a relatively small amount of energy available to animal species. This may be important in determining length of food chains, invertebrate abundance and diversity, and the relative importance of various trophic types.

5. Weakness of photoperiodic cues. In arctic and antarctic areas, the sun is continuously above the horizon for part of the growing season. Diurnal and seasonal information comes in the form of changes in light
intensity, quality, and angle of incidence rather than major changes involving alternation of light and dark periods. Under overcast conditions these cues may be masked altogether. This may raise problems in the daily and seasonal timing of physiological processes and activities.

Adaptation to Tundra Environments

For convenience, adaptation to the special problems of existence in the tundra is treated under several categories. Actually, these form a suite of interrelated adaptations expressed in various degrees and combinations by the various groups of invertebrate animals.

1. Microhabitat selection. When the annual heat budget is small, small deviations from average conditions may have great ecological and physiological importance. The annual aboveground heat budget of Barrow, Alaska (Figure 2a) expressed as C° days above freezing, is 238 C° days. If, by microhabitat selection, an animal were able to achieve an average 1°C increase over the 90 days of the growing season, the heat budget would increase by 90 C° days, or 32%.

Figure 2c and d shows the daily mean temperature recorded in 1972 and 1973 at a depth of 2 cm below the surface of a low polygon rim, a slightly elevated feature in the array of patterned ground that results from frost action in wet arctic and alpine sites (Hussey and Michelson, 1966). The smooth curve of Figure 2c is drawn to represent “average” conditions, taking into account excursions of air temperature from the long-term mean (Figure 2a). The total heat budget calculated from this curve is 440 C° days above freezing, an increase of 55% over air temperature. The effect is greatest where solar radiation is high and less where cloud cover and fog limit ambient radiation. Invertebrates clearly derive a significant thermal advantage in existing in the soil rather than the air. This could be one factor contributing to the dominance of soil-dwelling saprovores over surface-active herbivores in arctic tundra.

Where possible, animals may move during the day or season to optimize the heat budget. Haufe (1957) found that the larvae of mosquitoes aggregate in the surface waters of the warmest parts of pools, and move clockwise around the pool during the day as the warmest point changes due to the changing position of the sun. Corbet (1966) observed that females of *Aedes nigripes* at Lake Hazen oviposit around midday and only when directly insolated. Thus, their eggs are placed on the south-facing banks of ponds and experience warmer temperatures as a result. The eggs of *Aedes impiger* are deposited in cracks on south-facing banks, and derive a similar advantage.

The dense cushions of mosses and such characteristic tundra plants as *Saxifraga oppositifolia* and *Dryas integrifolia* may capture radiation and warm well above ambient temperature, providing a favorable heat budget for invertebrate development and activity (Courtin and Mayo, this volume). Kevan (1972) observed heliotropism—orientation toward the sun—in the flowers of several arctic plant species. This concentrates radiation on the reproductive structures, resulting in temperatures of up to 10°C above ambient (Kevan, 1973). Many arctic insects bask in flowers, and heliotropism may be a mechanism for attracting pollinators (Hocking and Sharpley, 1965).

Kevan and Shorthouse (1970) investigated basking as a mechanism of behavioral thermoregulation in arctic butterflies. By selection of substrate and orientation toward the sun, butterflies were able to elevate their body temperature 10°C or more above ambient. The dark color (melanism) and hairy body that characterize many arctic insects contribute to the capture and retention of the energy of radiation. *Belgica antarctica*, the southernmost occurring higher insect species, is likewise melanic and is frequently seen basking (Peckham, 1971).

High altitude melanism is a common feature of alpine insects (Mani, 1968). This is often attributed to the need for protection from ultra-violet radiation; however, the existence of parallel increases in the frequency of pigmented species with latitude and altitude (e.g., Rapoport 1969 for Collomella) suggests that absorption of radiation and increase in body temperature is the most important selective basis of melanism.

2. Life cycles. In speaking of temperate invertebrates the length of the life cycle is expressed as number of generations per season. In considering tundra invertebrates we find ourselves increasingly asking, How many years per generation? The known incidence of extended life cycles in tundra invertebrates is summarized in Table 2. The life cycles of few tundra invertebrates have been investigated; however, it seems certain that, when more data are available, this will prove to be a very common means of dealing with the short growing season and limited heat budget of the tundra.

Flexibility is another feature of the life cycle of arctic species. (Downes, 1965; Oliver, 1968; MacLean, 1973). During unfavorable years pupation may not occur, with individuals remaining as larvae for 1 or more additional years. This adaptation of extended and flexible life cycles is analogous to the perennial growth form of arctic plants. The future of the population is not dependent upon the success in any one year, as would be the case for annual species. The population perseveres even if unfavorable conditions lead to the failure of reproduction in any one year.
Table 2  Cases of Prolonged Life Cycles in High Latitude and High Altitude Invertebrates.

<table>
<thead>
<tr>
<th>Species</th>
<th>Order:Family</th>
<th>Location</th>
<th>Duration</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pardosa glaciata</td>
<td>Araneae:Lycosida</td>
<td>Lake Hazen, NWT</td>
<td>6–7 years</td>
<td>Leech (1966)</td>
</tr>
<tr>
<td>Tarentula exasperans</td>
<td>Araneae:Lycosida</td>
<td>Canada</td>
<td>6–7 years</td>
<td>Schmoller (1970)</td>
</tr>
<tr>
<td>Pardosa concinna</td>
<td>Araneae:Lycosida</td>
<td>Alpine tundra, Colorado</td>
<td>2 years</td>
<td>Schmoller (1970)</td>
</tr>
<tr>
<td>Gnaphosa muscorum</td>
<td>Araneae:Gnaphosida</td>
<td>Alpine tundra, Colorado</td>
<td>2? years</td>
<td>Richards (1964)</td>
</tr>
<tr>
<td>Gnaphosa nitidula</td>
<td>Araneae:Gnaphosida</td>
<td>Alpine tundra, Colorado</td>
<td>2? years</td>
<td>Kaufmann (1971)</td>
</tr>
<tr>
<td>Drassodes sp. nov. Pulvinaea</td>
<td>Homoptera:</td>
<td>Lake Hazen</td>
<td>As many as 5 years</td>
<td>Richards (1964)</td>
</tr>
<tr>
<td>allemerensis</td>
<td>Coccoidea</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pterostichus brevicornis</td>
<td>Coleoptera:</td>
<td>Taiga, Interior Alaska</td>
<td>14–36 months</td>
<td>MacLean, unpubl.</td>
</tr>
<tr>
<td>Pterostichus spp.</td>
<td>Carabidae</td>
<td>Barrow, Alaska</td>
<td>2 or more years</td>
<td></td>
</tr>
<tr>
<td>Gynaphora (=Byrdia) greeniandica</td>
<td>Lepidoptera:</td>
<td>Lake Hazen</td>
<td>2 or more years</td>
<td>Oliver et al. (1964)</td>
</tr>
<tr>
<td>G. roesi</td>
<td>Lymantriidae</td>
<td></td>
<td>&quot;Perhaps as many as 5&quot; years</td>
<td>Downes (1965)</td>
</tr>
<tr>
<td>Olethreutes inquietana</td>
<td>Lepidoptera:</td>
<td>Lake Hazen</td>
<td>&quot;at least 2 years&quot;</td>
<td>MacKay and Downes (1969)</td>
</tr>
<tr>
<td>Olethreutes mangelana</td>
<td>Tortricidae</td>
<td></td>
<td>2 years; exceptionally, 1 year</td>
<td></td>
</tr>
<tr>
<td>Tipula carinicornis</td>
<td>Diptera:Tipulida</td>
<td>Siberia</td>
<td>2 years</td>
<td>Chernov and Savchenko (1965)</td>
</tr>
<tr>
<td>Tipula carinicornis</td>
<td>Diptera:Tipulida</td>
<td>Barrow, Alaska</td>
<td>4 or more years</td>
<td>MacLean and Clement, in prep.</td>
</tr>
<tr>
<td>Tipula arctica</td>
<td>Diptera:Tipulida</td>
<td>Greenland</td>
<td>2 years</td>
<td>Niesen (1910)</td>
</tr>
<tr>
<td>Tipula excisa</td>
<td>Diptera:Tipulida</td>
<td>Norway</td>
<td>2 years</td>
<td>Hofvanger (1973)</td>
</tr>
<tr>
<td>Pedicia hannah</td>
<td>Diptera:Tipulida</td>
<td>Barrow, Alaska</td>
<td>4 or 5 years</td>
<td>MacLean, 1973</td>
</tr>
<tr>
<td>Culicoides sp.</td>
<td>Diptera:</td>
<td>Churchill, Manitoba</td>
<td>2 years</td>
<td>Downes (1962)</td>
</tr>
<tr>
<td>Procladius sp.</td>
<td>Caratopogonidae</td>
<td>Lake Hazen, NWT</td>
<td>3 or more years</td>
<td>Oliver (1968)</td>
</tr>
<tr>
<td>Diamesa vaillanovi</td>
<td>Diptera:</td>
<td>Finse, Norway</td>
<td>2 years; exceptionally, 1 year</td>
<td>Saether (1968)</td>
</tr>
<tr>
<td>Diamesa davisi</td>
<td>Chironomidae</td>
<td>Saskatchewan, Canada</td>
<td>2 years</td>
<td>Rempel (1936)</td>
</tr>
<tr>
<td>Chironomous hyperboreus</td>
<td>Diptera:</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
The existence of life cycles of more than 1 year leads to overlapping generations and the coexistence of several year-classes in a single population. Thus, the high density and biomass of certain tundra insect species may be a direct result of low annual productivity and the resulting prolonged life cycle (MacLean, 1973). Care must be taken in interpreting density and biomass values for tundra invertebrates.

While pupation may be prevented and the life cycle prolonged in unfavorable years, the reverse—accelerated pupation in favorable years—apparently does not occur (MacLean and Pitelka, 1971). Danks and Oliver (1972) argue that an obligate diapause prior to pupation is included in the life cycles of arctic insects as a mechanism preventing unseasonal emergence, for instance, late in the season in an unusually warm year. It should be noted that an extended life cycle is not necessarily a flexible one. A species may be rigidly bound in a life cycle that involves several years, and the coexistence of larvae in several stages of development (Dahl, 1970) is not, in itself, evidence of flexibility.

The length of the life cycle of arctic insects derives almost entirely from the larval period. The adult existence is usually brief, and is often devoted entirely to reproduction. Females of three abundant crane flies occurring near Barrow, Alaska emerge from pupation with fully developed ova, copulate within hours, and lay their complement of eggs within a day or so of emergence. In arctic blackflies (Simulidae) development of the eggs begins during pupation, and in at least two species the eggs are mature at the time of emergence (Downes, 1965). Reduction of adult life span reaches an extreme in the Norwegian species Prosimulium ursinum. This species is parthenogenetic. Most individuals fail to emerge from the pupa; the eggs are shed into the stream when the abdominal wall ruptures (Carlsson, 1962). Thus, there is essentially no adult stage.

Oliver (1968) observed that follicular development occurred in the pupae in chironomids at Lake Hazen, but maturity was not reached until 2½–4 days after emergence. Even in these species, however, the adults did not feed and egg maturation was completed using nutrient material accumulated during the larval stage. Surprisingly, some species can mature a second egg batch after the first has been laid (Oliver, 1968), a characteristic not seen in the arctic Tipulidae.

Ryan (personal communication) found that female moths of the genus Byrdia at Devon Island, Northwest Territory, Canada, have matured most of their complement of eggs in the pupal stage. Mating proceeds immediately, so that the first cluster of fertilized eggs is deposited on the cocoon itself.

Females of the antarctic midge Belgica antarctica apparently mature their eggs in the pupal stage, and eggs are generally deposited in a single mass of 30–50 eggs within a day or two of the emergence of the female (Strong, 1967). Females were observed to live for a week or so after oviposition, but no more than one egg mass was observed for a single female.

By completing most of the life cycle in the larval stage, usually protected by the soil, tundra invertebrate species limit the length of time that the critical reproductive phase is exposed to the uncertainties of the severe climate, and to surface-dwelling predators as well.

With the reduced adult life span, a morphological reduction of adult insects is often found. Wing reduction (brachyptery or aptery) is frequently found. Two of the three abundant crane flies near Barrow, Tipula carinifrons and Pedicia hannai, have brachypterous females. In P. hannai reduction involves leg length, eyes, antennae, and mouth parts as well (Tjeder, 1963). Byers (1969) argued that cold temperature, which limits the power of flight, is primarily responsible for the evolution of wing reduction; however, the tendency toward retention of wings by males indicates that there must be opposing selective pressures involved. Winter crane flies (Chionea spp.) gain a 4% advantage in egg production by replacing the flight muscles with eggs in the thorax (Byers, 1969), an advantage that would not accrue to males. Females of many species are so laden with mature eggs at emergence that, even if fully winged, flight would be difficult at best. With the reduced mobility that accompanies winglessness in females, the responsibility for mate location falls entirely upon the males, and wings may be retained for that purpose. Still, at the prevalent environmental temperatures encountered in midseason near Barrow, males of T. carinifrons and P. hannai are capable of feeble fluttering movement over the tundra surface at best, and do not engage in free flight. When brought into the laboratory and warmed to room temperature they are able to fly. On the Pribilof Islands, males of P. hannai, as well as females, are brachypterous (Tjeder, 1963).

In contrast to vertebrate homeotherms (Bergmann's rule), there is a tendency toward smaller body size in tundra representatives of a number of invertebrate taxa. Mani (1962) cited evidence for alpine insects. Hemmingsen and Jensen (1957) found that mean body length of Tipula arctica in Greenland decreases about 4.5% per 10° increase in latitude. This decrease is, presumably, the result of shorter growing seasons and lower temperatures, which reduce growth rate at higher latitudes. Thus, life cycle length and adult body size are both evolutionary responses to length and temperature of the growing season. Since potential fecundity is related to body size, decreased body size means reduced fecundity.
Alternatively, a species might maintain body size by increasing the life cycle length; this, however, increases the period of vulnerability to mortality prior to reproduction. The actual life cycle and morphological characteristics of any tundra species probably represent a compromise between considerations of fecundity and probability of survival in maximizing individual reproductive success.

Arctic mosquitoes offer a conspicuous contrast to the trend of prolonged life cycles, short adult life span, and morphological reduction of adults seen in many other tundra Diptera. All species, apparently, have annual life cycles. Eggs laid in summer hatch at melt-off as the following spring. Larval development occurs rapidly, leading to pupation and emergence of adults. Corbet and Danks (1973) investigated life cycle characteristics and phenology of the two high arctic mosquitoes, *Aedes nigripes* and *A. impiger*, at Lake Hazen, Ellesmere Island, Northwest Territory. They found that adult activity persisted for over a month after emergence has ceased. Both sexes took flower nectar as an energy source. During this prolonged activity period females were able to complete three or possibly even four gonadotrophic cycles.

The annual life cycle leaves arctic mosquitoes particularly vulnerable to the vagaries of the arctic climate. Cold weather at Lake Hazen during the summer of 1964 led to a severe reduction in egg laying, and hence emergence of adults in 1965 (Corbet and Danks, 1973). Two successive cold seasons could easily lead to extinction of the population. This is far less likely when several generations of larvae (future generations of adults) coexist in the relatively protected environment of the soil at any one time.

Autogeny—completion of ovarian development and egg laying without the benefit of a blood meal in biting flies—can be considered adaptive reduction of the life cycle. Corbet (1967) observed that both *Aedes impiger* and *A. nigripes* at Lake Hazen could lay reduced complements of eggs if deprived of a blood meal. This facultative autogeny gives individuals the advantage of high fecundity if a blood meal can be obtained, while allowing some amount of reproduction (and continuation of the population) even if poor weather or a shortage of suitable hosts should prevent the taking of a blood meal. *Aedes communis* is apparently always autogenous at Fort Churchill, Manitoba, although further south it appears to be a normal biting species (Hocking, 1960). Eight of the nine black fly species in arctic Canada are autogenous, as are the tundra species of *Culicoides* (Diptera: Ceratopogonidae) (Downes, 1965). Thus, if harrassment by biting flies becomes an annoyance in arctic tundra, one need only think of what it might have been but for autogeny!

One of the two antarctic midges, *Belgica antarctica*, is wingless, while the other, *Parochlus steinernii*, is winged. These species are believed to have life cycles of about 1 year, but with considerable flexibility, depending upon local circumstances and variation in seasons (Wirth and Gressitt, 1967; Peckham, 1971).

The life cycles of tundra microarthropods—mites and Collembola—remain to be investigated. Janetschek (1967) found the antarctic springtail *Gomphiocephalus hodgsoni* overwintering in all stages, with the possible exception of eggs. He concluded, on the basis of a statistical analysis of population size distribution, that the time needed to reach sexual maturity (minimum generation time) was 38.5 days at Cape Crozier; allowing two generations per season, and 49.2 days at Mount England, where one generation was completed per year. The full life cycle, however, extended over two seasons at Cape Crozier and three seasons at Mt. England. Peterson (1971) reported that this species may complete two generations in “good” summers, and only one generation in others. He found individuals overwintering in all stages, including the egg.

The life history of *Aeropedelhus clavatus*, a high altitude grasshopper occurring in the Colorado Rockies, was investigated by Alexander and Hilliard (1964). They found an obligate diapause, apparently involving more than one season, in the egg stage; however, postembryonic development and the life cycle are completed in a single season. The total period from hatching to adult is approximately 6 weeks. This is accomplished, in part, by a reduction in the life cycle from five juvenile instars, typical of most Acrididae, to only four. This is seen in other boreal Acrididae. Apparently this group adapts to tundra conditions by reduction rather than prolongation of the life cycle. The scarcity or absence of grasshoppers from tundra may indicate the limitation of this mode of adaption.

Extended life cycles have been observed in at least two subarctic beetles (Kauffmann, 1969, 1971); however, in these species the life cycle involves extension of adult life. Arctic carabid beetles overwinter in both larval and adult stages near Barrow, indicating a life cycle involving 2 or more years. The vast majority of arctic insects overwinter as larvae or prepupae, and perhaps the tendency to overwinter as adults limits the success of Coleoptera under arctic conditions.

3. Resistance to winter cold. In general, cold-climate insects may pass the winter in either of two manners: they may supercool, and thus avoid the formation of ice crystals, or they may freeze solid but, by various mechanisms, avoid tissue damage due to freezing. The actual physiological mechanisms are far from understood. The subject has recently been reviewed by Asahina (1969), Salt (1969), and Cloudsley-Thompson (1970), and will not be treated in detail here.

Several temperatures are of importance to poikilotherm under cold
important to tundra invertebrates. In the relatively warm 1972 summer season at Barrow (Figure 2) the daily minimum air temperature was 0°C or below on 29 days in June, 16 days in July, 9 days in August, and continuously following 7 September. Soil temperature at −2 cm, however, remained continuously above 0°C following thawing. This offers another important reason for the preponderance of soil-dwelling over surface-active invertebrates in arctic climates.

Resistance to cold in alpine invertebrates has not been investigated. Where temperatures may fall well below freezing each night due to radiation to a clear sky we might expect to find retention of supercooling or freezing-resistance mechanisms during the summer season. Schmoller (1971) has observed that the alpine spider and beetle fauna may be divided into day-active and night-active species which experience very different micro-climates. These differences may be reflected in adaptations relating to cold tolerance and metabolism.

4. Metabolic adaptations. The degree of metabolic adaptation to tundra conditions remains in dispute. Scholander et al. (1953) found only slight physiological adaptation in the metabolic rate (displacement of the metabolic rate/temperature curve toward cold temperatures) of terrestrial poikilotherms near Barrow, Alaska. They concluded that the most important adaptive mechanism was microhabitat selection. Aquatic invertebrates, in contrast, showed considerable but incomplete metabolic adaptation, relative to temperature and tropical forms. McAlpine (1965a) noted that most adult insects were collected walking rather than flying on Elr Ringnes Island, Northwest Territory, and Downes (1962) observed that bumblebees can forage and pollinate flowers in this way. In 1971 we collected large numbers of the moth Barrovia fasciata on sticky boards placed on the ground surface at Barrow; K. W. Philip (personal communication), collecting by conventional means at the same time, obtained none. Their distribution around the outside of each board indicated that the moths had walked onto the surface. These observations suggest that an evolutionary adjustment of behavior has occurred in response to reduced metabolic capacity.

Still, the existence of chill-coma temperatures below the tissue freezing point indicates that some adjustment of physiological capacity in response to low temperature must have occurred. We have found that arctic tundra crane fly larvae and adults, Sa'didae, and Enchytraeidae respire actively at +0.5°C Tilbrook and Block (1972) found cold adaptation, particularly in the immature stages, in the antarctic collembole Cryptopygus antarcticus, since these had a higher metabolic rate than temperate Collombola at comparable temperatures.

Metabolic rate or respiration, as measured by oxygen consumption
Larvae of both crane fly species show increasing \( Q_{10} \) values at low temperatures.

Hofsvang (1972) calculated linear regression lines for oxygen consumption and temperature for all stages of *Tipula excisa*; however, the goodness of fit was largely a result of the small number of data points involved. Calculations made from his data show that the relationship is more nearly exponential for adults, and falls off rapidly for early instar larvae.

Tilbrook and Block's (1972) data for the antarctic collembole *Cryptopygus antarcticus* show this tendency in the extreme. For the smallest size class (mean = 3.0 \( \mu \)g) the ratio of increase in metabolic rate is greater between 2\(^\circ\) and 6\(^\circ\) C than between 6\(^\circ\) and 10\(^\circ\) C. Metabolic rate changes 11.47-fold over the entire 8\(^\circ\) temperature range. For animals in the second size class (10.2 \( \mu \)g) the ratio of metabolic increase is independent of temperature, as predicted by the exponential model. For the three larger size classes \( Q_{10} \) is less between 2\(^\circ\) and 6\(^\circ\) C than between 6\(^\circ\) and 10\(^\circ\) C, indicating a steeper than exponential rise in metabolic rate with temperature. However, for the largest size class (92.8 \( \mu \)g) the metabolic increase is only 1.79-fold over the 2\(^\circ\)–10\(^\circ\) C range. Thus, in these insects the smallest animals show a large metabolic decline at low temperatures, while the largest animals show very little metabolic decline at low temperatures. Later data (Block and Tilbrook, 1975) collected from animals taken directly from the field showed that respiration rate of the smallest size class rose sharply as temperature was increased from 0\(^\circ\) to 5\(^\circ\) C, then fell slightly between 5\(^\circ\) and 10\(^\circ\) C. Animals of intermediate size gave a linear response to increasing temperature, while respiration rate of the largest animals fit the exponential model. The overall response from 0\(^\circ\) to 10\(^\circ\) C was greatest for the largest size classes, in contradiction of the data reported earlier for animals maintained in laboratory culture (Tilbrook and Block, 1972).

Thus, while the data are sparse, there appears to be a pattern of changing metabolic response to temperature as development proceeds. The significance of this can only be interpreted in relation to other parameters of the bioenergetic budget. The total amount of energy ingested is equal to the energy egested as feces, \((F)\) plus the energy of assimilation \((A)\):

\[
I = F + A
\]

the assimilated energy is partitioned into energy of metabolism or respiration, \((R)\) and production \((P)\):

\[
A = R + P
\]
Thus:

\[ I = F + R + P \]

Temperature and body size may affect each of these parameters. If low temperature has a severe depressing effect on the ability of an individual to ingest or assimilate energy, for example, then depression of the metabolic rate would be adaptive. Adaptation to tundra conditions involves the ability to maintain a positive energy balance (positive \( P \), or \( R \) less than \( A \)) at low temperatures, rather than simply maintaining a high metabolic rate.

We might imagine three distinct patterns in the metabolic response of an invertebrate animal to temperature (Figure 4). (I) The rate of assimilation may be greater than the rate of respiration at all temperatures. Such an organism could grow and complete the life cycle under both temperate and cooler arctic or alpine conditions. (II) The rate of assimilation increases more rapidly with increasing temperature than does respiration rate. Thus, the amount of energy available for growth increases with temperature. Such an organism may be unable to complete the life cycle at low temperatures because of an unfavorable energy balance. (III) The rate of respiration increases more rapidly with temperature than does assimilation. Such a pattern might occur in an obligate arctic or alpine organism that is able to maintain a positive energy balance only at low temperatures.

A particularly useful metabolic parameter is the ratio of energy of growth or production to respiration (\( P/R \)). MacLean (1973) found that the \( P/R \) ratio of the arctic crane fly *Pediccia hannai* is near 1 in the early larval stages, but falls to a very low value in the fourth and final instar. Thus, the accumulation of energy in growth becomes increasingly difficult. This may contribute to the long larval life of this species, rather than low temperature per se. At 0.5° and 5°C, metabolic rate is appreciable; however, no larval growth could be detected after 2 months in the laboratory at 5°C. In keeping with this, larval growth in the field is poor early and late in the season, when soil temperature is less than 5°C. Thus, *Pediccia hannai* appears to show the type II (Figure 4) metabolic pattern. If this is so, this species owes its existence in the arctic to the warmer days of midsummer and the occasional clear, warm days on which soil temperature rises above normal. The species would be an opportunist, tolerating arctic conditions but depending upon more temperate conditions for growth. Dalinjus (1965) and Peckham (1971) observed that maximum microhabitat temperatures have the greatest effect on the maturation of Antarctic microarthropods.

Hofsvang (1973) found that the \( P/R \) ratio of *Tipula excisa* in arctic-alpine Norway was 1.97 during the summer season, but 0.82 over the life cycle as a whole. The difference was in part explained by the fact that respiration continues during the winter although growth ceases.

In contrast, according to O. A. Saether (quoted in Hågvar and Østbye 1973), many larvae of the chironomid subfamily Orthocladiinae seem to grow only at temperatures below 5°C, and may be at rest during the summer when water temperature rises above 5°C. Thus, they seem to follow the type III (Figure 4) pattern with, perhaps, an obligate quiescence during the summer to minimize the period of negative energy balance. This represents an interesting and important mode of physiological adaptation to tundra conditions, and we should hope that additional data will soon be forthcoming.

Tilbrook and Block (1972), as discussed above, found the greatest metabolic depression with cold temperature in Collombola of the smallest size class. If the ability to secure and process food (i.e., assimilation) declined equally with temperature in all size classes, the smaller individuals would be at a distinct advantage at low temperature relative to the \( P/R \) ratio. They would be able to maintain a favorable individual energy balance (positive \( P \)) at lower temperatures and thus would tend toward the type I, or even type III (Figure 4) metabolic pattern. The relationship of the various parameters of the bioenergetic budget to temperature clearly requires investigation in temperate as well as tundra organisms if we are to understand physiological adaptation to the environment.

The integrated output of the bioenergetic budget under natural conditions is seen as growth rate. Haufe and Burgess (1956) determined the growth response of mosquito larvae to temperature near Ft. Churchill, Manitoba, by comparing development periods in pools of different temperature. The three species with geographic ranges extending into the tundra (*Aedes nigripes*, *A. impiger*, and *A. communis*) are the first mos-
quitoes to emerge each season at Churchill; hence, they complete
development with the smallest heat sum. The lowest threshold for development (34°F = 1.2°C) occurs in A. impiger. The thermal constant (days ×
degrees above the threshold) required to complete development in this
species is comparable to subarctic species; however, the low threshold
allows larvae of A. impiger to quickly complete development following
spring melt-off, even under arctic conditions. The other truly high arctic
mosquito, A. nigripes, requires a heat sum of about 20% greater than
that required by A. impiger (Corbet and Danks, 1973). Aedes nigripes is
the only mosquito occurring at Barrow and on Spitzbergen, indicating
that geographic range of arctic mosquitoes is not determined by metabolic
(or bioenergetic) adaptation alone.

Haufe and Burgess (1956) also reported a difference in thermal con-
stant between males and females of a given species. This allows males to
emerge several days before females. At lower temperatures, however,
the effect upon development time of this difference in thermal constant is
magnified and the difference in emergence dates of males and females is
increased. The absence of subarctic species from some tundra localities
may be due as much to dissynchrony in emergence of the sexes as to
absolute failure of larval development.

5. Timing mechanisms. Two distinct activity rhythms are of signifi-
cance to tundra invertebrates: seasonal and diurnal or diel. These have
been studied best in relation to the emergence and swarming activities of
adult insects, especially Diptera. Research on rhythms in other functions
and invertebrate groups might prove quite rewarding.

Snow melt in tundra locations usually occurs shortly before the
summer solstice, when photoperiodic cues are at a minimum. In many
species, at least of Diptera, development proceeds rapidly following snow
melt and the thawing of tundra ponds, so that the bulk of adult insect
activity occurs early in the season before a distinct pattern of alternating
light and dark periods develops. Emergence of adults of a species can be
strikingly synchronous. MacLean and Pitélka (1971) found that the peri-
od of time encompassing the middle 67% of the emergence of three
species of crane flies near Barrow varied from 3.8 to 11.6 days. The latter
occurred in an unusually cold season when the emergence was protract-
ed. Hadley (1969) observed a comparable degree of synchrony in a
small moorland crane fly, Metopiothrips ater, in Great Britain. Danks and
Oliver (1972) observed the emergence of a given species of aquatic chiron-
omids at Lake Hazen and found that emergence of a given species was
highly synchronized within a pond, but varied between ponds based
upon depth and exposure. Similar results for mosquitoes were reported

by Corbet and Danks (1973). Haufe and Burgess (1956), as discussed
above, used the variation in emergence patterns of mosquitoes in dif-
ferent ponds at Ft. Churchill to calculate temperature threshold and
thermal constant required for development.

Between-season and between-habitat variations in the timing of
emergence are clearly related to temperature. In the cold 1969 and 1973
seasons at Barrow, emergence was delayed and protracted in duration
(MacLean and Pitélka, 1971; MacLean and Clement, in progress). At
Lake Hazen, Danks and Oliver (1972) observed that (1) the time of first
emergence from the same pond in different years was related to pre-
emergence water temperature; (2) emergence was later and more syn-
chronous from deeper, colder water; and (3) emergence occurred later in
deeper, colder ponds. They concluded that emerging individuals were at
the same developmental stage (fully grown, final instar larvae) at the
beginning of each season, and pupated without further feeding immediately
following the thaw. Thus, timing of emergence is determined by meta-
bolic temperature summation, and synchrony results from the similarity
in thermal regime which the pupae experience. No external cues, such as
photoperiod, are necessary. Downes (1965) suggested that synchro-
nization in the absence of external cues is most easily achieved in spe-
cies that pupate at or soon after the melt-off. This may in part explain
the observation that many arctic insects emerge early in the season, be-
fore the thermal peak of the season.

At Barrow crane fly pupae are not found until shortly before emer-
gence begins; however, the emergence patterns fit the hypothesis of
Danks and Oliver. It appears that the mechanism initiating pupation is
easily triggered. Final instar larvae of Tipula corinifrons removed from
the tundra in August 1973, after nightly freezing of the tundra surface
had begun, initiated pupation when kept under warmer conditions (10°C
following brief exposure to room temperature during weighing) for a pe-
riod of time (L. E. Clement, research in progress). It appears that a par-
cular cohort of fourth instar larvae destined to complete the life cycle
at the next emergence period (and this does not include all of the larvae
in the fourth instar at a time; MacLean, 1973) is set for pupation by
freezing conditions. Pupation is then triggered by the next occurrence of
warm soil conditions. This is not likely to occur in fall because of the
shallow sun angle and diminishing photoperiod.

Downes (1963) suggested that dormancy in arctic insects may be a
direct response to prevailing temperature, rather than a diapause con-
trolled by more remote stimuli. This would favor rapid resumption of
growth when favorable conditions return in spring. It is apparent, how-
ever, that the external cue—freezing temperatures—is of great impor-
tance in timing the life cycle. Danks and Oliver (1972) refer to this as a "diapause" although, at least in crane flies, the obligate cessation of activity usually associated with diapause is lacking. Hofsvang (1973) found that larvae of *Tipula exixa* collected from Norwegian alpine tundra in winter became active after a few seconds warming in the palm of the hand. If this is truly a diapause, (a) it involves only temperature as both initiating and terminating stimulus, without the necessary intervention of photoperiod (the short days of fall and winter); and (b) it is easily broken. Such a mechanism is unlikely to occur in alpine tundra species; there, warm days may alternate with freezing nights throughout the summer season, and we may expect that preparation for pupation and emergence is set by some other environmental change.

There is a natural attempt to attribute synchronous emergence to the compression of events in the short arctic summer. Other factors may be equally or more important. The short functional adult life span makes prompt location of a mate particularly important. Mate location may be made more difficult by wing reduction in one or both sexes and the absence of mating swarms, and by low temperature which may decrease mobility. These factors make emergence into a high density population of particular selective advantage, thus selecting for intraspecific synchrony. MacLean and Pitelka (1971) point out that intense predation upon adult insects by birds (West and Norton, this volume) would select against insects emerging into a low density population. This would select for both intra- and interspecific synchrony of emergence as a predator swamping mechanism. Interspecific synchrony in emergence is certainly a conspicuous feature, at least among Diptera, in arctic tundra.

The diel periodicity of emergence seems to result from a direct response to environmental temperature (Corbet, 1966; Danks and Oliver, 1972). Air temperature is likely to be fluctuating around the lower threshold for mating activities, and changes in light intensity may not accurately indicate conditions above the ground or water. Further, diel changes in light intensity at high latitudes are relatively small. Syrjänäki (1968) found the mean ratio between night and day light intensities during July on Spitzbergen (78° N) to be 1.4. Such variations may be masked by changes in cloud cover.

Danks and Oliver (1972) found that the threshold for pupal ecdisis for chironomids at Lake Hazen (approximately 7°C) was higher than the threshold for pupation (4° or 5°C) or larval development (approximately 1°C). This promotes both seasonal and diel synchrony of emergence, and assures that the adults do not emerge into an environment in which they cannot fly. Such a mechanism leads us to expect the largest emergence on the first warm day following a sequence of cool (less that 7° for

chironomids at Lake Hazen) days. Our observations of crane fly emergence at Barrow support this hypothesis.

In some cases, particularly on warm days, Danks and Oliver (1972) recorded a bimodal pattern of emergence. The first peak occurred as the rising temperature passed the threshold for ecdisis. The second, later peak was attributed to accelerated pupal development at the maximum daily temperature.

For insects that have already emerged, some synchronization of activity via photoperiodism may occur. Thus, Corbet (1966) interpreted small morning and afternoon peaks in mosquito activity at Lake Hazen as vestiges of dawn and dusk maxima that characterize mosquito activity further south. Syrjänäki (1968) believed that photoperiodism may play a part in the midday maximum in activity of the chironomid *Smittia extrema* on Spitsbergen. *Trichocera borealis* (Diptera: Trichoceridae) showed no diel periodicity in swarming activity. Papi and Syrjänäki (1963) showed that the diel fluctuations in light intensity at 69° N are sufficient to set the sun orientation rhythm in a wolf spider, *Lycosa fluviatilis* (Araneae: Lycosidae). The meaningful question, as Danks and Oliver (1972) pointed out, is not whether organisms can detect the slight summer diel light intensity changes at high latitudes, but whether light is a useful measure of what is important for their existence.

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References


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