Seasonal Adaptations in Arctic Insects[1]

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Synopsis.   Many insect species live in the arctic and show a wide range of adaptations to its extreme severity and seasonality. Long, cold winters are met, for example, by cold hardiness and choice of protected sites. Cold hardiness includes both widespread tolerance to freezing and extreme supercooling ability, as well as unusual responses in a few species, such as lack of typical cryoprotectants. Adaptations to short, cool summers include activity at low temperatures, selection of warm habitats and microhabitats, melanism and hairiness coupled with basking behaviour, and prolonged or abbreviated life cycles. Diapause ensures that many species emerge early in summer, with brief synchronized reproduction that maximizes the time for offspring development before winter returns. Some species overwinter in sites that thaw earliest in spring, even if they are relatively exposed in winter. Other adaptations respond to year-to-year variability: for example, prolonged diapause can provide insurance against unsuitable summers. All of these adaptations are co-ordinated. For example, cold hardiness relies on physiological and biochemical adaptations but also on habitat choice and timing. Because the adaptations are complex, predicted climatic warming probably will have unexpected effects. In particular, an increase in temperature that increases summer cloud when sea ice melts would likely reduce temperatures for insect development and activity, because sunshine provides critical warmth to insects and their microhabitats. Changes in moisture will also be important. Moreover, responses differ among species, depending especially on their microhabitats. The complexity of the responses of insects to arctic conditions reinforces the need for research that is sufficiently detailed.

INTRODUCTION

The seasonal adaptations of insects to arctic conditions are especially instructive because more species of insects than of other kinds of animals live in the arctic. Although the arctic fauna is much reduced compared to temperate zones, more than 2,200 species of insects and their relatives have been reported from north of tree line in North America, and as many again probably remain to be discovered (Danks, 1981, 1990). Reduction in the fauna reflects the fact that only species with the requisite adaptations can survive in the north (*cf.*, Downes, 1962, 1964). Such adaptations tend to be shared by related taxa, and the insect fauna consists chiefly of groups favoured by habitat, marked cold tolerance, use of widely available food resources and other traits (*e.g.,* Danks, 1990).

The arctic environment constrains insects in somewhat different ways than for the conspicuous vertebrates. In particular, insects are cold-blooded and so (with few exceptions) they cannot withstand cold by generating heat. Moreover, their small size means that they are affected by conditions at a very small scale within the microenvironments that they occupy. For example, sunshine increases the temperature of some plant parts to more than 20°C above ambient (*e.g.,* Sørensen, 1941; Corbet, 1972; Mølgaard, 1982). The surface soil is warmer than the lower layers. High arctic ponds warm up rapidly as sunshine heats the bottom, but cool down slowly because of the high specific heat of water, and so remain above 12°C for some weeks during a summer with mean air temperatures of only 5°C (Oliver and Corbet, 1966; Corbet, 1972). Most arctic insects live in these warmer sites.

Aspects of arctic climates that challenge insects include severity (cold temperatures, limited heat accumulation for growth), seasonality (wide differences between summer and winter), short term unpredictability (such as the potential for sudden changes in temperature, even freezing events, during summer) and variability (year-to-year changes in the factors governing development and survival) (Danks, 1999). The relative richness of faunas from different polar zones suggests that severity has the greatest influence on whether or not particular species can live in a given zone (Danks, 1999).

Arctic insects thus require ways of coping especially with long, cold winters and short, cool, unpredictable summers. In turn, because mean temperatures may be close to the limits for insect life even in summer, these species must be able to survive even when conditions vary greatly about the mean. Many relevant earlier studies are reviewed by Danks (1981), so that specific citations here emphasize later work.

Some adaptations of arctic insects are shared with those of alpine zones (Mani, 1962, 1968; Sømme, 1989; Sømme and Block, 1991), but alpine habitats differ in several important ways, such as different seasonal and daily patterns of temperature and a greater supply of allochthonous food (Danks, 1999).

ADAPTATIONS

Adaptations to long, cold winters

One set of adaptations serves to withstand the cold and dryness of winter (Table 1). Although not all of

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TABLE 1. *Adaptations of arctic insects to long, cold winters.*

Adaptation	Notes	Example
Physiological and structural		
Cold hardiness	A complex of physiological adaptations	Different species have different sets of adaptations
	More than one system: frozen or unfrozen, with cryoprotectants	
	Ongoing dehydration prevents freezing in a few species	Some springtails and other invertebrates
	Unexpected patterns in some species, e.g. absence of normal cryoprotectants	
	Requires energy	
	Freezing may conserve energy and water	
Desiccation resistance	Cold habitats are dry	Gall sawflies
	Many physiological adaptations	Different species have different sets of adaptations
	Small individuals are most vulnerable	Many arctic insects are small
Cocoons	Potential protection against inoculative freezing	Some moths
	Protection against wind-borne ice crystals	Species that overwinter in exposed sites
	Protection against mechanical damage by ice formation in aquatic habitats	Chironomid midges
Ecological		
Choosing protected sites	Snow insulates overwintering sites	Most species
	Coverings may protect against desiccation, and against wind-borne ice crystals	
Timing		
Diapause	Suppressed development favours resistance, conserves energy, prevents premature emergence, and is crucial to life-cycle timing	Many species, though difficult to demonstrate from short field seasons

the elements of cold hardiness that are known in insects as a whole (reviews by Sømme, 1982, 1999; Zachariassen, 1985; Cannon and Block, 1988; Storey and Storey, 1988; Block, 1990; Lee and Denlinger, 1991; Danks, 1996, 2000*b*; Bale, 2002) have been reported from the arctic, the major trends have been confirmed there, together with some interesting variants. Some arctic species are able to survive in frozen soil for several years (*e.g.,* springtails and some mites survived in soil when kept below −20°C in the laboratory for 4 years: Coulson and Birkemoe, 2000).

Physiological adaptations for cold hardiness have been most studied. Most arctic species are freezing tolerant: they survive winter in a frozen state with much of the water converted to extracellular ice. For example, the freezing-tolerant fly *Heleomyza borealis* survives temperatures down to −60°C (Worland *et al.*, 2000). Even in frozen insects, a core of water associated with biological structures (''unfreezable water,'' usually between 10 and 30%: Block, 1996, 2002) remains unfrozen. Frozen insects use energy and lose water more slowly than unfrozen ones at the same temperature (Irwin and Lee, 2002).

Most species use cryoprotectants of low molecular weight, such as glycerol and other polyhydric alcohols, to protect tissues during freezing and thawing (for arctic species see Ring, 1981, 1982, 1983; Ring and Tesar, 1980, 1981; Kukal *et al.*, 1988*b*, 1989; Kukal, 1991). Typical freezing-tolerant species also make nucleators to initiate freezing at relatively high subfreezing temperatures (Duman, 2001), thereby avoiding the very

rapid growth of ice crystals that takes place once the first crystal forms in cold supercooled fluids. Nucleation is time dependent, which makes tolerance of freezing rather than supercooling a common strategy in the long arctic winter.

However, some arctic species (and most temperate ones) supercool instead, remaining unfrozen even at extremely low temperatures, down to −62°C in some arctic gall midges (Ring, 1981, 1983; Ring and Tesar, 1981; Miller, 1982; Miller and Werner, 1987). Typical insect species depend on various cryoprotectants to lower the supercooling point and protect supercooled tissues (references above, and see Ring 1981 for arctic species), and also evidently have effective means of masking the nucleators that are present. Antifreeze proteins (see below) enhanced by glycerol and other low molecular weight substances can play such a masking role (Duman, 2002).

Some temperate insects use another method of cold hardiness, large peptide or protein molecules (termed antifreeze proteins or thermal hysteresis proteins) that act by inhibiting the growth of ice crystals at the ice-water interface (Duman, 2001), although perhaps they constrain internal nucleation sites rather than embryonic ice crystals (Wilson and Leader, 1995). These compounds are most effective at temperatures close to freezing, and have not been reported in arctic insects during winter.

A few arctic species with permeable cuticles resist freezing by tolerating dehydration, as in the springtail *Onychiurus arcticus* (Worland, 1996; Holmstrup and

Sømme, 1998; Worland *et al.*, 1998). Water is lost from the supercooled animal to surrounding ice in winter, because the vapour pressure of ice is lower than that of supercooled water at the same temperature. In *O. arcticus* and some other invertebrates, this loss ensures that the concentration of solutes always remains high enough at a given temperature to prevent freezing (Holmstrup and Westh, 1994; Holmstrup and Zachariassen, 1996; Sømme and Birkemoe, 1997; Holmstrup and Sømme, 1998; Holmstrup *et al.*, 2002).

Some arctic insects show unexpected patterns of cold hardiness. The beetle *Xylophagus* sp. is freezing tolerant although it lacks the usual cryoprotectants (Ring, 1981, 1983). Several freezing-tolerant arctic species have very low supercooling points (Ring, 1981, 1983), and the alpine beetle *Pytho deplanatus* can survive freezing even after extreme supercooling to −54°C (Ring, 1982), despite the fact that most freezing-tolerant species are killed when freezing follows extreme supercooling. Finally, it is worth noting that synthesis of cryoprotectants requires energy, a potential constraint that may be significant in the resource-limited arctic (*cf.*, Danks *et al.*, 1994). Degradation of mitochondria has been reported in one arctic species, the lymantriid moth *Gynaephora groenlandica* (Kukal *et al.*, 1989; Levin *et al.*, 2003), and may be linked to energy balance as well as to cold hardiness.

Cold air contains little moisture and so can dry out the organisms exposed to it, especially those that are small. Therefore, during all kinds of cold hardiness many insects are also desiccation resistant (*e.g.,* Bennett *et al.*, 2001; Williams *et al.*, 2002). Physiological adaptations inactivate part of the water content ("osmotically inactive water") and the behaviour of water in cells and tissues is controlled especially through solute production and ion transport (Danks, 2000*a*). Some of the low molecular weight solutes known for cryoprotection, notably trehalose (see Ring and Danks, 1998), play similar roles in protection against desiccation (Danks, 2000*a*).

In a few species the cocoons built for winter contribute to cold hardiness, at least by preventing inoculative freezing by keeping ice crystals away from the surface of the body. Arctic as well as temperate chironomid midges build special winter cocoons that are distinct from those made in summer. The winter cocoons are less flimsy and are tightly applied to the characteristically folded bodies of the larvae (Danks, 1971, fig. 6). These cocoons have been supposed to protect against mechanical damage caused by the expansion of water as it freezes around the larvae. In arctic ponds, larvae become visibly dehydrated before freezing, apparently as water is drawn out of them at the bottom of the pond where solutes accumulate, forced out of the thickening layer of frozen surface water. Such dehydration before freezing probably enhances cold hardiness (see Zachariassen, 1985 for general discussion).

The microenvironment of overwintering sites is at least as important in allowing winter survival as are physiological adaptations. Some organisms that live all their lives in the relatively stable soil have few special adaptations and survive unfrozen despite relatively high supercooling points, but typical insects choose sheltered sites for the winter, apparently using precise features of light, temperature, moisture, touch, gravity and other factors (Danks, 1991). Snow is an important insulator against low temperatures, and a cover of snow or vegetation also helps to resist desiccation and to protect immobile overwintering individuals against lethal abrasion by wind-blown ice crystals. Therefore, many arctic insects overwinter in plant clumps, under stones, in shallow depressions, and so on. Nevertheless, a surprising number of insects especially in the high arctic overwinter in relatively exposed rather than sheltered areas. For example, some moth caterpillars overwinter on exposed ridges (Danks and Byers, 1972; Danks, 1981). Overwintering mosquito eggs are placed on the warmest south-facing sides of ponds which thaw earliest (Corbet and Danks, 1975). Such habits allow development to begin as early as possible in the year and reproduction to be completed before winter returns. Evidently, for many species the need to complete the life cycle is more critical than avoiding the coldest places in winter.

Adaptations for overwintering are coordinated, or at least coincide, with suppression of development. Some species are merely quiescent, and thus active whenever temperatures are warm enough, but most others appear to enter diapause, a programmed suppression of development (typically cued by photoperiod, temperature or other factors) that starts well in advance of the adverse conditions (Danks, 1987*a*). Many observations hint at the presence of diapauses in arctic insects. Such a program provides a resting stage that tends to resist adverse conditions, reduces metabolism to low levels and so conserves energy, prevents unseasonable warm spells from restarting development (to the adult, to another stage, or to a vulnerable moulting stage) that would be fatal near the end of the season, and helps to resynchronize individuals towards simultaneous spring emergence. Such diapauses may even occur several times during the life cycle. For example, caterpillars of the high arctic geometrid moth *Psychophora sabini* moult each spring to the next instar (Danks and Byers, 1972). Apparently, diapauses stop development so that overwintering takes place at the end of each instar. Again, larvae of the fly *Heleomyza borealis* pupate and emerge only after temperatures rise following a low-temperature stimulus below about −15°C (Worland *et al.*, 2000).

Adaptations to short, cool summers

A second set of adaptations reflects the fact that summers are short and cool (Table 2). A number of species have limits (thresholds) of activity close to freezing. Two arctic mosquito larvae are active at temperatures near 1°C (Haufe and Burgess, 1956), several degrees lower than in their temperate relatives. High

TABLE 2. *Adaptations of arctic insects to short, cool, unpredictable summers.*

Adaptation	Notes	Example
Physiological and structural		
Low activity thresholds	Some species are active even close to 0°C	Several kinds of mites, spiders, springtails and insects
Endothermy	Heat generated by activity of flight muscles	Bumble bees warm up to fly
Increased metabolic rate	Basic level of metabolism is elevated, to speed development at low temperatures	Relatively few species, e.g. a small number of springtails, beetles and aquatic arthropods
Rapid development	Some groups develop more rapidly, especially if small in size	Mosquitoes, some other flies
Summer cold hardiness	Frost possible even in summer	Many high arctic species
Autogeny	Some biting flies develop eggs rapidly without a blood meal	Some mosquitoes, black flies
Melanism	Dark colour absorbs heat	Many species
Hairiness	Hairs trap absorbed heat	Larger insects, such as hairy caterpillars
Reduced antennae, enlarged genitalia, brachyptery, aptery	Correlated with ground rather than aerial mating	Some chironomid midges
Ecological		
Choosing early thawing sites	Allows reproduction before winter returns	Moth larvae on exposed ridges; mosquito eggs on south-facing pond margins
Selection of warm habitats	Locally favourable sites, at various scales, are occupied	Butterflies and other insects
Opportunistic activity	Activity when warm enough regardless of the time of day	Many species
Basking	Specific behaviours to absorb solar radiation	Butterflies, mosquitoes, other species
Timing		
Multi-year life cycle	Development exploits limited resources of food and heat over several years	Many species
Abbreviated life cycle	Life cycle completed during a single summer	Aphids, mosquitoes, some psyllids, etc.
Early spring emergence	Reproduction starts as early as possible in the short summer	Chironomid midges, many other species
Brief synchronized reproduction	All offspring are produced relatively early in the year	Many species

arctic bumble bees (which like temperate species can generate heat by "shivering" the flight muscles: Heinrich, 1993; Heinrich and Vogt, 1993) can fly at subzero air temperatures (Bruggemann, 1958).

The basal metabolic rate is increased in a few species (*e.g.,* Scholander *et al.*, 1953; Sømme and Block, 1991). However, there is no such metabolic compensation in many species (review by Danks, 1981, pp. 275–276). MacLean (1975) pointed out that activity is only fruitful if the energy acquired can be assimilated more rapidly than it would be respired, and this may not be feasible at low temperatures. The high Q_{10} shown for the arctic springtail *Onychiurus arcticus* means that individuals of this species can take advantage of small increases in the temperature of their habitats (Block *et al.*, 1994). Moreover, not all habitats are cold (Corbet, 1972; Birkemoe and Leinaas, 2000). Even with metabolic rates comparable to those of temperate species, however, many arctic species develop rapidly: small insects belonging to groups characterized by rapid development, such as aphids and small flies, are relatively well represented in the arctic.

Typical arctic species are more cold hardy in summer than their temperate-zone relatives (*e.g.,* Kukal *et al.*, 1988*b*; Bale *et al.*, 1994). Indeed, freezing temperatures occur in most high arctic sites even during July. The physiological basis of this summer cold hardiness is uncertain (*cf.*, Kukal *et al.*, 1989; Kukal, 1991), but perhaps antifreeze proteins (which are most effective at temperatures near freezing) will be found in some species (Danks *et al.*, 1994). Rapid cold hardening in response to cold might also be expected in summer. It has already been reported from many temperate species, as well as some antarctic ones (Worland and Convey, 2001). Rapid cold hardening allows individuals to acquire cold hardiness within a few hours when exposed to decreasing temperatures.

Short summers reduce many potential resources. In typical biting flies the female feeds on vertebrate blood, which is used as a source of nutrients for egg development. In the arctic the shortness of the season is coupled with the fact that the numbers of hosts may be limited, and a greater proportion of biting flies than in temperate regions is autogenous: such species develop their eggs from larval food stores without feeding on blood in the adult stage. For example, about 2.5% of black flies as a whole are obligately autogenous (even lacking mouth parts competent for blood-feeding) but 25% of species from northwestern North America are autogenous (Currie, 1997) as are most of the arctic species (Danks, 1981). The two species of high arctic mosquitoes have several options for egg development, including both obligate and facultative autogeny (Corbet, 1967). Some individuals develop

eggs immediately without blood-feeding; some feed on blood if a host is available within a few days, but without a host they revert to autogenous egg production. Of course, many more eggs can be developed if a blood meal has been taken. The high arctic species *Aedes impiger*, for example, develops an average of about 3 eggs by facultative autogeny and 6 eggs by obligate autogeny, but an average of about 50 eggs when blood fed (Corbet, 1967). These options maximize potential reproduction in cold and unpredictable environments.

Several structural features are relatively well developed in arctic species, including melanism and hairiness (examples cited in Danks, 1981). Melanic individuals are suffused to a greater or lesser extent with the black pigment melanin, which allows them to absorb solar radiation more effectively. Hairs, especially when the insects are large, allow the absorbed heat to be retained because the warm boundary layer of air next to the dark cuticle is protected from disturbance (*e.g.,* Kevan *et al.*, 1982). The temperature of pupal cocoons of the moth *Gynaephora groenlandica* is increased by both orientation (Kukal *et al.*, 1988a) and structure. An outer pale layer and an inner dark layer serve to enhance heating of the cocoons in sunshine (Kevan *et al.*, 1982 as *G. rossi*; Lyon and Cartar, 1996).

Even when it is too cold or windy for flight, mating on the ground is still possible, and structural changes in antennae, wings and genitalia are associated with ground-mating in some arctic nematocerous flies with temperate relatives that mate in the air, as in some species of chironomids (review by Danks, 1981, p. 274; Butler, 2000).

Ecological adaptations to acquire heat in summer are as important as physiological or structural ones. Many species choose early thawing sites for overwintering (see above). During summer, nearly all species choose relatively warm sites amongst those available. At a larger scale, butterflies occupy sheltered valleys or gullies warmed by the sun, and they frequent extensive patches of darker vegetation (*e.g.,* Kevan and Shorthouse, 1970). At a smaller scale, many species sit in warm microsites, such as the south-facing aspect of surface irregularities, or the centres of parabolic flowers that track the sun during the day (Kevan, 1975, 1989). The arctic-alpine bug *Nysius groenlandicus* lives in the warmest and driest places (Böcher and Nachman, 2001).

The daily pattern of warm days and cooler nights familiar in temperate zones is replaced in the arctic by continuous summer daylight with a much less rigid pattern of warmth and coolness. Arctic species from some characteristically nocturnal or crepuscular groups, such as noctuid moths, are active during the day. Unlike the strictly programmed diel activity of many temperate insects, most arctic insects are active whenever it is warm enough independent of the time of day. For example, daily emergence of midges from

shallow ponds is governed by water temperature (Danks and Oliver, 1972b).

Site selection and specific behaviours, coupled with structural attributes, facilitate heat gain. Mosquitoes and many other insects bask in flowers, orientating their bodies to absorb solar radiation. In arctic butterflies, several types of basking behaviour are known, depending on the location of heat-absorbing dark pigments and how they are exposed (Kevan and Shorthouse, 1970). During dorsal basking, wings are held open with the darker uppersides facing the sun (as in *Boloria* fritillaries). During lateral basking, the wings are closed and their darker undersides slanted to face the sun (as in *Colias* species). In feeding blue butterflies (Lycaenidae), the wings are held slightly open to allow body basking, augmented by the hairiness of the dark body. Ground contact may be added, by which heat can be absorbed from warm dark substrates (as in *Boloria*). Caterpillars of high arctic *Gynaephora* moths also bask, adjusting the orientation of their bodies and sheltering from wind to maintain an optimal temperature (Kevan *et al.*, 1982, 1988a; Kukal, 1990, 1991; Bennett *et al.*, 1999a). Arctic bumble bees fly close to the ground, potentially profiting from heat radiated from the soil (Richards, 1973, p. 132).

Many adaptations reflect needs for the life cycle as a whole. Large species cannot complete development in one season, and so must feed and grow in summer and survive at the larval stage through several successive winters. Detailed studies have established that life cycles last 7 years or more in some arctic moths and midges (Ryan and Hergert, 1977; Butler, 1982; Kukal and Kevan, 1987; Kevan and Kukal, 1993; Morewood and Ring, 1998). Various crane flies, spiders, springtails and other species have life cycles of 3 to 5 years (MacLean, 1973; Lantsov, 1982; review by Danks, 1981). In many other species not yet studied in detail there is evidence of long life cycles, such as simultaneous occurrence of multiple instars, or a moult each spring by several independently synchronized instars (*cf.*, *Psychophora sabini* above). Larvae of the moth *Gynaephora groenlandica* rapidly increase or decrease metabolic rate many fold in response to feeding or starvation (Bennett *et al.*, 1999b), thus maximizing feeding but conserving energy during the short season.

Alternatively, life-cycle requirements can be met by accelerating summer development to complete a generation each year, allowing a fixed resistant stage such as the egg or adult to overwinter, as in arctic species of mosquitoes, bumble bees and some other groups (*e.g.,* Richards, 1973; Böcher, 1975; MacLean, 1983; Winchester *et al.*, 1993). In the high arctic aphid *Acyrthosiphon svalbardi*, the fundatrix that hatches from the overwintering egg produces sexual morphs (and some viviparae that produce sexual morphs), which in turn produce overwintering eggs (Strathdee *et al.*, 1993). The many intervening summer generations of parthenogenetic viviparae typical of temperate aphids have been eliminated (although recently the unexpected alate morph has been reported: Hodkinson *et al.*,

TABLE 3. *Adaptations of arctic insects to long-term variability.*

Adaptation	Notes	Example
Prolonged diapause	Provides insurance against severe years	Probably many species, though relatively few studies
Life-cycle patterns	Life cycles constructed in various ways to offset arctic constraints, especially through delays	See text
Parthenogenesis	Mating activity is unnecessary	Many species, including midges, caddisflies, mayflies
	Well adapted genotypes buffered against change	

2002). One of the high arctic species of bumble bees is a nest parasite of the other, eliminating the worker caste and so reducing the time required for nest establishment (Richards, 1973).

Insects that feed on temporally restricted parts of the host plant, such as new leaves or flowers, must match their development to that of the plant (Danks, 1987*b*). Arctic psyllids that attack willow catkins apparently can make such a match only in the central part of the host-plant range (MacLean and Hodkinson, 1980; MacLean, 1983).

Several life-cycle adaptations ensure that particular stages are present at the appropriate season. Even when larval development is flexible, the timing of adult emergence is closely controlled in many species. In particular, species in the arctic normally emerge early in the summer, and many are related to species of the temperate spring; the "late season" equivalent in temperate faunas is absent. Such precipitate emergence allows reproduction to be completed during the short summer. In high arctic chironomid midges only those larvae that have completed feeding in a given year emerge the following spring; all other larvae, even if they must feed just a little after the winter, remain dormant the rest of the summer and emerge as early as possible in the following season. These species were termed "absolute spring species" by Danks and Oliver (1972*a*). Reproduction of the springtail *Hypogastra tullbergi* is confined to a short period following snow melt, after a diapause that ends following exposure to cold (Birkemoe and Leinaas, 1999). For further examples see Danks (1999, table 3). Such traits lead to a brief period of synchronized reproduction early in the year, maximizing the likelihood that offspring will reach the overwintering stage before winter returns.

Adaptations to long-term variability

A third set of adaptations reflects the need to cope with variability over more than one season (Table 3). Certainly each individual summer or winter is important, but insects are also adapted to the long-term likelihood of climatic events such as a series of worse than average or better than average summers, or an occasional very cold year.

Some individuals of many insect species from unpredictable habitats (deserts, the cones of trees, etc.) remain in diapause for several successive years, providing insurance (bet hedging) against years when most of the population would emerge into circumstances with few resources or extreme weather (*cf.*, Danks, 1987*a*, table 27). In the arctic, relatively limited observations have confirmed that species from several different taxa, such as muscid and anthomyiid flies, olethreutid moths and tenthredinid sawflies (Chernov, 1978), include individuals that remain in diapause for several years, so that the phenomenon must be widespread.

In the crane fly *Pedicia antennata* and in some chironomid midges, delay is facultative, whereby prepupae do not pupate and develop to the adult stage if the summer is very cold, but instead remain as prepupae for another winter (Oliver, 1968; MacLean, 1973). Other patterns of activity have been supposed to correspond with seasonal constraints such as a decline in food plant quality as the season progresses, or the presence of parasitoids (*e.g.,* Kukal and Kevan, 1987; Danks *et al.*, 1994).

Finally, parthenogenesis is more common in insects from the arctic than in faunas elsewhere. Arctic species of mayflies, scale insects, midges, caddisflies and other groups are known to be parthenogenetic (Danks, 1981). Parthenogenesis not only removes the necessity for mating when summer conditions are cool and unpredictable, but also buffers the population against risk (Downes, 1965, pp. 270–271). Responding too rapidly to conditions that change (*e.g.,* a series of very warm summers) by short term selection after recombination would remove well adapted genotypes in favour of those that might be vulnerable when more typical severe conditions return. Predominant or universal parthenogenesis reduces or prevents the recombination that follows sexual reproduction.

POTENTIAL RESPONSES TO ENVIRONMENTAL CHANGE

Given these adaptations for the arctic environment, what would be the expected results of change? As already noted, insects survive in the arctic through many coordinated adaptations, such as dark pigments and basking, or long life cycles, repeated cold hardiness and energy use. Moreover, the effects of change on arctic insects are filtered through their relationships with habitat, especially because solar radiation is so important for increasing the temperatures of microsites or of individual insects. Therefore, the effects of change will be complex and vary among species (*e.g.,* Danks, 1992; Hodkinson *et al.*, 1998).

In such a context, the changes in climate that have been predicted are inexact because they are based chief-

ly on mean air temperatures. Warming trends in climate should permit additional species to survive farther north or augment populations of existing species, because a dramatic effect might be expected from even a modest increase in temperature when current temperatures operate so close to the limits for life for insects and the effective growing season is so short (*cf.*, Block and Convey, 2001). However, the expectation for insects that there will be more generations per year (*e.g.,* Strathdee *et al.*, 1993; Bale, 1999), more stable and persistent populations, and addition of species currently prohibited by low heat sums is too simple. Winters may be shorter but they will still be very cold, while concomitant changes in insulating snow cover will have other effects on these poikilotherms. Summers may be longer, but this change will not necessarily improve conditions for insects because the microhabitat temperatures and moisture relationships important to insects do not all coincide with changes in mean ambient temperature (Danks, 1992). For example, climatic warming in the Canadian western high arctic, where islands in the Arctic Ocean are relatively small, is likely to melt permanent or seasonal sea ice to expose more open ocean. In turn, this open ocean will probably lead to increased cloudiness in summer. The resulting reduction in sunshine would make insect microhabitats cooler and thus more than offset any increase in mean air temperature. The insect fauna of the northwestern arctic is already much less diverse than that of the east because of greater summer cloud cover (Danks and Byers, 1972). Effects in the eastern arctic, where the islands are larger, may well be different.

Again, the high arctic is a polar desert, where moisture as well as cold constrains life. The effects of climatic warming on local moisture regimes are not easy to predict, and information for arctic mites and springtails suggests that these species are more likely to be influenced by changed moisture regimes than by changed temperatures (Hodkinson *et al.*, 1996; Webb *et al.*, 1998; Hayward *et al.*, 2000).

It will also be difficult to predict the ecosystem effects of climatic change. Insects are engaged in surprisingly complex food webs even in the highest arctic (*e.g.,* Bliss, 1977; Danks, 1980, fig. 3). Herbivorous insects are much reduced in more severe sites, dropping out much faster than the plants on which they could feed (Danks, 1987*b*, 1993). Many insects depend on plants for warm microclimates, nectar or pollen, and many arctic plants are at least partly insect pollinated (Kevan, 1972, 1973). Climate change will therefore lead to changes in the dynamics of herbivores and pollinators, but we have only general indications of what might happen (*e.g.,* Danks, 1992). Species that live above ground and below ground are affected very differently (Bale *et al.*, 1997; Hodkinson *et al.*, 1998). Most arctic plants are low and clump forming and rely for seasonal growth or seed development on sunshine. They would be affected in some of the same ways as insects by changes in cloud cover.

Insects normally respond to changed environments chiefly by movement to or from areas that are newly or no longer suitable rather than by new adaptations. For instance, relatively rapid movements following the retreat of glaciers in North America have been shown from insect fossils (Matthews, 1979; Ashworth, 1996; Matthews and Telka, 1997). The short life cycles and the potential for dispersal of many insects allows a rapid response to environmental changes. Insects of various kinds dispersing by air into arctic areas from sources many hundreds of kilometers away have been reported by both land-based and ship-based observers (Elton, 1925; Lokki *et al.*, 1978; review by Danks, 1981, pp. 349–350; Coulson *et al.*, 2002*b*). Arctic soil arthropods survive for more than 2 weeks in or on seawater, an ability that would allow prolonged ocean transport (Coulson *et al.*, 2002*a*).

Humans have introduced other species, although except for some soil forms few establish out of doors in polar climates (Danks, 1981; Pugh, 1994). Climatic warming might favour introduced species because they rely on warmer (though moister) habitats than most of the native fauna (Gabriel *et al.*, 2001; Chown *et al.*, 2002).

There are no direct data to assess the potential effects of contamination by air-borne pollutants on arctic insects. However, evidence elsewhere shows that even modest contamination, for example by pesticides or heavy metals, has a variety of sublethal effects, including slowed development (partial review by Rosenberg *et al.*, 1986). Because rapid development during the short summer is so important for arctic insect life cycles, even a small reduction in growth rate might have severe consequences. Insects with long life cycles are potentially vulnerable too, because damage to the population or its habitat removes many year-classes simultaneously.

CONCLUSIONS

The information summarized in Tables 1–3 shows that arctic existence is generally possible only through multiple adaptations through the life cycle, involving co-ordinated physiological, structural, ecological and timing features (Danks, 1981; Chernov and Lantsov, 1992). For example, effective cold hardiness comes not just from physiological responses such as the build up of cryoprotectants, but also from the choice of microhabitats, life-cycle timing and dormancy, and energy budgeting. By the same token, the major constraint for a given insect species may not be the most conspicuous one. The need for early spring development and reproduction outweighs the need for additional protection from cold in many species, which therefore overwinter in early thawing but relatively exposed sites. Most life cycles are not merely flexible in order to take advantage of any opportunity for development (Danks, 1999). Rather, at least at some stages they are closely structured, because critical parts of the life cycle such as reproduction must coincide with favourable conditions. This need for precise timing of the reproductive stage generally outweighs the alter-

native strategy of simply developing whenever it is warm enough.

Given the close and co-ordinated relationships of insects with the constraints of arctic environments, especially low temperatures and their effects on metabolism, the short growing season, and the resulting importance of sunshine in raising microhabitat temperatures, future changes such as the climatic warming that has been predicted will have complex and sometimes counter-intuitive effects. For example, changes in moisture regimes affect the suitability of habitats for insects through both the amount and seasonal supply of moisture and the duration of sunshine controlled by cloudiness. Such changes are driven by global circulation patterns but also by more local effects such as island size, relief and the extent of sea ice in summer. Warming that increases cloud cover decreases the temperature of important insect habitats.

This brief review shows that research on insect adaptations in the arctic can give valuable insights and is favoured by the fact that many species with different ways of life occur there. It confirms that potential changes in arctic systems are more complex than has often been appreciated, suggesting in turn that the proper assessment of environmental changes in natural systems must include relatively sophisticated biological analyses. In particular, the premature use of simple ''indicators'' will almost certainly prove misleading.

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