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Temperature/Development Relationships and Life History Strategies of Arctic *Gynaephora* Species (Lepidoptera: Lymantriidae) and Their Insect Parasitoids (Hymenoptera: Ichneumonidae and Diptera: Tachinidae), With Reference to Predicted Global Warming

by

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A Dissertation Submitted in Partial Fulfillment of the Requirements for the Degree of

DOCTOR OF PHILOSOPHY

in the Department of Biology

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ABSTRACT

Increases in temperature and precipitation predicted under global warming are expected to be most pronounced and thus have their greatest impact on ecosystems at high latitudes. Insects constitute a major component of the foodwebs of terrestrial ecosystems and should be among the first organisms to show noticeable responses to predicted global warming, especially in the Arctic where climatic conditions are often limiting. However, interactions among species must also be taken into account. The genus *Gynaephora* Hübner (Lepidoptera: Lymantriidae) is represented in North America by two species, *G. groenlandica* (Wocke) and *G. rossii* (Curtis), and their geographic distributions overlap broadly across the Canadian Arctic. Previous studies have examined the biology, ecology, and physiology of these two species and have revealed many adaptations to the Arctic environment, but the immature stages of these insects have been misidentified even in recently published reports. Both species are found at Alexandra Fiord, Ellesmere Island, a High Arctic oasis largely isolated by expanses of ocean and icecap, and the population of *G. groenlandica* at this site is thought to be limited mainly by parasitoid-induced mortality rather than by climatic conditions.

Field observations, surveys, and temperature-manipulation experiments were conducted at Alexandra Fiord during the spring and summer of 1994, 1995, and 1996; laboratory rearing was conducted under controlled conditions at the University of Victoria in the spring of 1996 and 1997. Immature stages of both species of *Gynaephora* were described and illustrated, and all species of insect parasitoids using *Gynaephora* species as hosts at Alexandra Fiord were identified. Life histories and seasonal phenologies for *Gynaephora* species and their insect parasitoids were elucidated from field studies, and temperature/development relationships for selected stages of most of these species were derived from laboratory rearing. The results of field studies and laboratory rearing were compared and used to formulate predictions about the responses of these insects to predicted global warming.

Immature stages of the two species of *Gynaephora* are easily distinguished by differences in the colour patterns, form, and overall length of the larval hairs and by the structure of their cocoons. Both species of *Gynaephora* complete metamorphosis and reproduction within a single growing season but spread larval development over a number of years. In *G. groenlandica*, seven larval instars and annual moulting combine to produce a seven year life cycle whereas *G. rossii* develops through six larval instars at a rate of two or three moults per year, resulting in a three or four year life cycle.

The parasitoid complex at Alexandra Fiord consists of three primary parasitoids, *Hyposoter pectinatus* (Thomson) (Hymenoptera: Ichneumonidae), *Exorista* n.sp. (Diptera: Tachinidae), and *Chetogena gelida* (Coquillett) (Diptera: Tachinidae), and one hyperparasitoid, *Cryptus leechi* Mason (Hymenoptera: Ichneumonidae). All of the parasitoids are univoltine, although *H. pectinatus* may undergo delayed development in some cases, and each of the primary parasitoids relies primarily on a single larval instar for hosts whereas the hyperparasitoid attacks the primary parasitoids during their metamorphosis.

Seasonal phenologies of the parasitoids provide optimal access to new hosts but parasitoid-avoidance strategies of *Gynaephora* larvae ensure that a proportion of their populations escape parasitism. Laboratory rearing showed that the relative timing of host and parasitoid seasonal phenologies is maintained over a broad range of temperatures; therefore, temperature increases predicted under global warming are unlikely to have any great effect on host-parasitoid interactions. However, increased cloudiness associated with the predicted increase in precipitation might have profound effects resulting from lower ground-level temperatures caused by a lack of solar heating. The extent of this effect is uncertain but might lead to reproductive failure in *Gynaephora* species, with similar repercussions for the insect parasitoids.

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DEDICATION

This dissertation is dedicated to my wife, Petra Morewood, for sharing my love of the Arctic and of critters great and small. Without her support and encouragement, this dissertation might never have been completed.

INTRODUCTION

The Greenhouse Effect and Global Warming Scenarios

The greenhouse effect and global warming are not new issues. Indeed, the first quantitative discussion of changes in the earth's surface temperature resulting from changes in atmospheric carbon dioxide was published more than 100 years ago by Arrhenius (1896, cited by Handel and Risbey 1992) and the first quantitative discussion of anthropogenic increases to the greenhouse effect was published less than 50 years later by Callendar (1938, cited by Handel and Risbey 1992). These authors attempted to explain climatic changes on geological time scales, such as the occurrence of ice ages, and the trend of increasing temperatures observed early in this century, respectively, in terms of changes in the atmospheric concentration of carbon dioxide (Handel and Risbey 1992). The latter analysis was largely ignored due to the onset of World War II and the beginning of a cooling trend in the 1940s; however, within a couple of decades, concern about anthropogenic global warming resurfaced, leading to the publication of a vast amount of literature on the subject. For example, the annotated bibliography of Handel and Risbey (1992) included more than 600 publications and, according to the authors, these represented only a small selection of the many thousands that had been published up to that time. The proliferation of published information related to global warming has continued to increase unabated.

The greenhouse effect itself is indisputably real. Carbon dioxide and certain other trace gases in the earth's atmosphere, such as methane and nitrous oxide, are largely transparent to incoming shortwave radiation from the sun but absorb longwave radiation that is reradiated from the surface of the earth. The end result of this phenomenon is that average temperatures at the earth's surface are approximately 33°C warmer than they would be if these gases were not present in the atmosphere (Sagan and Mullen 1972; Jones and Henderson-Sellers 1990; Schneider 1993). The current debate and resulting concerns, then, are not about whether the greenhouse effect exists but rather whether anthropogenic increases in the atmospheric concentration of carbon dioxide and other trace gases will

cause a significant increase in the greenhouse effect. Such an increase has been termed global warming and the extent and potential effects of this global warming have been the subject of much discussion and debate.

The main impetus for predictions of global warming is the fact that atmospheric concentrations of carbon dioxide are increasing, primarily due to human activities such as the burning of fossil fuels and to a lesser extent deforestation. Atmospheric concentrations of carbon dioxide have risen from approximately 280 parts per million by volume (ppmv) in preindustrial times (Goodness and Palutikof 1992) to approximately 365 ppmv today (Weaver[1], personal communication 1999) with well over half of this increase occurring since the middle of the 20th century (*cf.* Bolin *et al.* 1986). This rapid rise in carbon dioxide, to levels that appear to be unprecedented in recent earth history, has led to the suggestion that the most serious aspect of global warming for biological systems is its potential rapidity compared to past climatic changes (Schneider 1993), although there is evidence that past climatic changes may have occurred much more rapidly than is generally believed (Broecker 1987; Cuffey *et al.* 1995).

Predictions about the extent of global warming that might result from increased atmospheric concentrations of carbon dioxide have been generated mainly through mathematical modelling. The models used have ranged from zero-dimensional, time-independent, energy balance models that simply provide an overall average temperature, through three-dimensional, time-dependent, atmospheric general circulation models (GCMs), to coupled atmosphere-ocean GCMs (Cubasch and Cess 1990; Schneider 1992). Most of the modelling has been conducted using atmospheric GCMs that contain relatively simple representations of the oceans, the use of coupled atmosphere-ocean GCMs having been limited by the much greater computer power required to run such models (Cubasch and Cess 1990). However, simulations conducted using coupled models were generally consistent with simulations produced by the simpler atmospheric GCMs (Gates *et al.* 1992) and the constraint imposed by available computer power has been greatly diminished in recent years (Weaver, personal communication 1999).

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A major drawback to predictions of climate change based on GCM simulations is that these are not necessarily accurate. At least 27 different GCMs have been developed by climate modelling groups around the world (Gates *et al.* 1996), but most of the scenarios of climate change resulting from increased carbon dioxide have been derived from only six of them (Maxwell 1992). These GCMs produce results that differ from one another and none of them is entirely accurate in simulating the current climate, even in a broadly averaged way (AES 1994; Gates *et al.* 1996). Although GCM simulations are generally consistent in a qualitative way, both among models and in comparison to current climatic conditions, their quantitative differences may be significant. Differences in simulated temperatures, for example, may be only a few degrees (Gates *et al.* 1990), but this is the same order of magnitude as the overall increase in temperature predicted in global warming scenarios. Simulation of other climatic factors, such as precipitation, is even less accurate and less consistent among models (Gates *et al.* 1990; AES 1994). This is not to say that these models are inherently faulty; rather, the inaccuracies and variability among models simply reflect the fact that current knowledge of, and ability to simulate, the complexities of the climate system, while steadily improving, is still incomplete (Cubasch and Cess 1990; Gates *et al.* 1996).

Increased atmospheric carbon dioxide will almost certainly result in higher temperatures at and near the surface of the earth; the questions that remain are related to the magnitude and distribution of the increase in temperatures. The overall consensus is that the average global surface air temperature will increase by between 1°C and 3.5°C by 2100 relative to 1990, with a "best estimate" of 2°C based on a "mid-range" scenario for emissions (Houghton *et al.* 1996; Kattenberg *et al.* 1996). Precipitation is also expected to increase overall, due to increased evaporation associated with higher temperatures; however, the distribution of precipitation is much more variable and decreases have been predicted for some areas (Mitchell *et al.* 1990). Other effects are even more uncertain and lie, for the most part, within the realm of speculation. "However, *prevailing uncertainty does not mean that the problem can or should be dismissed*" (Bolin *et al.* 1986, original emphasis).

Implications of Global Warming for Insects

The prospect of global warming has generated great concern about its potential impact on biological systems. This concern has focussed mainly on ecosystems as they relate to economic interests such as agriculture and forestry (*e.g.* Warrick *et al.* 1986), but has also extended to biological systems with less direct economic potential, such as arctic ecosystems (Chapin *et al.* 1992; Riewe and Oakes 1994; Henry and Molau 1997; Heal *et al.* 1998). Insects loom large in any consideration of terrestrial ecosystems because of their taxonomic and numerical abundance, their importance in foodwebs, and their impact on agriculture, forestry, and other human interests. Furthermore, because they are ectothermic and have relatively short generation times and often great dispersal capabilities, insects might be expected to respond rapidly to climatic warming.

Changes in temperatures and precipitation associated with global warming are expected, over the long term, to result in large-scale shifts of ecosystems, although such shifts may be limited by other factors such as geology and soils (Rizzo and Wiken 1992). It should also be noted that large-scale shifts of ecosystems would not occur uniformly but would produce changes in ecosystem structure and composition due to differences in the responses and dispersal capabilities of different species (*e.g.* Pielou 1991). Similarly, the geographic distribution of insect species would be expected to expand northward, although this would depend on the availability of suitable resources such as foodplants. Although plants may not disperse as rapidly as insects, this will not necessarily hinder insect range expansion because, in some cases at least, the current ranges of insects are more restricted than those of their potential host plants (*e.g.* MacLean 1983). In addition, many insects are generalist predators or scavengers and therefore would be less limited by the availability of specific food sources (Schwert and Ashworth 1990). In any case, the most immediate responses should occur where the insects already exist.

The most certain effect associated with global warming due to increased atmospheric concentrations of carbon dioxide is higher temperatures. Temperature has long been considered the dominant factor controlling insect development and survival (Messenger 1959). The geographic distribution of an insect species may be limited by cold

temperatures in winter, which can be lethal, or by summer temperatures that are insufficient for the insect to complete its development and reproduce. In multivoltine species, summer temperatures and the length of the growing season may limit the number of generations that the insects can complete each year. Therefore, increased temperatures associated with global warming would be expected to allow insects to expand their range into higher latitudes and, in some multivoltine species, increase the number of generations that develop in areas where they currently occur.

Collier *et al.* (1991) and Porter *et al.* (1991) examined the potential response of insects to predicted global warming, both cases involving multivoltine pests of agriculture in Europe. Using a simulation model designed to predict development of the cabbage maggot, *Delia radicum* (L.) (Diptera: Anthomyiidae), Collier *et al.* (1991) found that an increase of 3°C in daily mean temperatures would allow the insects to become active about one month earlier than under current conditions, but that an increase of 5°C or more was required for an additional generation to complete development. Porter *et al.* (1991) compared the thermal requirements for development of the European corn borer, *Ostrinia nubilalis* (Hübner) (Lepidoptera: Pyralidae), with a GCM-produced scenario for global warming in Europe and concluded that this insect could expand its range northward as much as 1220 km and complete an additional generation in most of its current range.

An important consideration in assessing the effects of increased temperatures on insects is the effects of such temperature increases on organisms with which the insects interact, such as foodplants and natural enemies (Watt *et al.* 1990; Cammell and Knight 1992). Of particular importance for insect herbivores is the relative effect of increased temperatures on development of the insect *versus* development of its foodplant because many species of insect herbivores are limited by declining nutritional quality of the plant as it matures. A striking example of this was reported by Ayres (1993), wherein a 1°C increase in daily mean temperature enhanced growth and survival of larvae of the autumnal moth, *Epirrita autumnata* (Borkhausen) (Lepidoptera: Geometridae), feeding on birch trees to the extent that their rate of population increase was up to 2.9 times greater than it was under ambient temperatures. Functional responses of insect predators to increased

temperatures tend to be enhanced to a greater extent than the numerical response of their prey (Cammell and Knight 1992) and thermal requirements for development of many insect parasitoids are known to differ from those of their hosts (Uvarov 1931, cited by Lawton 1994; Messenger and Force 1963; Force and Messenger 1968; Campbell *et al.* 1974; Nealis *et al.* 1984; Ravlin and Haynes 1987; Lajeunesse and Johnson 1992; Mao and Kunimi 1994), such that higher temperatures often tend to favour the natural enemies. These types of responses indicate the need to take interactions among species into account.

Global Warming and Insects in the Arctic

Effects of global warming, in terms of increased temperatures and changes in precipitation, are expected to be most pronounced in polar regions, primarily due to positive feedback from reduced snow and ice cover (Manabe and Wetherald 1980; Robock 1983; Everett and Fitzharris 1998). Maxwell (1992) presented data focussed on the North American Arctic, derived from simulations by four different GCMs that were developed by climate modelling groups in North America. Because the cooling effect of atmospheric aerosols had not yet been incorporated into those models, they tended to overestimate temperature increases, particularly in summer (Gates *et al.* 1996). However, the data they produced might still be taken to represent a "worst case" scenario. In different areas of the North American Arctic, the data presented by Maxwell (1992) indicate summer temperature increases of 1°C to 7°C, averaging 3°C to 4°C, and winter temperature increases of 3°C to 15°C, averaging 7°C to 9.5°C, with intermediate spring and fall values. Simulated changes in precipitation ranged from a 30% decrease to a 70% increase, with 15-30% increases on average. Increases in precipitation were slightly more pronounced in winter and spring than in summer and fall, but were most consistent among models for the fall. Higher winter temperatures and increased precipitation should result in greater snowfall; however, both observational records and GCM simulations indicate that this will not result in a longer duration of snow cover. Rather, higher temperatures should increase snowmelt during winter and lead to a much earlier onset of the main spring melt and this, combined with later freeze-up, could lengthen growing seasons by a month or more (Maxwell 1992).

Increased temperatures, both in summer and in winter, and longer growing seasons might be expected to benefit insects in the Arctic because these changes would tend to ameliorate the constraints imposed by the characteristically low temperatures and short growing seasons.

Life cycles of arctic insects often show modifications that allow these insects to complete their development and reproduce within the constraints imposed by the short growing seasons and low summer temperatures of arctic environments. Danks (1981) considered the key aspects of arctic insect life cycles to be voltinism and phenology. Voltinism refers to the number of generations completed each year or, conversely, the number of years required to complete a generation. Phenology refers to the seasonal position of occurrence of different life stages, most notably, in this case, the reproductive stage and the stages adapted for winter dormancy. The latter are also relevant to voltinism, especially in arctic insects.

Dormancy is known to occur in all life stages of insects, although usually only in a single stage in a given species. Among the endopterygote insects in general, which dominate the arctic fauna, approximately 40% of the species studied enter the state of diapause as larvae (Danks 1987). This predominance of larvae as the overwintering stage is even more pronounced among arctic insects. Danks (1978) calculated that of the 90 species for which the overwintering stage was known, 92% overwintered as larvae at Hazen Camp, Ellesmere Island. The importance for arctic insects of overwintering in the larval stage is that this allows for the life cycle to be extended over more than a single year and this is considered to be a characteristic adaptation of insects to arctic conditions (Danks *et al.* 1994).

In contrast with insects from lower latitudes, which are predominantly univoltine or multivoltine, Arctic insects normally take at least one year to complete their life cycle and the proportion of species that extend their life cycle over more than one year increases with increasing latitude (Danks 1981). In addition to species with prolonged larval stages from high latitudes or high elevations, Danks (1992b) cited many examples, representing several different orders of insects, of speciés in which extension of larval development for more

than one year was correlated directly with low temperature or with increasing elevation or latitude. Overwintering in the larval stage removes the necessity of completing development within a single growing season, which may be risky where the growing season is very short and temperature conditions may be unfavourable, and allows the larval stage to be extended as necessary until development can be completed. For species such as this, higher temperatures and longer growing seasons should enable the larvae to complete more growth and development each year and this might lead to a decrease in overall generation time and an increase in population levels. Kennedy (1994) reported a potential example of this from Signy Island in the Maritime Antarctic. Populations of soil arthropods were sampled in control plots and within cloches that had been in place for one, three, or eight years. Population levels were higher within the cloches than in the control plots and showed a progressive increase with age of the cloches; furthermore, the most abundant species showed an increased proportion of small individuals, suggesting increased reproduction (Kennedy 1994).

In contrast with the above species, which overwinter as larvae and can extend this life stage as required to complete development, some arctic insects can overwinter only in the egg or adult stage and therefore must complete at least one generation each year. Examples of such species include aphids (Homoptera: Aphididae) and *Aedes* mosquitoes (Diptera: Culicidae), which overwinter in the egg stage (Danks 1981), and bumblebees (Hymenoptera: Apidae) and *Hydroporus* diving beetles (Coleoptera: Dytiscidae), which overwinter as adults (Richards 1973 and deBruyn 1993, respectively). Longer growing seasons with higher temperatures would be expected to benefit such species by allowing more individuals to complete development to the appropriate stage. As an example of the converse effect, populations of mosquitoes have been known to decline following unfavourable years (Corbet and Danks 1973). The only experimental study of the effect of increased temperatures on the life history of an arctic insect that has been published to date involved the high arctic aphid *Acyrthosiphon svalbardicum* Heikinheimo (Homoptera: Aphididae), which must develop through two generations to reach the overwintering egg stage (Strathdee *et al.* 1993a). This species also produces a third generation that usually

fails to mature; however, an average increase in temperature of 2.8°C during the growing season allowed the aphid to complete this extra generation, resulting in an eleven-fold increase in the number of overwintering eggs produced (Strathdee *et al.* 1993b). Similar responses might be expected from mosquitoes, individual females of which will produce more than one batch of eggs, given the opportunity. Such species, currently limited by the requirement that they complete at least one generation each year, would be expected to extend their ranges and/or become more abundant in their currently occupied ranges (Danks 1992a).

The comments about species interactions in the previous section also apply to insects in the Arctic, with some modification. Herbivorous insects in general are relatively poorly represented in the Arctic, making up a decreasing proportion of the total insect fauna with increasing latitude (Danks 1990). The decline in diversity of insect herbivores is much greater at high latitudes than the decline in diversity of vascular plants, suggesting that herbivorous insects are limited more by climatic conditions than by the availability and suitability of food resources. In contrast, the Hymenoptera are quite well represented in the Arctic and representation of the family Ichneumonidae, the members of which are almost all insect parasitoids, is second only to the dipteran family Chironomidae in the High Arctic (Danks and Masner 1979; Danks 1981). This suggests that interactions with parasitoids might be an important factor to take into account when assessing the responses of arctic insects to climatic change.

The Experimental Animals

North American *Gynaephora* Species

Members of the genus *Gynaephora* Hübner (Lepidoptera: Lymantriidae) are considered to be adapted to cool temperate and arctic climates (Ferguson 1978; Spitzer 1984), although very little information has been published concerning species not found in North America. These include the type species, *G. selenitica* (Esper), which is native to Europe (Patocka 1991), as well as "a highly endemitic group of [perhaps seven] species

occurring only in the Central Asian Highlands" that have been placed in a separate subgenus, *Dasorgyia* Staudinger (Spitzer 1984). The genus *Gynaephora* is represented in North America by two species, *G. groenlandica* (Wocke) and *G. rossii* (Curtis), which along with *G. selenitica* constitute the subgenus *Gynaephora, sensu stricto* (Ferguson 1978; Spitzer 1984).

The geographic distribution of *G. groenlandica* is almost entirely limited to Greenland and islands of the Canadian Arctic archipelago; that of *G. rossii* includes most of the North American Arctic (excluding Greenland) and Siberia, with isolated populations occurring in alpine areas of Japan, New England, and the southern Rocky Mountains (Ferguson 1978; Mølgaard and Morewood 1996). Japanese populations of *G. rossii* have been given subspecific names (Inoue 1956) but none of these was recognized by Ferguson (1978). Similarly, Ferguson (1978) considered *G. lugens* Kozhantshikov, a name applied to Siberian populations of *Gynaephora* (Kozhantshikov 1950), to be a synonym of *G. rossii*. Russian taxonomists, however, continued to follow Kozhantshikov (1950; Dubatolov[2], personal communication 1996), although a reexamination of morphological characters has recently cast doubt on the distinction between *G. lugens* and *G. rossii* (Dubatolov 1997, and personal communication 1997).

Gynaephora rossii was originally described under the generic name *Laria* Schrank (Curtis 1835) whereas *G. groenlandica* was originally described as belonging to the genus *Dasychira* Hübner (Homeyer 1874). Prior to Ferguson (1978) establishing *Gynaephora* as the correct name for the genus, these species were variously referred to under the generic names *Laria* (Grote 1876; Packard 1877; Scudder *et al.* 1879), *Dasychira* (Anonymous 1892; Skinner and Mengel 1892; Dyar 1896; Nielsen 1907, 1910; Johansen 1910; Henriksen and Lundbeck 1918), and *Byrdia* Schaus (Henriksen 1939; Forbes 1948; Inoue 1956; Munroe 1956; Bruggemann 1958; Downes 1962, 1966; Oliver 1963) as well as *Gynaephora* (Dyar 1897; Gibson 1920; Johansen 1921; Kozhantshikov 1950; Wolff 1964; Oliver *et al.* 1964; Downes 1964, 1965; Oliver 1968). This inconsistency in nomenclature has led to at least one review (Strathdee and Bale 1998) discussing *Byrdia groenlandica*

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and *Gynaephora groenlandica* as different species.

Gynaephora groenlandica has the distinction of ranging to the most northerly point of land in Canada (Ward Hunt Island, 83°N; Downes 1964) as well as northernmost Greenland (Wolff 1964) and is considered to be a high arctic endemic species (Munroe 1956; Downes 1964), whereas *G. rossii* has a typical arctic/alpine distribution; the ranges of the two species overlap broadly across the Canadian Arctic archipelago (Figure 1). *Gynaephora* species are among the largest and most conspicuous terrestrial arthropods found in the Canadian Arctic and early accounts of these insects are numerous, mostly consisting of descriptions and natural history observations (Curtis 1835; Homeyer 1874; Grote 1876; Packard 1877; Scudder *et al.* 1879; Skinner and Mengel 1892; Dyar 1896, 1897; Nielsen 1907, 1910; Johansen 1910, 1921; Gibson 1920; Forbes 1948; Bruggemann 1958). Later authors emphasized the apparent adaptations of these insects and others to the extreme conditions of the arctic environment (Downes 1962, 1964, 1965; Oliver *et al.* 1964; Oliver 1968). More recent studies have investigated the biology, ecology, and physiology of arctic *Gynaephora* species in order to elucidate and understand the various ways in which they are adapted to arctic conditions (Ryan 1977; Ryan and Hergert 1977; Schaefer and Castrovillo 1979(1981); Kevan *et al.* 1982; Kukal 1984; Kukal and Kevan 1987; Kukal *et al.* 1988a, 1988b, 1989; Kukal and Dawson 1989; Kevan and Kukal 1993; Kukal 1995; Lyon and Cartar 1996).

One adaptation to the short arctic growing season that *G. groenlandica* has in common with many arctic insects is a prolonged life cycle with larval development spread over a number of years (Danks 1981, 1992b; Kukal and Kevan 1987; Danks *et al.* 1994). Metamorphosis and reproduction are accomplished within a single summer and require most of the growing season to complete; however, subsequent larval activity is confined to a brief period of about three weeks immediately following snowmelt, after which the larvae spin hibernacula and become dormant until the next spring (Kukal and Kevan 1987; Kukal 1995). Estimates of the length of the life cycle of this species have grown progressively longer from "more than one year" in northeast Greenland (Nielsen 1910) and "probably ... at least three or four years" at Lake Hazen, Ellesmere Island (Downes 1964) through "an estimated 10 years" at Truelove Lowland, Devon Island (Ryan and Hergert 1977) to

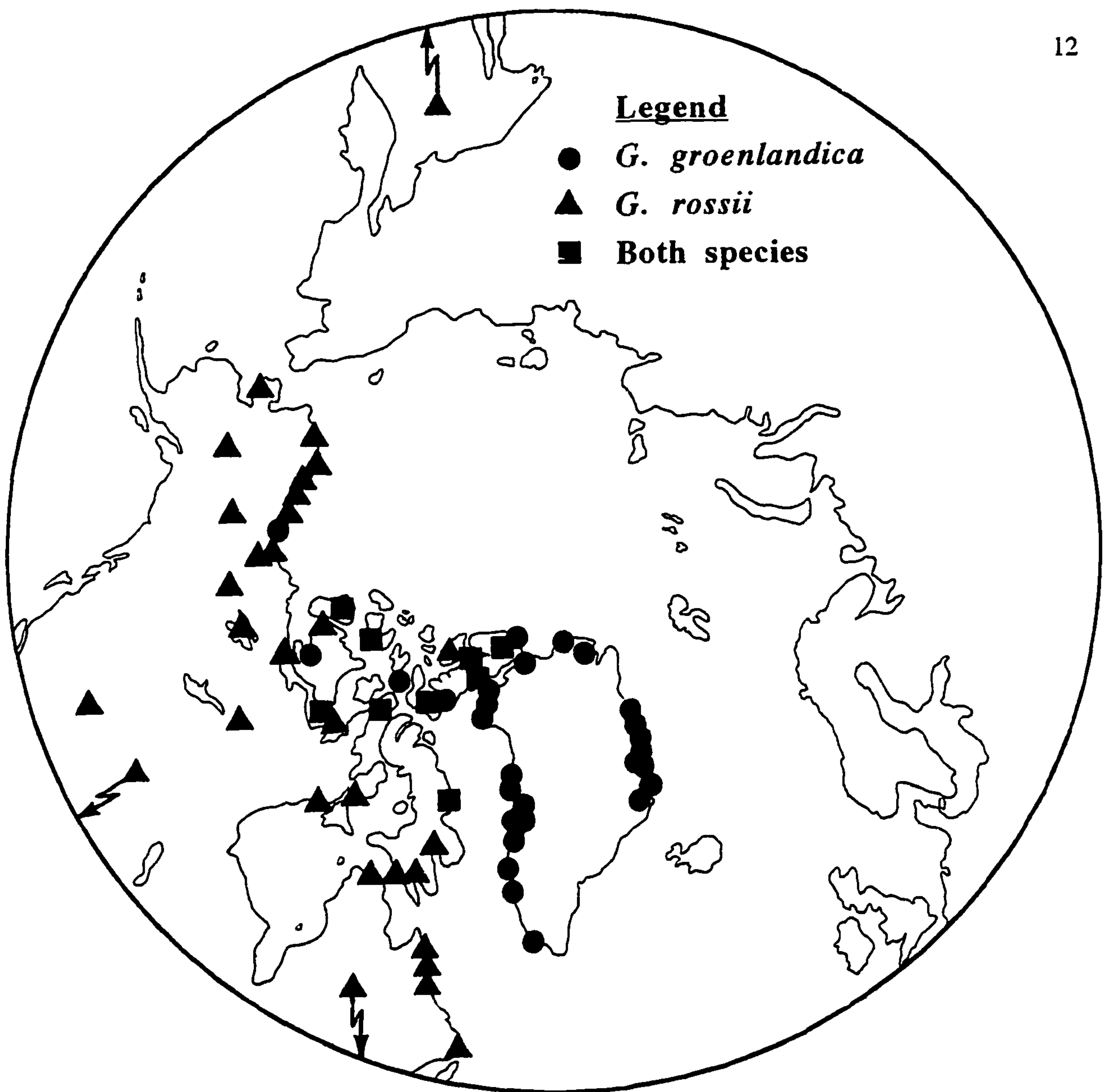

Figure 1. Geographic distribution of *Gynaephora groenlandica* and *Gynaephora rossii*, compiled from Johansen (1921), Wolff (1964), Ryan and Hergert (1977), Ferguson (1978), Lyon and Cartar (1996), and personal observations. *Gynaephora rossii* is also known from Siberia but specific records could not be obtained to include here; symbols with arrows indicate southern alpine populations (see text). Basemap modified from Molau and Mølgaard (1996).

"an estimated 10 years" at Truelove Lowland, Devon Island (Ryan and Hergert 1977) to 14 years at Alexandra Fiord, Ellesmere Island (Kukal and Kevan 1987). This last estimate was the first to be based on detailed observations of development of the insects in the field and the resulting 14-year figure has been cited frequently in subsequent publications. Ryan and Hergert (1977) included both *G. groenlandica* and *G. rossii* in their studies and did not distinguish between the two species (see below), so there is very little published information on the life history of *G. rossii* in the North American Arctic.

Despite the attention that arctic *Gynaephora* species have received, there remains confusion regarding identification of the immature stages. For example, Kevan *et al.* (1982) ostensibly studied *G. rossii* but published photographs of a larva, cocoons, and even an adult that are clearly *G. groenlandica*. Furthermore, Ryan and Hergert (1977) considered the two species to be "identical in their food choices and development, and almost identical morphologically"; however, there are considerable differences, both morphologically and ecologically.

Insect Parasitoids of North American *Gynaephora* Species

A number of insect parasitoids have been previously reported to use North American *Gynaephora* species as hosts (Table 1). Some of these host associations are well-documented; however, others are unconfirmed or otherwise equivocal.

Hyposoter pectinatus (Thomson) (Hymenoptera: Ichneumonidae) is well known as a solitary larval endoparasitoid of *G. groenlandica*, this host association being reported first from eastern Greenland (Nielsen 1907, 1910; Johansen 1910) and later from Alexandra Fiord, Ellesmere Island (Kukal and Kevan 1987). Specimens from Greenland were initially described as a new species, *Limneria Deichmanni* (Nielsen 1907), and later recognized to be conspecific with the European *Anilasta pectinata* Thomson (Roman 1930; Henriksen 1939), which had been reared from *Dicallomera fascelina* (L.) (Lepidoptera: Lymantriidae) (Roman 1930), a palaearctic species very closely related to *Gynaephora* (Ferguson 1978). This parasitoid is currently placed in the genus *Hyposoter* Foerster and is known only from eastern Greenland, Europe, and Ellesmere Island, with

Table 1. Insect parasitoids reported to use North American *Gynaephora* species as hosts.

Parasitoid	Locality	Reference
	Gynaephora groenlandica	
<u>Ichneumonidae</u>		
Hyposoter pectinatus	Eastern Greenland	Nielsen 1907, 1910; Johansen 1910
	Alexandra Fiord, Ellesmere Island	Kukal and Kevan 1987
<u>Tachinidae</u>		
Periscep[illegible] stylata	Eastern Greenland	Nielsen 1907, 1910; Johansen 1910; Henriksen and Lundbeck 1918
Exorista fasciata *	Eastern Greenland	Nielsen 1907; Henriksen and Lundbeck 1918
Peleteria aenea *	Eastern Greenland	Henriksen and Lundbeck 1918
Exorista n.sp.	Alexandra Fiord, Ellesmere Island	Kukal and Kevan 1987
	Gynaephora rossii	
<u>Ichneumonidae</u>		
Amblyteles sp.*	Western Arctic Coast	Johansen 1921
Hyposoter pectinatus *	Western Arctic Coast	Johansen 1921
Pterocormus byrdiae	Yukon & NWT	Heinrich 1956a, 1956b
Nepiera sp.	Mt. Katahdin, Maine	Schaefer and Castrovillo 1979(1981)
Unidentified	Mt. Daisetsu, Japan	Schaefer and Castrovillo 1979(1981)
<u>Tachinidae</u>		
Chetogena gelida	North Coastal Alaska	Malloch 1919
	Mt. Katahdin, Maine	Schaefer and Castrovillo 1979(1981)
	Gynaephora (both species or species not specified)	
<u>Braconidae</u>		
Rogas sp.	Truelove Lowland, Devon Island	Ryan and Hergert 1977
Apanteles sp.*	Ellesmere Island	Mason, cited by Ryan and Hergert 1977
<u>Tachinidae</u>		
Chetogena gelida	Truelove Lowland, Devon Island	Ryan and Hergert 1977
Exorista sp.	Ellesmere Island	Wood, cited by Ryan and Hergert 1977

*Equivocal or unconfirmed records (see text).

G. groenlandica as the only reported host in North America (Carlson 1979; Kukal and Kevan 1987). However, Johansen (1921) mentioned an unidentified ichneumonid parasitizing *G. rossii* on the western Arctic coast of North America which "...spun itself to the ground, the caterpillar skin above protecting it from discovery..." as does *H. pectinatus*, suggesting that this parasitoid might also attack *G. rossii.* This host association was confirmed at Alexandra Fiord in 1992 (Morewood, unpublished) during fieldwork that led to the current study.

Periscepsia stylata (Brauer & Bergenstamm) (Diptera: Tachinidae) is a gregarious larval endoparasitoid reported to parasitize *G. groenlandica* in eastern Greenland (Nielsen 1907, 1910; Johansen 1910; Henriksen and Lundbeck 1918). This species has been reported under the generic names *Peteina* Meigen (sometimes misspelled as *Petina*) and *Petinarctia* Villeneuve, but is currently placed in the genus *Periscepsia* Gistel (Wood 1987; O'Hara and Wood 1998). It is known from eastern Greenland, Sweden, and much of the North American Arctic (Henriksen 1939; Stone *et al.* 1965; specimens in the Canadian National Collection of Insects, Ottawa), with the only host record being *G. groenlandica* in eastern Greenland.

Exorista fasciata (Fallén) (Diptera: Tachinidae) is also a gregarious larval endoparasitoid reported to parasitize *G. groenlandica* in eastern Greenland. It was initially reported from Greenland as *Eutachina larvarum* (L.) (Nielsen 1907) and later reidentified as *Tachina fasciata* Fallén (Henriksen and Lundbeck 1918). This species is currently placed in the genus *Exorista* Meigen and is widespread in Europe and northern Asia (Stone *et al.* 1965; Belshaw 1993; Richter and Wood 1995) where it parasitizes various Lepidoptera larvae, mainly Lymantriidae and Lasiocampidae (Henriksen and Lundbeck 1918; Belshaw 1993; Eichhorn 1996). Kukal and Kevan (1987) reported a new species of *Exorista* parasitizing *G. groenlandica* at Alexandra Fiord, Ellesmere Island. This species is not *E. fasciata*, but the earlier report from Greenland might represent this new species misidentified as *E. fasciata* due to inadequate taxonomic knowledge at that time.

Peleteria aenea (Staeger) (Diptera: Tachinidae) may also parasitize *G. groenlandica* but this host association has not been documented. This species has been reported under

the generic names *Echinomyia* Meigen and *Peleteriopsis* Townsend, but is currently placed in the genus *Peleteria* Robineau-Desvoidy and is known from Greenland and the North American Arctic (Nielsen 1907; Henriksen and Lundbeck 1918; Henriksen 1939; Oliver 1963; Stone *et al.* 1965). The only host association for this parasitoid is the suggestion by Henriksen and Lundbeck (1918) that it parasitizes *G. groenlandica*, although it was not reared from any host.

Johansen (1921) reported an "*Amblyteles* sp." (Hymenoptera: Ichneumonidae) as a solitary endoparasitoid of *G. rossii* prepupae and pupae on the western Arctic coast of North America; however, the palaearctic genus *Amblyteles* Wesmael is not considered to be represented in the North American fauna, all North American species listed under this generic name having been reassigned to various other genera (Heinrich 1961; Carlson 1979). Unfortunately, no specimens reared from *G. rossii* were collected (*cf.* Brues 1919), so the identity of this parasitoid cannot be confirmed; however, the host association, locality, and higher taxonomic status (subfamily Ichneumoninae) suggest that this record might represent the following species.

Pterocormus byrdiae (Heinrich) (Hymenoptera: Ichneumonidae) is the only species of ichneumonid parasitoid reported from *G. rossii* in the Arctic. Known from the northern Yukon and northwestern Northwest Territories, this species was reared from *G. rossii* and originally described as *Ichneumon byrdiae* (Heinrich 1956a). Heinrich (1956b) concluded that it was this species, not *Ichneumon lariae* Curtis, that had been reared from *G. rossii* by Curtis (1835). The latter species is known from Greenland, where one specimen was reared from the pupa of an unidentified species of Noctuidae (Heinrich 1956b), as well as the Northwest Territories, and both species are now placed in the genus *Pterocormus* Foerster (Carlson 1979).

Two species of ichneumonid parasitoids have been reported from alpine populations of *G. rossii*. A single specimen of an undetermined species of *Nepiera* Foerster was reared from a *G. rossii* larva from Mt. Katahdin, Maine, and of 78 *G. rossii* pupae collected from Mt. Daisetsu, Japan, 10 had been killed by an "ichneumonid similar in habits to *Coccygomimus* [Saussure] spp. based on the emergence hole", although no

specimens were obtained (Schaefer and Castrovillo 1979(1981)).

Chetogena gelida (Coquillett) (Diptera: Tachinidae) is a gregarious larval endoparasitoid reported from both arctic and alpine populations of *G. rossii*. This species has been reported under the generic names *Euphorocera* Townsend and *Spoggosia* Rondani, both of which are now considered synonyms of *Chetogena* Rondani (sometimes misspelled as *Chaetogena*) (Wood 1987; O'Hara and Wood 1998). This parasitoid has been reared from puparia "from inside of the cocoons of a lepidopteron, *Dasychirus* sp. (?)", almost certainly *G. rossii*, collected on the north coast of Alaska (Malloch 1919), and from larvae and prepupae of *G. rossii* collected at Alexandra Fiord (Morewood, unpublished) and on Mt. Katahdin, Maine (Schaefer and Castrovillo 1979(1981)). *Chetogena gelida* is also known from Siberia (Ryan 1981; Richter and Wood 1995) where it has been reported to parasitize *G. rossii* (*lugens*) (Chernov 1975, cited by Ryan and Hergert 1977), but it has not been recorded in Japan (Schaefer and Shima 1981).

Ryan and Hergert (1977) reported *C. gelida* reared from cocoons, and an undescribed species of *Rogas* Nees (Hymenoptera: Braconidae) reared from larvae, of both species of *Gynaephora* at Truelove Lowland, Devon Island. They also cited unpublished records of *Exorista* sp. and a species of *Apanteles* Foerster (Hymenoptera: Braconidae), almost certainly now placed in the genus *Cotesia* Cameron (Sharkey[3], personal communication 1997), as parasitoids of *Gynaephora* on Ellesmere Island, noting that they did not find these parasitoids at Truelove Lowland (Ryan and Hergert 1977). The former is almost certainly the undescribed species of *Exorista* reported by Kukal and Kevan (1987) from Alexandra Fiord, but the latter probably represents a spurious host association. There are specimens in the Canadian National Collection of Insects in Ottawa labelled as "probably" from *Gynaephora*, based on the fact that they were reared from cocoons found in association with a *Gynaephora* cocoon. Larvae of *Cotesia* emerge from their hosts and spin their cocoons elsewhere, however, and at Alexandra Fiord their cocoons have been found on willow leaves and under small stones and they have been reared from larvae of Noctuidae and Nymphalidae but not Lymantriidae (Morewood,

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unpublished).

The only reported hyperparasitoids of the parasitoids of North American *Gynaephora* species are the gregarious "chalcid larvæ" (Hymenoptera: Chalcididae?) mentioned by Johansen (1921) as parasitizing pharate adults of *C. gelida* within their puparia on the western Arctic coast of North America, and *Cryptus leechi* Mason (Hymenoptera: Ichneumonidae) (Morewood 1996), the occurrence of which will be reported in some detail here.

The Study Site

The site selected for field studies, and for the collection of insects for laboratory studies, was Alexandra Fiord (78°53'N 75°55'W) on the east coast of Ellesmere Island (Figure 2) in the Canadian Arctic. This site has been subject to a considerable amount of ecological research (*cf.* Svoboda and Freedman 1994) and also is subject to ongoing studies as part of the International Tundra Experiment (ITEX), a collaborative network of researchers working at arctic and alpine sites with the overall objective of understanding the responses of tundra vegetation to global warming (Molau and Mølgaard 1996; Henry and Molau 1997; Hollister 1999).

The Alexandra Fiord study site consists of a small (about 8 km^2) lowland valley bounded by glaciers to the south, upland polar desert and fellfield to the east and west, and the fjord itself to the north. It is described as a "polar oasis", noted for its relatively lush vegetation compared to the surrounding polar desert (Freedman *et al.* 1994), and is known to support populations of both species of *Gynaephora*, although *G. groenlandica* appears to be far more abundant there than *G. rossii* (Morewood 1994). Due to the isolation of this site, being almost completely surrounded by expanses of ocean and icecap, ecological changes that might occur with global warming are likely to be predominated by direct responses of organisms to changes in their physical environment and resulting changes in the interactions among species, rather than invasions of additional species expanding their ranges northward in response to more favourable climatic conditions. In addition, it has

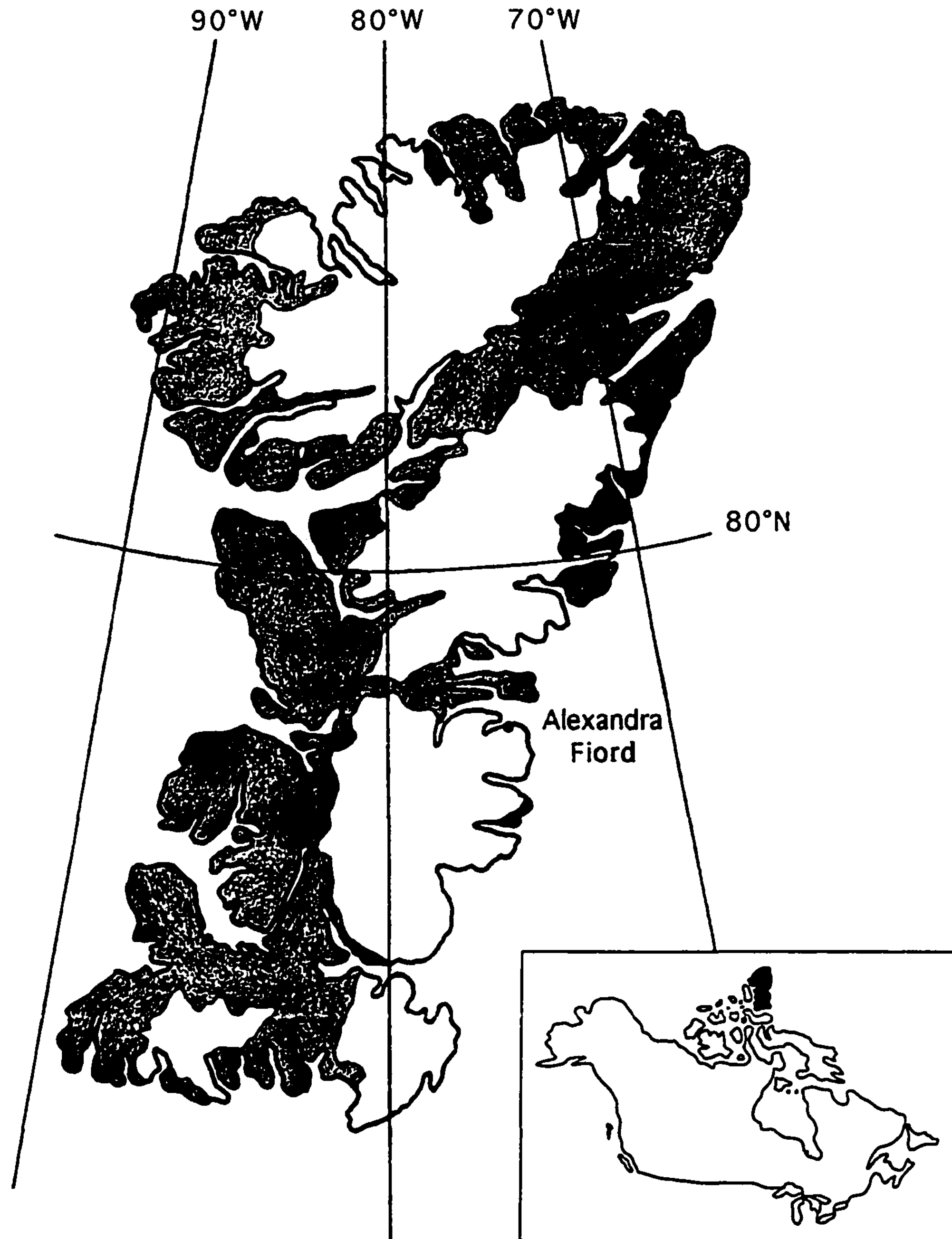

Figure 2. Location of the Alexandra Fiord lowland (•) on the east coast of Ellesmere Island in the Canadian Arctic; nonshaded areas of Ellesmere Island represent major icecaps. Basemaps of Ellesmere Island and Canada modified from Svoboda and Freedman (1994) and deBruyn (1993), respectively.

been suggested that the population of *G. groenlandica* at Alexandra Fiord is limited by parasitoid-induced mortality rather than by the constraints of the physical environment (Kukal and Kevan 1987; Kevan and Kukal 1993) and that "populations of *G. groenlandica* and its parasitoids are in fine balance" (Kevan and Kukal 1993). As such, and considering that the number of interacting species is likely to be far fewer than in comparable systems at lower latitudes, *Gynaephora* species and their insect parasitoids at Alexandra Fiord offer the opportunity to investigate a tractable system within which host-parasitoid interactions are thought to be at least as important as direct environmental constraints.

Objectives

The overall objective of this dissertation was to generate hypotheses regarding the responses of arctic *Gynaephora* species and their insect parasitoids to predicted climate change at Alexandra Fiord, Ellesmere Island, and to provide baseline information against which these hypotheses might be tested in the future. Specific objectives were

(1) to describe and illustrate the immature stages of *G. groenlandica* and *G. rossii*, with emphasis on differences between the two species, so as to help prevent future misidentifications of these insects;

(2) to provide basic life-history information for both species of *Gynaephora* and each species of parasitoid, with emphasis on seasonal synchronization among populations, against which future changes might be measured; and

(3) to investigate temperature/development relationships of key life stages of these species in order to project how or whether predicted climate change might alter the pattern of development of individual species and the interactions among species.

MATERIALS AND METHODS

Studies were conducted through observations, detailed surveys, and experiments in the field at Alexandra Fiord and through rearing under controlled conditions in the laboratory at the University of Victoria. Basic statistical tests were conducted as described by Zar (1984) but some aspects of the study required more specialized analyses and these are described under "Head-capsule Widths and Number of Larval Instars in *Gynaephora* Species" below. All adult parasitoids reared from *Gynaephora* species during the course of this study, both in the field and in the laboratory, were identified to determine whether any additional species were using *Gynaephora* species as hosts. All host remains were retained and ultimately dissected to measure the head-capsule width (HCW) of the primary host, to record the number of parasitoids per host, and to investigate the fate of the parasitoids, including stage of development attained and incidence of hyperparasitism.

Field Studies

Fieldwork was conducted at Alexandra Fiord from 6 June to 15 August 1994, from 29 May to 17 August 1995, and from 25 May to 13 August 1996. Conducting fieldwork during three consecutive summers allowed for some assessment of year-to-year variation and also allowed for monitoring of individual insects through more than one growing season. Field studies were largely confined to the central area of the Alexandra Fiord lowland (Figure 3) because the "deciduous dwarf shrub – graminoid" plant community of Muc *et al.* (1989), which supports the highest density of *Gynaephora* (Kukal and Kevan 1987; personal observations), is most extensive in that area.

Larvae, cocoons, adults, and eggs of both species of *Gynaephora* were observed and photographed in the field and were collected for rearing and for more detailed examination. Dimensions of eggs and maximum widths of isolated larval head capsules viewed from the front were measured to the nearest 0.05 mm using a stereomicroscope (Meiji Zoom Stereo EMZ-1) equipped with an ocular micrometer, at a magnification of 20X. Head capsules are shed intact by all but the final instar; occasional head capsules that

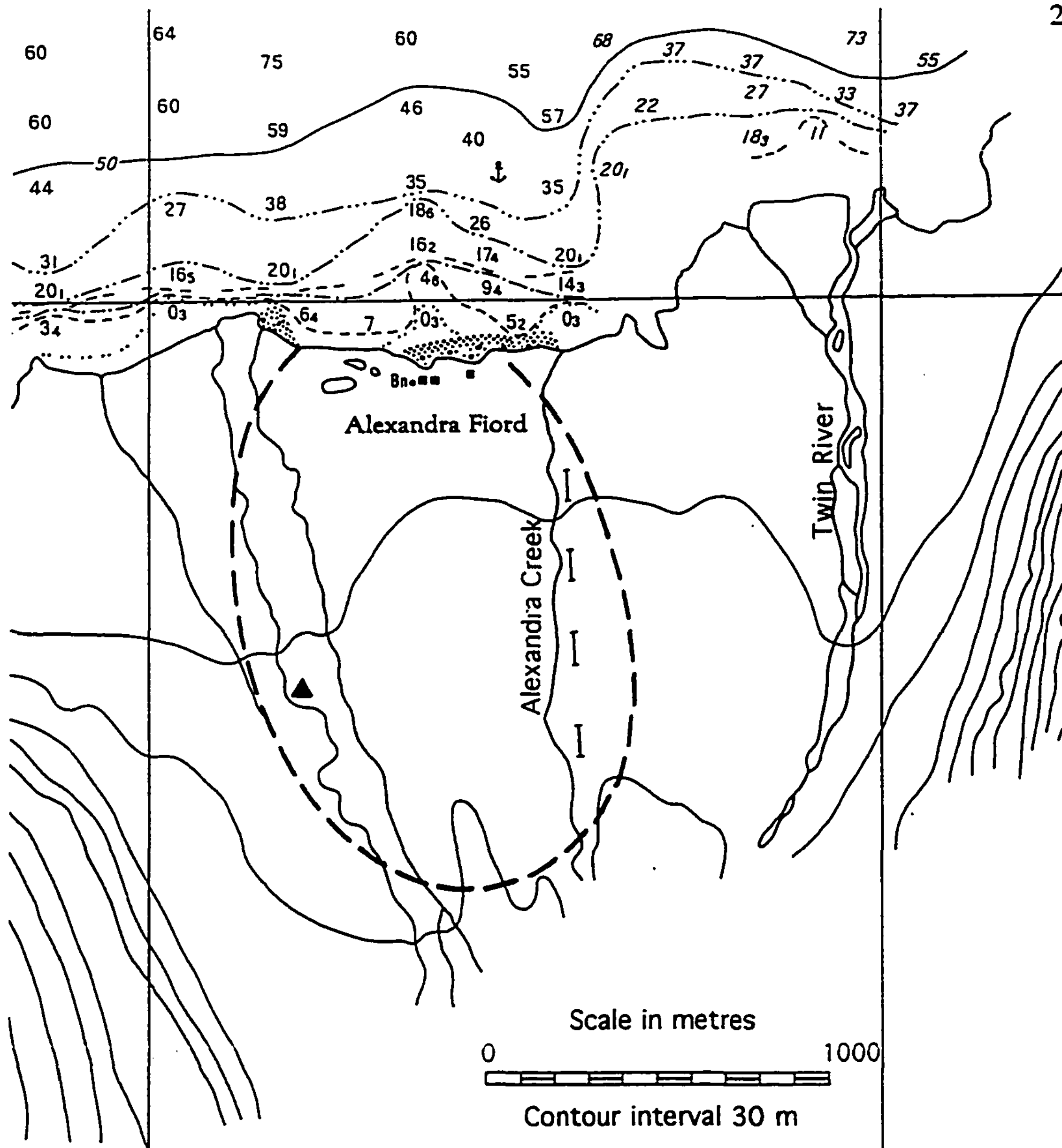

Figure 3. Map of the Alexandra Fiord lowland showing the location of the RCMP buildings used as a base camp (small filled rectangles adjacent to the fjord; "Bn" denotes an old navigation beacon), the site of the experimental corrals and open-top chambers (filled triangle), the transects used for *Gynaephora* surveys (short lines immediately east of Alexandra Creek), and the approximate boundary of the main study area (heavy dashed line). Basemap from Anonymous (1981) with stream names assigned by Sterenberg and Stone (1994).

were accidentally split, broken, or distorted were not measured. Early larval instars were determined by rearing larvae from eggs and measuring head capsules shed at each moult. Additional head capsules, mostly of older instars, were collected from naturally moulted exuviae found on the tundra. Head capsules of final-instar larvae split along the epicranial suture and ecdysial lines during the moult to the pupal stage, making it impossible to measure naturally moulted head capsules for the final instar. Therefore, head capsules were collected from larvae that had been killed by parasitoids prior to pupation, leaving their head capsules intact, but after they had spun cocoons, indicating that they were in their final stadium. Sample statistics for head-capsule widths (HCWs) of the larval instars of *G. groenlandica* were calculated by simply dividing the distribution of measured HCWs at low points between the peaks. Because very few data were obtained for the intermediate (fourth and fifth) instars of *G. rossii*, mean HCWs for these two instars were estimated by extrapolating from the mean HCWs of the first three instars according to the Brooks-Dyar rule, which holds that the HCW of a given species tends to increase by the same ratio at all moults (Dyar 1890; Daly 1985). Due to overlap in HCW between instars of *G. groenlandica* and the very limited number of HCW measurements for the intermediate instars of *G. rossii*, the given HCW should be considered approximations only. Descriptions of the later instars were obtained by measuring the head capsules of larvae examined in detail and assigning these larvae to the appropriate instar. These descriptions were supplemented with field observations of larval phenotypes, especially larvae that were spinning cocoons, indicating that they were in their final stadium. Descriptions of larvae follow the terminology used by Ferguson (1978).

Photographs of larval hairs and portions of cocoons were taken through the stereomicroscope at a magnification of 30X. Maximum lengths and widths of cocoons viewed from above were measured to the nearest millimetre using a plastic ruler; sexes were subsequently determined from the morphology of caudal segments of the pupal exuviae. Maximum lengths and widths of pupae in ventral view were measured to the nearest half millimetre using a plastic ruler; very few pupae were measured because most were left to develop within their cocoons for other studies. Descriptions of pupae follow

the terminology of Mosher (1916) and were formulated to be comparable to those published by Patocka (1991).

Foodplant preferences were determined by recording the plant species and part of the plant eaten by all *Gynaephora* larvae that were observed actively feeding on the tundra in 1995 and 1996; these observations were limited to free-ranging larvae, excluding larvae held in corrals or otherwise confined for other studies.

Eggs of *Gynaephora* species were screened for parasitism. Unhatched eggs from egg masses that had otherwise hatched in the field were held individually in Falcon® dishes (Becton Dickinson and Company, Lincoln Park, New Jersey), small Petri dishes with tight-fitting lids, indoors at the field site and monitored for emergence of adult parasitoids until the end of the field season. These eggs were overwintered at the field site and monitored again from the beginning of June to the end of July of the following year.

Field Surveys

Standardized surveys were conducted each year using four transects established in the deciduous dwarf shrub – graminoid plant community along the east bank of Alexandra Creek (Figure 3). Each transect was 90 m in length and was marked at 10-m intervals with yellow tent pegs (Figure 4); surveys consisted of slowly walking the transects in the early afternoon (1200-1600 h EST) and recording all *Gynaephora* observed within one metre on each side of the transect line. Surveys were initiated as soon as was feasible each year and were repeated every second day until no *Gynaephora* larvae were observed in at least two consecutive surveys and no other study insects remained in the transects (*i.e.*, *Gynaephora* pupae or parasitized *Gynaephora* that had not yet produced adults of *Gynaephora* or the parasitoids, respectively). When the numbers of larvae observed in the transect surveys began to decline, all free-ranging *Gynaephora* larvae observed in the course of fieldwork throughout the study area were recorded each day until the end of the field season.

Development of individual insects dispersed throughout the primary study area (*cf.* Figure 3) was monitored in 1995 and 1996 during their immobile developmental stages. *Gynaephora* larvae that were killed by parasitoids or were found spinning cocoons

Figure 4. Yellow tent pegs marking one of the transects used for standardized surveys.

(or at any subsequent stage of development) were marked using survey flags (*cf.* Figure 5) with notes made on their exact position relative to the flag. All flagged insects were checked at the end of each day (usually 2000-0200 h EST) and their stage of development noted. Dates of cocoon-spinning, pupation, adult emergence, egg-laying, and hatching for *Gynaephora* species and dates of cocoon-spinning for *H. pectinatus*, pupariation for *C. gelida* and *Exorista*, and adult emergence for all three species of parasitoid were recorded, as well as the fate of any insects that failed to complete these developmental sequences.

Field Experiments

Gynaephora life histories and effect of temperature on development

Small *Gynaephora* larvae were retained under field conditions using small "corrals" constructed by removing the bottoms from four-litre plastic pails and setting the sides of these pails into the tundra to form circular walls approximately 10 cm high (Figure 5). These corrals were either placed around eggs masses found on the tundra, which were then allowed to hatch *in situ*, or stocked with larvae from egg masses hatched indoors. All corrals were placed so as to ensure that there was some arctic willow (*Salix arctica* Pallas, a main foodplant for *Gynaephora* larvae), as well as other vegetation, within each corral. Corrals placed around egg masses were covered with coarse netting (*ca.* 2-cm mesh) to prevent predation by birds.

Gynaephora larvae from eggs hatched indoors were reared in large Petri dishes and provided with the youngest available shoots of arctic willow, which were replenished as necessary to maintain a plentiful supply of fresh food, usually every second or third day. Temperatures indoors were maintained near 20°C most of the time but ranged as low as 15°C and as high as 25°C. Of the *G. groenlandica* larvae reared in this way, 100 first instars and 100 second instars were placed in small corrals, with the different instars in separate corrals, in early August of 1994 and left to overwinter under field conditions. Larvae were recovered from the corrals in early June of 1995, as soon as the snow had

Figure 5. Small corral used to retain small *Gynaephora* larvae under field conditions and to protect egg masses from predation by birds.

melted within the corrals. They were again reared indoors through the growing season, to minimize losses and allow for the collection of moulted head capsules, and then returned to the corrals in early August. Larvae of *G. rossii* that were reared from eggs hatched indoors in 1995 were placed in a small corral in early August, left to overwinter under field conditions, and recovered once the snow had melted within the corral in July of 1996. The larvae were again reared indoors through the growing season in 1996 and then transported to the University of Victoria for laboratory rearing in the spring of 1997, along with additional larvae that had been reared from eggs laid in 1996. In addition, the corrals that had been placed around egg masses of *G. groenlandica* left to hatch *in situ* in 1994 were left in place until the end of the field season in 1996, at which time the corrals were searched and the recovered larvae transported to the University of Victoria for laboratory rearing in the spring of 1997.

Individual development of older larvae of *G. groenlandica* was monitored by holding such larvae in larger corrals (approximately 0.8 m diameter) constructed from plastic lawn-edging set into the tundra to form walls several centimetres high. Twenty-four such corrals were established in 1995 within approximately 100 m of the ITEX meteorological station in the deciduous dwarf shrub – graminoid plant community (*cf.* Figure 3). These corrals were placed so as to include as much arctic willow as possible, as well as other vegetation, within each corral. Small (1.0 m bottom diameter, 0.8 m top diameter, 0.3 m height) hexagonal open-top chambers (OTCs) of the type used in ITEX studies to passively increase daytime temperatures were placed over 12 of these corrals, and the other 12 served to approximate ambient conditions as controls (Figure 6). Details of the construction and performance of the OTCs are given by Marion (1996), Marion *et al.* (1997), and Stenström *et al.* (1997). Larvae held in the corrals were marked with small spots of Liquid Paper® to ensure that the same individuals were being monitored, because more than one individual was held in each corral and additional larvae occasionally entered the corrals by climbing the wires used to anchor the walls from the outside.

A single larva of *G. groenlandica* was placed in each of the 24 corrals on 13 June

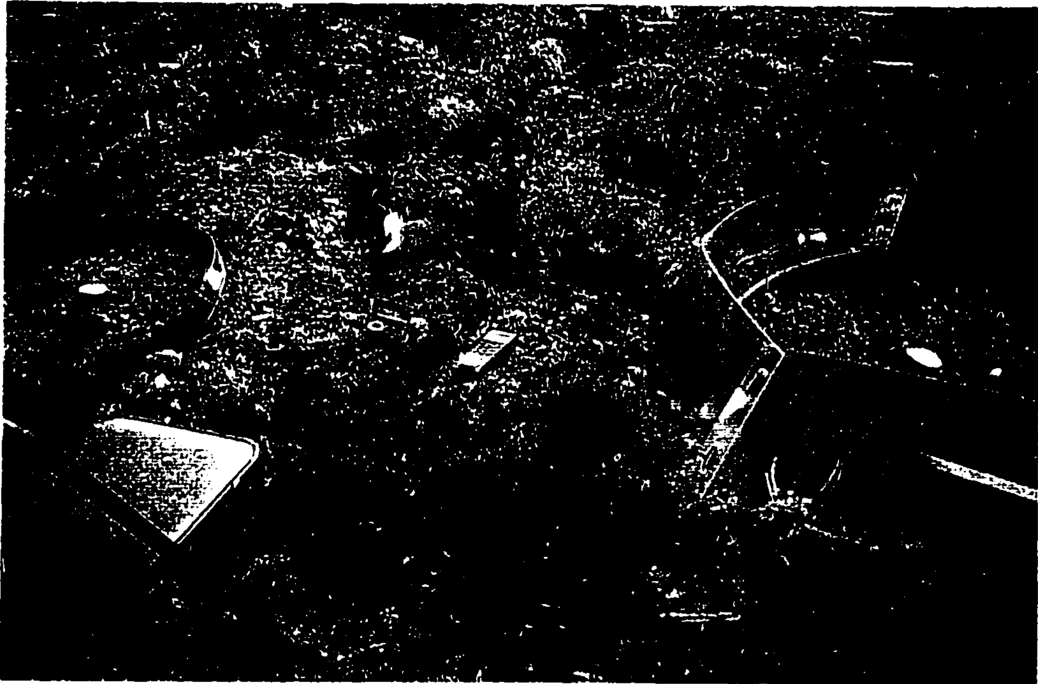

Figure 6. A pair of large corrals, within and without an open-top chamber, used for rearing fourth to seventh instar larvae of *Gynaephora groenlandica* under field conditions (tin can lids were placed to shade thermocouples for temperature measurements).

1995 and a second larva was placed in each corral (plus one additional larva to replace one of the original larvae which had been killed by *H. pectinatus*) on 23 June 1995, a few days before the end of their active season. All larvae were checked daily from the day they were placed in the corrals until the end of the field season (17 August), and in early August each corral was carefully searched and the location of each larval hibernaculum was mapped to facilitate monitoring of larval emergence the following spring. Development of all of the corralled larvae was monitored from the day they emerged from their hibernacula in 1996 until the end of the field season that year (13 August). Fresh larval mass was measured to the nearest 0.01 g using an Ohaus® portable field balance approximately every three days for as long as they remained alive and active, and dates of all changes in developmental status were recorded. Relative growth rate (RGR) was calculated from fresh larval mass as described by Waldbauer (1968) except that initial mass, rather than mean mass, was used to compensate for differences in absolute mass among larvae because mean mass is itself a function of RGR (Raubenheimer and Simpson 1992). At the end of the field season in 1996, the 17 remaining larvae that had not pupated or been killed by parasitoids were collected (all in hibernacula) and transported to the University of Victoria for laboratory rearing as described below.

Behavioural observations were made on four *G. groenlandica* larvae, two in each of a representative OTC and control corral, for three hours (1330-1630 h EST) on five different days with favourable weather (mostly sunny with light winds) spread over the portion of the season that *G. groenlandica* larvae were active in 1996. The behaviour of each larva was recorded as feeding, moving, or basking (not feeding or moving) each minute throughout the three-hour period. At the same time, shaded air temperatures near ground level (*ca.* 1 cm) were measured in both the OTC and the control corral every ten minutes using a hand-held digital thermometer (Fluke 52 K/J) with chromel/alumel (Fluke 80PK-1) thermocouples (Figure 6).

Reproductive isolation of *Gynaephora* species

In 1995 and 1996, experiments were conducted to investigate reproductive isolation of the two species of *Gynaephora*. A preliminary experiment was conducted in July of 1995, stimulated in part by the fact that males of both species had been attracted to a cage containing virgin females of *G. groenlandica*. Four males of *G. rossii* thus attracted were placed in the cage with four calling females of *G. groenlandica* and were held there for several hours under nearly continuous observation. To ensure that mating was not inhibited by capture or cage conditions, two males of *G. groenlandica* that were also attracted by the calling females were later added to the same cage.

A more detailed experiment was conducted in July of 1996. On each of three days with sunny weather and light winds, one to four virgin females of one or the other species were placed in an outdoor cage and monitored for a period of three hours (1000-1300 h EST). Males attracted to the cage were captured, identified, and counted; males that escaped or eluded capture were not counted because they might have returned and thus been counted more than once. Heterospecific males were placed in the cage with the calling females (to a maximum of ten on 13 July) while conspecific males were sequestered in a separate cage. At the end of each three-hour period, some of the conspecific males were introduced into the cage with the females. These experiments were evaluated simply in terms of the relative numbers of males attracted (1996 only) and the incidence of heterospecific and/or conspecific mating (both years).

Effect of temperature on primary parasitoid metamorphosis

Parasitoid-killed *Gynaephora* were collected and held in four light mesh cages on the tundra to monitor the emergence of adult parasitoids in 1994 and 1995. Two of these cages were placed within small OTCs and the other two were placed on the tundra nearby to serve as controls (Figure 7), with one OTC and one control cage for each host species. In 1994 these cages were stocked from 8 June until no new parasitoid-killed hosts were found, in 1995 the cages were stocked from 13 June until 22 June only, and in both years

Figure 7. Light mesh cages, within and without open-top chambers, used to monitor emergence of adult parasitoids.

the cages were checked and all adult parasitoids removed at the end of each day (usually between 2200 h and 0200 h EST) until the end of the field season. Temperatures near ground level (among the host remains) within each of the four cages were measured sporadically at different times of the day and under various weather conditions through the month of June in 1994 using a hand-held digital thermometer and thermocouples as described above.

Voltinism of the primary parasitoids

Two approaches were used to determine voltinism of the primary parasitoids, depending on the type of parasitoid. Because *Exorista* and *C. gelida* lay macrotype eggs externally on their hosts, living *Gynaephora* larvae parasitized by these flies could readily be identified as such by the presence of eggs. Larvae of *G. groenlandica* collected for laboratory rearing that were not bearing tachinid eggs when they were collected were placed in two of the stock corrals described under "Laboratory Rearing" below, one of which was covered with light mesh (Figure 8) to exclude adult parasitoids while the other was left uncovered. Thus, any larvae in the uncovered corral that became parasitized by tachinid flies would have been attacked after they were placed in the corral and emergence of adult flies the following spring would indicate that the tachinids are univoltine. This method could not be used with *G. rossii* because too few unparasitized larvae were found; however, four eggs were laid by a mated female of *C. gelida* on a *G. rossii* larva held indoors at the field site in 1995 and this host larva was then placed in a small corral in the field to determine whether the *C. gelida* eggs would develop to adults in one year.

Because *H. pectinatus* inject their eggs into the host, parasitism by these wasps could not be detected until the wasp larvae were fully grown and began to spin their cocoons. However, *H. pectinatus* adults readily mated, and females readily accepted *G. groenlandica* larvae that were offered for oviposition, even when they were confined in small containers. Therefore, in 1995, mated females of *H. pectinatus* were held indoors, provided with male and female willow catkins as sources of pollen and nectar, and offered larvae of *G. groenlandica*. Larvae that were apparently accepted for oviposition ("stung")

Figure 8. Large "stock" corrals used to retain *Gynaephora* larvae in the field so they could be collected at the end of the field season for laboratory rearing the following spring (one corral is covered with light mesh to exclude adult parasitoids).

were reared indoors at the field site until the end of the field season and then placed in a small corral to overwinter in the field before being recovered the following spring.

Laboratory Rearing

For laboratory rearing, *Gynaephora* larvae were collected from the tundra in July and August of 1995 and 1996 and held in four large "stock" corrals, constructed as for the OTC and control corrals except that each of these stock corrals encompassed an area of approximately two square metres (Figure 8). In order to avoid any influence on the transect surveys, no *Gynaephora* larvae were collected from east of Alexandra Creek. At the end of the field season the larvae (in hibernacula) were collected from the stock corrals, along with a number of larvae collected from hibernacula found on the open tundra in 1996. Approximately 200 larvae were collected in this way each year and transported to the University of Victoria. There they were "overwintered" through a series of low temperatures, from 5°C gradually down to –25°C over eight to ten weeks, –25°C for approximately three months, and then gradually back up to 0°C over four to five weeks.

On 1 March in both 1996 and 1997, each larva was randomly assigned to one of three controlled-environment chambers for rearing at one of three different constant temperatures, such that approximately 50 to 75 larvae were assigned to each temperature. Rearing was conducted under continuous light and approximately 70% relative humidity in 10 x 10 x 10-cm rearing units constructed from Plexiglas and lined with leaf litter (Figure 9). Rearing temperatures were standardized among controlled environment chambers using the hand-held digital thermometer and thermocouples described under "Field Experiments" above. Temperature variation within the chambers was monitored throughout the rearing period by a Barigo® minimum-maximum thermometer placed in each chamber. Cuttings from local willows (*Salix scouleriana* Barratt in Hooker), consisting of twigs with buds and expanding leaves, were provided and readily accepted as food by the *Gynaephora* larvae. Because these willows usually do not begin development until late March, cuttings were collected regularly beginning in early February, placed in water, and brought indoors to stimulate bud-burst, ensuring a steady

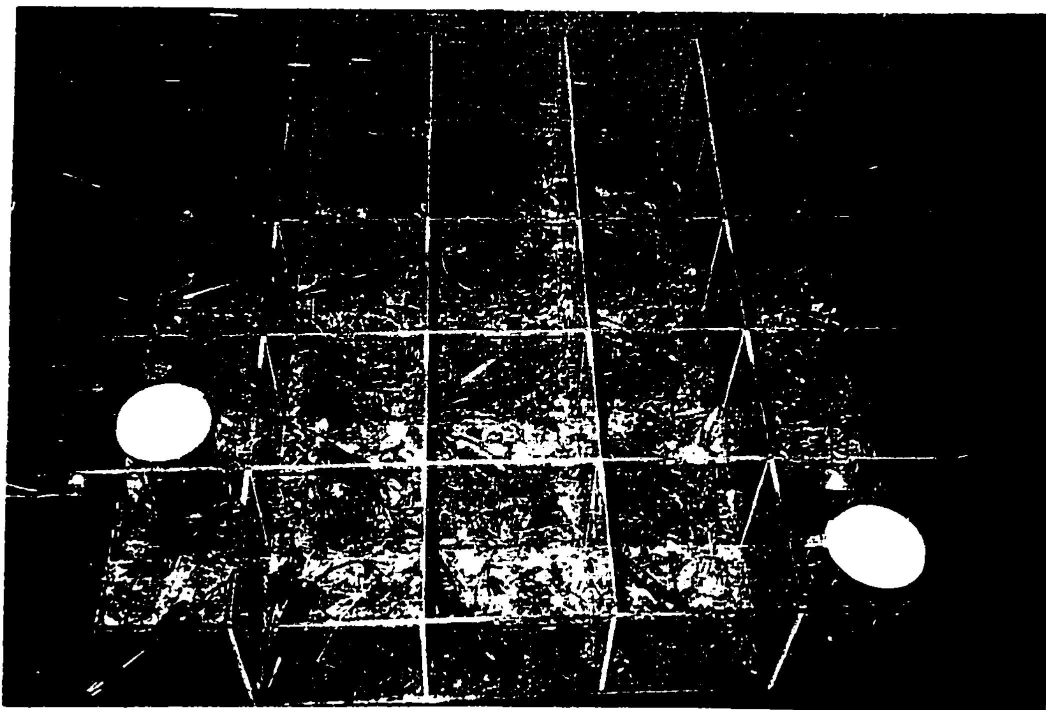

Figure 9. Individual rearing units for laboratory rearing (parasitoid-killed larvae were placed in plastic vials to monitor emergence of adult parasitoids).

supply of cuttings at approximately the same stage of development. Larvae were provided with cuttings as the available food (buds and expanding leaves) was consumed, in most cases daily. These cuttings were placed in small green plastic vials with rubber lids made for cut flowers (Econoplastik Inc., St-Jean Port-Joli, Québec) which were filled with an aqueous solution of Floralife® cut flower food (Horticultural Technologies Ltd., Kitchener, Ontario). *Gynaephora* larvae that died or that spun cocoons and pupated were placed into large (30-dram) plastic vials with perforated lids to monitor emergence of adult parasitoids or moths (*cf.* Figure 9).

The hyperparasitoid *C. leechi* was obtained through dissections of host remains retained from field studies. Puparia of *Exorista* or *C. gelida*, or cocoons of *H. pectinatus*, that were found to contain cocoons or living larvae of *C. leechi* were overwintered along with the *Gynaephora* larvae in the laboratory and were placed in large plastic vials (as above) in the controlled environment chambers to monitor the emergence of adult hyperparasitoids in the spring.

In the spring of 1996, laboratory rearing was conducted at temperatures of 10°C, 20°C, and 30°C. All insects were checked daily and the dates of all changes in developmental status up to the spinning of hibernacula and the emergence of adult *Gynaephora* and adult parasitoids were recorded. In the spring of 1997, laboratory rearing was conducted at temperatures of 15°C, 20°C, and 25°C. Larvae of *G. groenlandica* were weighed every three days for as long as they remained alive and active, using the same portable balance that was used in the field, and RGR for these larvae was calculated as described under "Field Experiments" above. All insects were checked daily and the dates of all changes in developmental status up to the spinning of hibernacula and the emergence of adult *Gynaephora* and adult parasitoids were recorded.

In 1997, three pairs of *G. groenlandica* adults were induced to mate by placing recently-emerged males and females in small (30 x 30 x 30-cm) screen cages and placing the cages in the breeze produced by the cooling system in the Cunningham Building's Equipment Room (113) at the University of Victoria. Each mated female was allowed to oviposit for 24 h in the controlled environment chamber in which she was reared, after

which each egg mass was divided into three groups of equal numbers of eggs. One group of eggs from each egg mass was placed into each of the controlled environment chambers (at 15°C, 20°C, or 25°C) and the dates of hatching were subsequently recorded.

Temperature/development relationships were constructed from laboratory-rearing data for selected stages of *G. groenlandica*, *H. pectinatus*, *Exorista* n.sp., and *Cryptus leechi*; too few *G. rossii* and *C. gelida* were obtained for laboratory rearing to conduct such analyses for these species. Lower temperature thresholds for development and overall thermal requirements to complete development were estimated from linear regression of temperature and mean development rate, the x-intercept and reciprocal of the slope of the regression line representing the "developmental zero" temperature and "thermal constant" in degree-days, respectively (Wigglesworth 1972).

Head-capsule Widths and Number of Larval Instars in *Gynaephora* Species

Because the range of HCWs for adjacent instars of *G. groenlandica* overlapped, the "expectation-maximization" (EM) algorithm (Dempster *et al.* 1977; Redner and Walker 1984) for population mixtures was used to calculate maximum-likelihood estimates of population parameters for the HCW of each instar. This procedure is based on the "steepest descent" method of Hasselblad (1966) and was applied to HCWs of the navel orangeworm (*Amyelois transitella* (Walker)) by Beaver and Sanderson (1989). One of the equations presented by Beaver and Sanderson (1989) was unfortunately misprinted (Beaver[4], personal communication 1996) and others are here modified slightly to facilitate computation; therefore, all of the equations are reproduced in the following outline of the procedure.

A multimodal HCW distribution can be considered a population of measurements consisting of a mixture of k subpopulations, each subpopulation j representing a larval instar and comprising a proportion p_j of the overall population such that the proportions for all instars sum to 1. If HCWs for instar j are normally distributed with a mean of μ_j and a

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variance of σ_j^2, their distribution is described by the function

$$f_j(x;\mu_j,\sigma_j^2) = \frac{\exp[-(x-\mu_j)^2 / 2\sigma_j^2]}{\sqrt{(2\pi\sigma_j^2)}} \quad [1]$$

and the combined distribution for the overall population is described by the function

$$f(x) = \sum_{j=1}^{k} p_j f_j(x;\mu_j,\sigma_j^2). \quad [2]$$

The EM algorithm is an iterative procedure involving two steps, estimating the unknown parameters and maximizing the fit to the sample data of the function defined by those parameters. Applied to population mixtures, the two steps can be combined within the iteration procedure and computed through the equations

$$\mu_j^{(n+1)} = \sum_{i=1}^{N} y_i x_i w_{ij}^{(n)} / \sum_{i=1}^{N} y_i w_{ij}^{(n)} \quad [3]$$

$$\sigma_j^{2(n+1)} = \sum_{i=1}^{N} y_i (x_i - \mu_j^{(n)})^2 w_{ij}^{(n)} / \sum_{i=1}^{N} y_i w_{ij}^{(n)} \quad [4]$$

$$p_j^{(n+1)} = \sum_{i=1}^{N} y_i w_{ij}^{(n)} / \sum_{i=1}^{N} \sum_{j=1}^{k} y_i w_{ij}^{(n)} \quad [5]$$

wherein n denotes the iteration number, i the HCW category, N the total number of HCW categories, x_i the HCW value for category i, and y_i the frequency of HCWs in category i;

w_{ij} is a weighting factor accounting for the proportion of the HCW frequency contributed by each instar and calculated as

$$w_{ij}^{(n)} = \frac{p_j^{(n)} f_j (x_i; \mu_j^{(n)}, \sigma_j^{2(n)})}{\sum_{j=1}^{k} p_j^{(n)} f_j (x_i; \mu_j^{(n)}, \sigma_j^{2(n)})}. \qquad [6]$$

Initial parameter estimates for the EM algorithm were the sample statistics determined as described under "Field Studies" above. Calculations were performed by a program in FORTRAN (see Appendix) run on the University of Victoria's mainframe computer system and the procedure was terminated once there was no change from one iteration to the next within the first five significant figures of any of the parameters.

The EM algorithm converges on parameter estimates that maximize the likelihood of obtaining the observed data from a population described by the estimated parameters, given a set number of subpopulations. Because not all of the peaks in the distribution of measured HCWs were well-defined, the EM algorithm was used to fit the data to a combined distribution comprising seven larval instars ($k = 7$) and also to one comprising six larval instars ($k = 6$). The logarithm of the likelihood function (Hasselblad 1966) for each distribution was approximated as

$$L = \sum_{i=1}^{N} y_i \operatorname{Log} f(x_i) \qquad [7]$$

with $f(x_i)$ defined by equation [2]. Twice the difference in log-likelihoods, which has an approximate χ^2 distribution with three degrees of freedom, the difference in the number of parameters for the two models (Beaver and Sanderson 1989), was used to test the relative goodness of fit of the two models to the sample data.

Boundary points for HCWs of adjacent instars were selected so as to minimize the probability of misclassifying an individual with respect to instar, based on HCW alone, using the likelihood-ratio method described by Beaver and Sanderson (1989).

To determine whether HCWs of *G. groenlandica* conform to the Brooks-Dyar rule (equal growth ratios at all moults), two approaches were used. First was the exponential growth function

$$Y = a\exp(bX) \quad [8]$$

wherein X denotes the instar number and Y the mean HCW for that instar, and $\exp(b)$ is the growth ratio (Gargiullo and Berisford 1982). After transforming the HCWs to natural logarithms, linear regression was used to estimate the constants a and b, and equation [8] was then used to calculate the mean HCW for each instar as predicted by the Brooks-Dyar rule. Observed mean HCWs (as estimated from the sample data through the EM algorithm) were compared to expected mean HCWs (predicted by the Brooks-Dyar rule) using χ^2 goodness-of-fit analysis. Second, individual larval growth ratios were determined by measuring the head capsules of recently moulted larvae as well as their respective exuviae. These measurements were limited to free-ranging larvae found on the tundra and the growth ratio was defined as the HCW of a larva divided by the HCW of its exuviae. Larval moults for which individual growth ratios had been determined were assigned to instar according to the HCW of the exuviae, using the boundary points selected above. Linear regression was then used to determine the relationship between instar and growth ratio, a relationship that should be nonsignificant (a slope of zero) according to the Brooks-Dyar rule.

RESULTS

Generally, sample statistics are given as mean ± standard deviation, followed by the sample size in brackets, and are rounded off to the level of precision of the original data; statistical tests were conducted before rounding off the sample statistics.

Descriptions of Immature Stages of *Gynaephora* Species

Eggs

Eggs are laid in masses covered by hairs rubbed from the abdomen of the female, typically on the cocoon from which the female emerged but also frequently on vegetation or the ground (Figure 10). The eggs of both species are smooth, creamy white, and roughly spherical but somewhat flattened.

***G. groenlandica*:** 1.60 ± 0.05 mm in diameter by 1.35 ± 0.05 mm in height (n = 10).

***G. rossii*:** 1.40 ± 0.05 mm in diameter by 1.10 ± 0.05 mm in height (n = 10).

The eggs of *G. rossii* are significantly smaller than those of *G. groenlandica* ($t_{(1)18} = 15.345$, $P < 0.0005$ for diameter; $t_{(1)18} = 15.545$, $P < 0.0005$ for height) and this difference is visible even to the unaided eye.

Larvae

Larvae of both species are large and very hairy, superficially resembling larval Arctiidae (Figure 11). The following general description, outlining the basic arrangement of verrucae and hairs, is applicable to all instars of both species; modifications and species-specific differences are described in the subsequent sections. Differences only are noted in the specific descriptions; larvae of a given instar correspond to the description given for the previous instar except as described otherwise.

The head capsule is black and bears many hairs. Addorsal, subdorsal, supraspiracular, subspiracular, and subventral verrucae are present on the mesothorax, the metathorax, and abdominal segments 1 through 8. The addorsal verrucae are fused with

Figure 10. *Gynaephora groenlandica* (A-D). Female ovipositing on the cocoon from which she emerged; male still present to the right (A). Female (arrow) ovipositing on the ground near the cocoon from which she emerged (B). Egg mass partially depredated by foraging birds; note small tears in the cocoon where eggs were removed (C). Egg mass (arrow) on a lichen-covered rock (D).

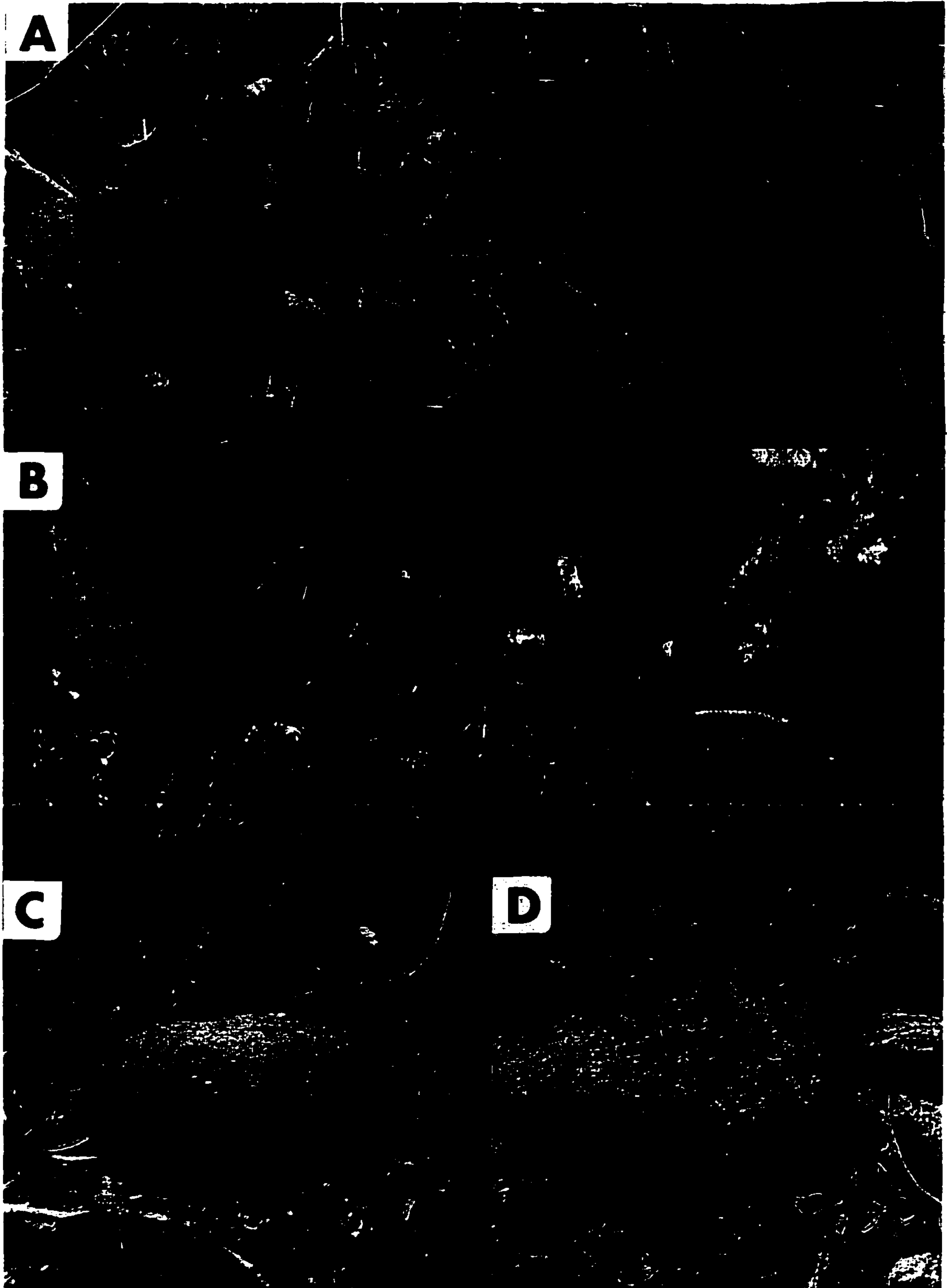
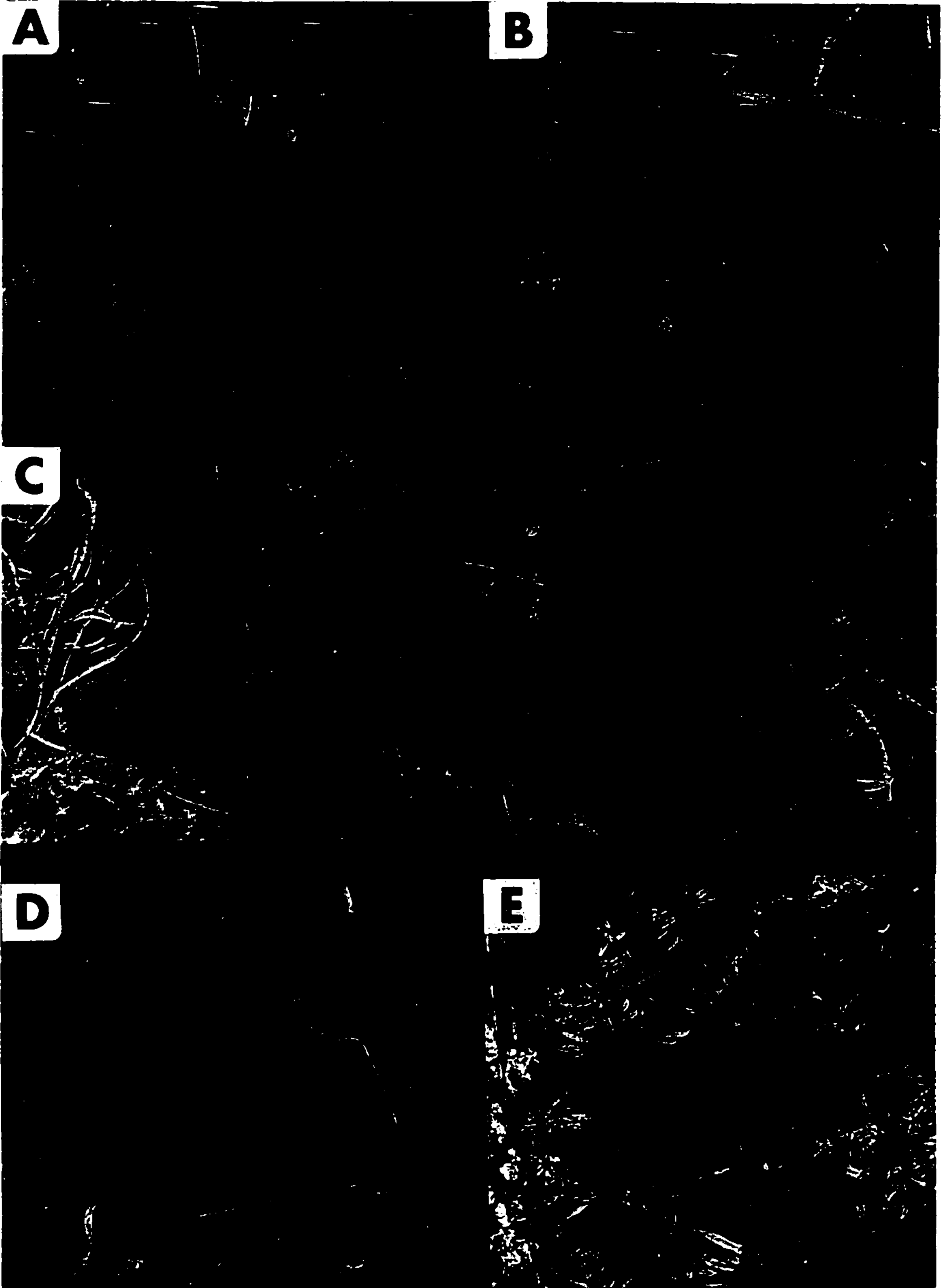

A
B
C
D

Figure 11. *Gynaephora groenlandica* (A-C) and *Gynaephora rossii* (D-E). Fifth-instar larva (head to the right) with the characteristic black and yellow dorsal hairtufts and rudimentary dorsal posterior hair pencil (A). Seventh-instar larva (head to the left) with the four black dorsal hairtufts typical of the final instar (B). Larvae showing the range of colour of larval hairs with the most recently moulted larva on the left (C). Typical larva, showing grey tufting produced by the plumose larval hairs (D). Larva lacking grey plumose hairs (E).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the subdorsal verrucae on the prothorax and abdominal segment 9. On the prothorax, the supraspiracular verrucae are greatly reduced, sometimes lacking hairs, and the subspiracular verrucae are enlarged and oriented anteriorly. Except as just noted, all verrucae bear from one to many hairs. The hairs arising from the addorsal and subdorsal verrucae are generally thicker than those arising from the supraspiracular, subspiracular, and subventral verrucae. The hairs arising from the supraspiracular and subspiracular verrucae, and from the dorsal verrucae on abdominal segment 9, are up to two or three times as long as the longest hairs arising from the addorsal, subdorsal and subventral verrucae. The cuticle, including the verrucae, is entirely black except where noted below. There are well developed whitish dorsal glands on abdominal segments 6 and 7 in all instars except the first.

***G. groenlandica*:** First instar HCW = 0.70 ± 0.05 mm (n = 202). The larvae correspond to the general description above. The cuticle between the verrucae is black. The hairs arising from the addorsal and subdorsal verrucae are black, the hairs arising from the subspiracular and subventral verrucae are brown, and the hairs arising from the supraspiracular verrucae are mixed. All of the hairs are spinulose.

Second instar HCW = 0.95 ± 0.05 mm (n = 177). All of the verrucae bear a mixture of black and brownish yellow hairs. The hairs arising from the supraspiracular, subspiracular, and subventral verrucae are predominantly yellow. The hairs arising from the addorsal and subdorsal verrucae are predominantly yellow on the mesothorax and metathorax, black on abdominal segments 1, 2, and 8, and yellow on abdominal segments 3 through 5.

Third instar HCW = 1.30 ± 0.05 mm (n = 124). The hairs are denser than in the previous instars, beginning to obscure the underlying verrucae from which they arise. The predominance of black and yellow hairs in separate tufts, as noted in the second instar, is more pronounced.

Fourth instar HCW = 1.80 ± 0.15 mm (n = 77). All of the hairs are brown except the following. Black hairs arise from the mesal portions of the addorsal and subdorsal verrucae on abdominal segments 1, 2, and 8, and form tufts that are much denser and

somewhat longer than the surrounding dorsal hairs. Yellow hairs arise from the addorsal verrucae on abdominal segments 3 and 4, and form tufts that are denser but not longer than the surrounding dorsal hairs.

Fifth instar HCW = 2.35 ± 0.15 mm (*n* = 251); sixth instar HCW = 3.05 ± 0.20 mm (*n* = 379). The hairs are longer and denser than in the fourth instar, most notably the hairs arising from the supraspiracular, subspiracular, and subventral verrucae, and the dorsal verrucae on abdominal segment 9. Some of the hairs arising from the dorsal verrucae on the prothorax and from the subdorsal verrucae on the mesothorax and metathorax are as long as the hairs arising from the supraspiracular verrucae. The lengths of the black and yellow dorsal tufts are somewhat variable, sometimes nearly even and sometimes with the black tufts distinctly longer than the yellow tufts. The black tuft on abdominal segment 8 is longer and more slender than those on abdominal segments 1 and 2, resembling more the rudimentary hair pencil that it represents (Figure 11A).

Seventh instar HCW = 3.95 ± 0.20 mm (*n* = 571). The colour pattern of the dorsal hairtufts on abdominal segments 1 through 5 is somewhat variable. Typically, on abdominal segments 1 through 4, the hairs arising from the addorsal verrucae are black and those arising from the subdorsal verrucae are black mesally and yellow laterally; occasionally this pattern is developed to a lesser extent also on abdominal segment 5. This produces an overall appearance of four, or occasionally five, central black tufts fringed laterally with yellow (Figure 11B). Rarely, the pattern of two black tufts on abdominal segments 1 and 2, followed by two yellow tufts on abdominal segments 3 and 4, is retained in this final instar.

With the exception of the distinctive black and yellow tufts, the larval hairs of *G. groenlandica* show considerable variation in overall colour, depending on how recently an individual has moulted. Freshly moulted larvae appear silvery brown overall, but the brown hairs quickly darken and then very gradually fade to golden yellow (Figure 11C) during the course of the stadium.

***G. rossii*:** First instar HCW = 0.60 ± 0.00 mm (*n* = 90). The larvae correspond to the general description above. The cuticle between the verrucae is pale compared to the

verrucae. The hairs are uniformly grey in colour. All of the hairs are spinulose.

Second instar HCW = 0.85 ± 0.05 mm (*n* = 44). Some of the hairs arising from the addorsal verrucae on abdominal segments 1, 2, and 8 are plumose. One or two of the hairs arising from the supraspiracular verrucae on each abdominal segment are plumose. All of the other hairs are spinulose. The cuticle between the verrucae is generally somewhat paler than the verrucae.

Third instar HCW = 1.25 ± 0.05 mm (*n* = 35). The hairs are denser than in the previous instars, beginning to obscure the underlying verrucae from which they arise. Some of the hairs arising from the addorsal verrucae on the mesothorax and metathorax, as well as on abdominal segments 1, 2, and 8, are plumose. Some of the hairs arising from the subdorsal verrucae and most of the hairs arising from the supraspiracular and subspiracular verrucae on all segments except the prothorax are plumose. The other hairs are spinulose and either black or yellow, those arising from thoracic verrucae and from the addorsal verrucae on abdominal segments 3 through 5 being predominantly yellow.

Fourth instar HCW approximately 1.80 mm. The grey plumose hairs are denser and more prominent; otherwise, the fourth instar is very similar to the third instar.

Fifth instar HCW approximately 2.60 mm. Some to most of the hairs arising from all of the verrucae are plumose. The hairs arising from the addorsal and subdorsal verrucae are quite uniform in length, giving a "clipped" appearance in lateral view. The hairs arising from the supraspiracular and subspiracular verrucae are up to twice as long as those arising from the dorsal verrucae. The longer plumose hairs are grey and the shorter spinulose hairs are black or yellow, as in the third and fourth instars.

Sixth instar HCW = 3.55 ± 0.20 mm (*n* = 338). All of the hairs are black except as noted in the following. The thoracic verrucae bear a mixture of black and yellow hairs that do not form distinct tufts. The addorsal and subdorsal verrucae on abdominal segments 1 through 8 bear dense tufts of relatively short hairs; those arising from the addorsal verrucae and the mesal portion of the subdorsal verrucae are black, and those arising from the lateral portion of the subdorsal verrucae are yellow. This produces the appearance of a black tuft fringed laterally with yellow on each abdominal segment, the pattern becoming less distinct

caudally. Variable numbers of longer grey plumose hairs arise from all verrucae, usually obscuring the pattern of black and yellow tufts to some extent, sometimes completely, and giving the impression of lint accumulated among the larval hairs (Figure 11D).

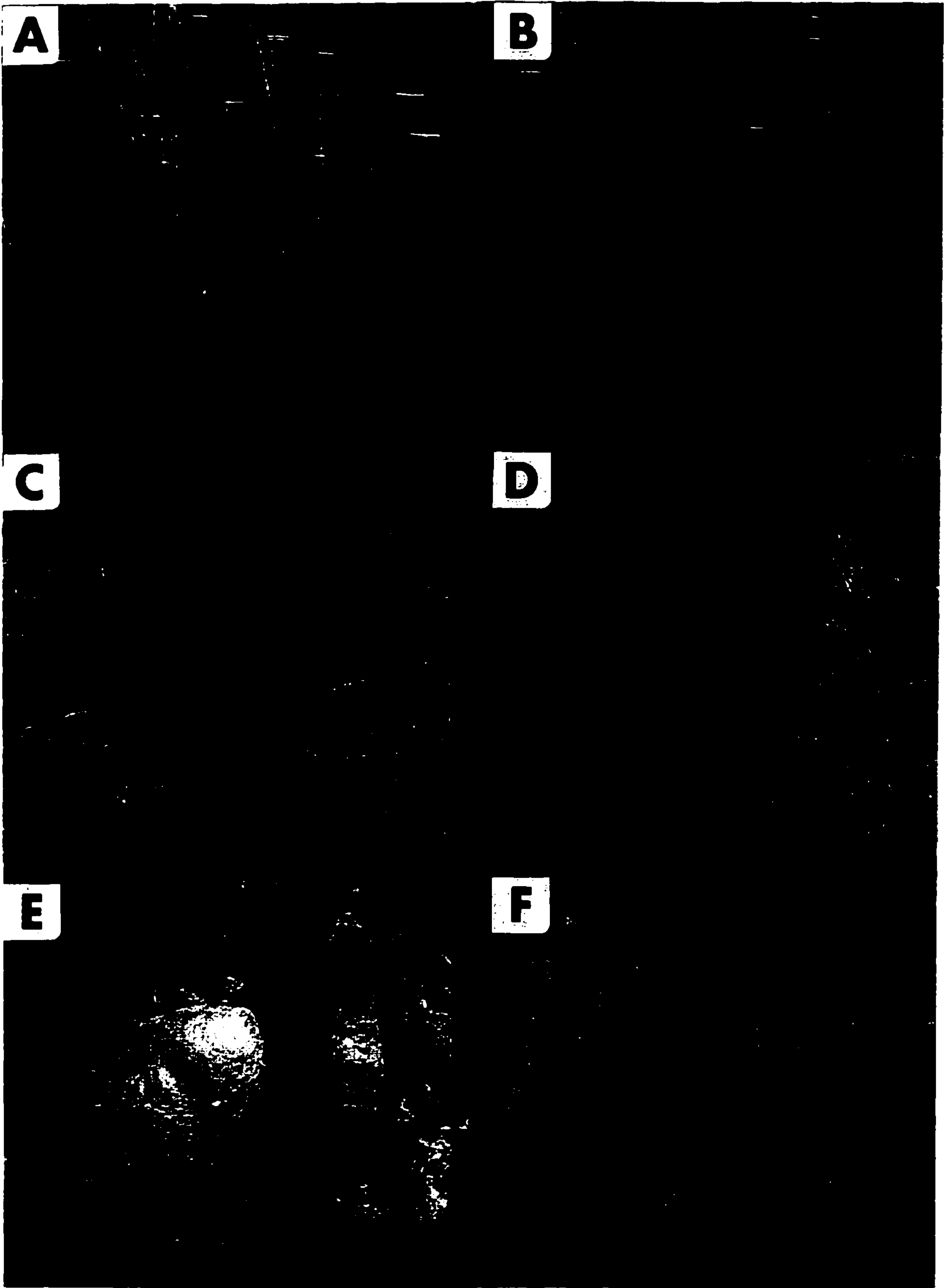
In rare individuals, the grey plumose hairs are replaced by black spinulose hairs that do not obscure the pattern of black and yellow tufts (Figure 11E). Rearing of such larvae produced either adults of *G. rossii* or adults of the tachinid parasitoid *Chetogena gelida* (Coquillett), which is extremely host-specific to larvae of *G. rossii*, at least at this site (see "Parasitoids of *Gynaephora* Species" below).

In general, larvae of *G. rossii* are smaller than larvae of *G. groenlandica* and have much shorter hairs of more uniform length. The pattern of black and yellow dorsal hairtufts is quite different in the two species and is not obscured by other hairs in *G. groenlandica* but is usually obscured at least partially by grey plumose hairs in *G. rossii*. The long spinulose (Figure 12A) or plumose (Figure 12B) larval hairs are characteristic of *G. groenlandica* and *G. rossii*, respectively, produce a contrast in overall appearance, and are quite distinct when viewed under magnification. These hairs are also readily distinguished after they have been incorporated into cocoons (Figures 12C & 12D).

Hibernacula

Hibernacula are spun with silk, much like pupal cocoons (see below) except that no larval hairs are incorporated, the structure consists of a single layer in both species, and hibernacula are never spun in exposed locations. Larvae confined within enclosures on the tundra generally spin hibernacula in clumps of vegetation or in litter and incorporate litter into the structure, making it well camouflaged. Such hibernacula are rarely found on the open tundra, probably due to their cryptic nature; however, hibernacula are commonly found beneath or between loosely piled rocks (Figure 12F). Hibernacula spun in high-density stock corrals were often found to contain two or more larvae; however, hibernacula spun in experimental corrals or found on the open tundra never contained more than a single larva.

Figure 12. *Gynaephora groenlandica* (A, C, E, F) and *Gynaephora rossii* (B, D, E). Spinulose larval hairs (A). Plumose larval hairs (B). Portions of the outer (right) and inner (left) layers of the pupal cocoon (C). A portion of the pupal cocoon (D). Complete cocoons of *G. groenlandica* (left) and *G. rossii* (right) (E). Larval hibernacula; the opening in the occupied hibernaculum was the result of removing an overlying rock (F).


A
B
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D
E
F

Cocoons

Cocoons are spun on the surface of the tundra and anchored to the substrate, not concealed in any way but rather located in exposed sites with maximum insolation, on substrates of vegetation, litter, bare soil, or rock. The cocoons of *G. groenlandica* are much larger than those of *G. rossii* (Figure 12E), mainly due to the difference in structure (see below).

***G. groenlandica*:** Cocoons are constructed in two distinct layers with a considerable air space between the layers. The outer layer is ovoid, with dimensions of 32 ± 3 mm in length by 19 ± 2 mm in width (n = 279), comprised of a thin layer of silk with some larval hairs, and cream coloured to deep yellow or grey, depending on the number and relative proportions of black and yellow larval hairs incorporated and the extent of weathering. The inner layer is oblong-ovoid, with dimensions of 28 ± 3 mm in length by 13 ± 1 mm in width (n = 279), comprised mainly of larval hairs tied together with silk, and correspondingly deeper in colour than the outer layer. The cocoons of females, with outer layer dimensions of 34 ± 3 mm by 20 ± 2 mm and inner layer dimensions of 30 ± 2 mm by 14 ± 1 mm (n = 124), are significantly larger ($t_{(1)277}$ = 6.463 for outer length, 3.576 for outer width, 12.970 for inner length, 9.770 for inner width; $P < 0.0005$ in all cases) than those of males, with outer layer dimensions of 31 ± 3 mm by 19 ± 2 mm and inner layer dimensions of 26 ± 2 mm by 13 ± 1 mm (n = 155).

***G. rossii*:** Cocoons are constructed in a single layer roughly equivalent to the inner cocoon of *G. groenlandica*, oblong-ovoid, with dimensions of 26 ± 2 mm in length by 13 ± 1 mm in width (n = 56), comprised of a single layer of silk with many larval hairs incorporated, and dark grey to light grey, depending on the extent of weathering.

The cocoons of females, with dimensions of 27 ± 2 mm by 13 ± 1 mm (n = 17), are significantly larger ($t_{(1)54}$ = 2.852, $0.0025 < P < 0.005$ for length; $t_{(1)54}$ = 2.143, $0.01 < P < 0.025$ for width) than those of males, with dimensions of 25 ± 2 mm by 12 ± 1 mm (n = 39).

Pupae

The pupae of both species (Figure 13) are reddish-brown, darkening to black as the pharate adults mature but often retaining some areas of reddish-brown cuticle, most notably along the caudal margins of the abdominal segments. The pupae are very hairy. The hairs arise from the scars of the larval verrucae and are brown to golden yellow and always simple, not plumose or spinulose. The dorsal hairs are long, dense, and erect; the ventral hairs are much shorter, sparser, and recumbent. The labrum is trapezoidal with rounded corners and a caudal margin varying from straight to strongly concave. The maxillae are short, slightly longer than the labial palps, and the coxae of the prothoracic legs are distinctly visible caudad of the maxillae. The prothoracic legs (excluding the coxae) border on each other for about as long as the length of the maxillae. The antennae are short, extending only about halfway to the caudal margin of the wings. The wingtips are separated by the ends of the metathoracic legs. The ventral surface of abdominal segments 9 and 10 tapers steeply towards the cremaster, which is short and conical, somewhat flattened dorsoventrally, with a rounded apex bearing a group of short hooked setae.

***G. groenlandica*:** The pupae have dorsal hairs up to 4 mm in length and ventral hairs up to 2 mm in length. Hairs are usually absent from the ventral surface of abdominal segment 9 and are always absent from the ventral surface of abdominal segment 10. The maxillae usually curve mesad and often meet beyond the ends of the labial palps. The ventral surface of the cremaster has fine longitudinal grooves in females which are less apparent in males. Female pupae, with dimensions of 24.0 ± 2.0 mm in length by 9.5 ± 0.5 mm in width ($n = 3$), are significantly larger ($t_{(1)4} = 3.255$, $0.01 < P < 0.025$ for length; $t_{(1)4} = 7.071$, $0.001 < P < 0.0025$ for width) than male pupae, with dimensions of 19.5 ± 1.0 mm in length by 7.5 ± 0.5 mm in width ($n = 3$).

***G. rossii*:** The pupae have dorsal hairs up to 3 mm in length and ventral hairs up to 1.5 mm in length. Hairs are always present on the ventral surface of abdominal segment 9 and are usually present on ventral surface of abdominal segment 10. The maxillae are roughly straight or slightly curved mesad but never meet beyond the ends of the labial

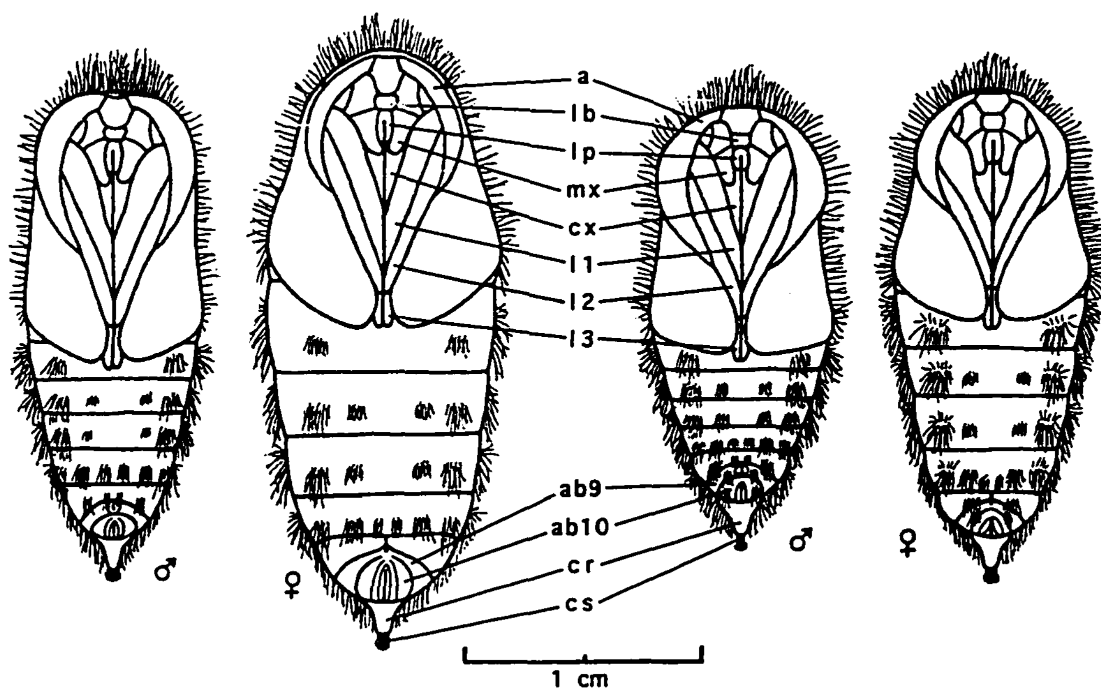


Figure 13. Pupae of *Gynaephora groenlandica* (left) and *Gynaephora rossii* (right) in ventral view. Abbreviations: a = antenna, ab = abdominal segment, cr = cremaster, cs = cremastral setae, cx = coxa of the prothoracic leg, l1 = prothoracic leg, l2 = mesothoracic leg, l3 = metathoracic leg, lb = labrum, lp = labial palp, mx = maxilla.

palps. The ventral surface of the cremaster is smooth. Female pupae, with dimensions of 19.0 ± 1.0 mm in length by 8.0 ± 0.5 mm in width ($n = 2$), are larger than male pupae, with dimensions of 17.0 ± 1.0 mm in length by 7.0 ± 0.5 mm in width ($n = 3$), the difference being statistically significant for length ($t_{(1)3} = 2.402$, $0.025 < P < 0.05$) but not for width ($t_{(1)3} = 2.049$, $0.05 < P < 0.10$), probably due, at least in part, to the small sample size.

The pupae of *G. groenlandica* are generally larger than those of *G. rossii*, the difference being more pronounced for females ($t_{(1)3} = 3.349$, $0.01 < P < 0.025$ for length; $t_{(1)3} = 5.563$, $0.005 < P < 0.01$ for width) than for males ($t_{(1)4} = 3.545$, $0.01 < P < 0.025$ for length; $t_{(1)4} = 2.121$, $0.05 < P < 0.10$ for width). Considerable variation was seen among individuals in exact shapes and relative dimensions of morphological features, even in the small number of pupae examined in detail. Therefore, differences between species, as described above, were limited to those most consistent and clearly visible; nonetheless, these differences should be regarded with caution.

Differences between *G. groenlandica* and *G. rossii* in the immature stages are outlined in Table 2. Voucher specimens, including eggs, most larval instars, pupae, cocoons, and adults of both species, have been submitted to the Canadian National Collection of Insects, Ottawa, Ontario.

Life Histories and Biology

Of the species included in this study, the only one for which detailed life history data had been previously published is *G. groenlandica* (Kukal and Kevan 1987). During the course of this study, however, it became clear that much of the previously published life history data could not be used as a baseline because the insects were not developing as described by Kukal and Kevan (1987) even though that study was conducted at the same site. Therefore, key life history parameters of *G. groenlandica* were investigated in detail, as described in the following sections. Similar data were collected for *G. rossii*, but because *G. rossii* were encountered much less frequently than *G. groenlandica*, a similarly detailed analysis of life history data could not be conducted for *G. rossii*.

Table 2. Morphological differences between high arctic *Gynaephora* species in the immature stages. For measurements, the full range found in this study is given.

Stage Morphological feature	*G. groenlandica*	*G. rossii*
Eggs		
Diameter (mm)	1.55 – 1.70	1.35 – 1.45
Height (mm)	1.30 – 1.40	1.05 – 1.15
Larvae		
Cuticle between verrucae		
First instar	black	pale
Second instar	black	paler than verrucae
All subsequent instars	black	black
Form of larval hairs		
First instar	all spinulose	all spinulose
Second instar	all spinulose	some plumose
All subsequent instars	all spinulose	many plumose
Colour of larval hairs		
First instar	black and brown	uniformly grey
All subsequent instars	varying shades of brown with distinct dorsal tufts of black and yellow	longer plumose hairs grey, shorter hairs black and yellow
Cocoons		
Colour	cream to deep yellow, occasionally grey	grey
Outer layer		
length (mm)	25 – 40	21 – 30
width (mm)	14 – 26	11 – 16
Inner layer		
length (mm)	19 – 35	N/A*
width (mm)	10 – 17	N/A*
Pupae		
Length (mm)	19.0 – 26.0	16.0 – 19.5
Width (mm)	7.5 – 9.5	7.0 – 8.0

*N/A = not applicable; this structure does not occur in *G. rossii*.

Gynaephora Species

Head-capsule widths and number of larval instars

The distribution of HCWs for *G. groenlandica* showed a number of distinct peaks but no gaps separating the peaks, indicating that the range of HCWs for individual instars overlapped (Figure 14). Parameters estimated through the EM algorithm produced a greater log of the likelihood function for seven instars (-810.48) than for six (-814.64), and $\chi^2_3 = 2(-810.48 - (-814.64)) = 8.301$ ($0.025 < P < 0.05$), indicating that the seven-instar model produced a significantly better fit to the data (Figure 15). Regression of mean HCW and instar number for *G. groenlandica* yielded the constants $a = 0.5441$ and $b = 0.2906$ ($r^2 = 0.993$), and thus a growth ratio of 1.34. Observed and expected mean HCWs did not differ significantly ($\chi^2_4 = 0.038$, $P > 0.999$), suggesting that the observed mean HCWs conform to the Brooks-Dyar rule, although there were apparent deviations in the fourth and seventh instars (Table 3). Growth ratios measured for individual larvae ranged from 1.02 to 1.50 with a mean of 1.30 ± 0.09 ($n = 98$), a value very similar to that produced by regression analysis of the observed mean HCWs with respect to the Brooks-Dyar rule. In addition, regression of individual growth ratios by instar was not statistically significant, although the relationship did show a negative slope (Figure 16), suggesting a tendency for growth ratios to decline slightly at progressively later moults.

The distribution of HCWs for *G. rossii* also showed distinct peaks for the first three instars and the final instar, and these peaks were clearly separated, but too few data were obtained to distinguish the intermediate instars (Figure 14). Growth ratios measured for individual larvae ranged from 1.42 to 1.53 with a mean of 1.48 ± 0.06 ($n = 4$) and growth ratios calculated from the mean HCWs of the first three instars were 1.42 and 1.47 for the first two moults. Extrapolating from the mean HCWs of the first three instars using 1.45 as an estimate of the overall average growth ratio suggested a total of six instars, with an overestimate of the mean HCW for the final instar, compared to the sample data, similar to that found for *G. groenlandica* (Figure 14).

Figure 14. Frequency distribution of measured head-capsule widths for *Gynaephora groenlandica* (above) and *Gynaephora rossii* (below). Solid columns represent head capsules shed by larvae reared from eggs, open columns represent naturally moulted head capsules collected from the field, and stippled columns represent head capsules of larvae killed by parasitoids after spinning cocoons. Inverted triangles indicate mean head-capsule widths estimated according to the Brooks-Dyar rule.

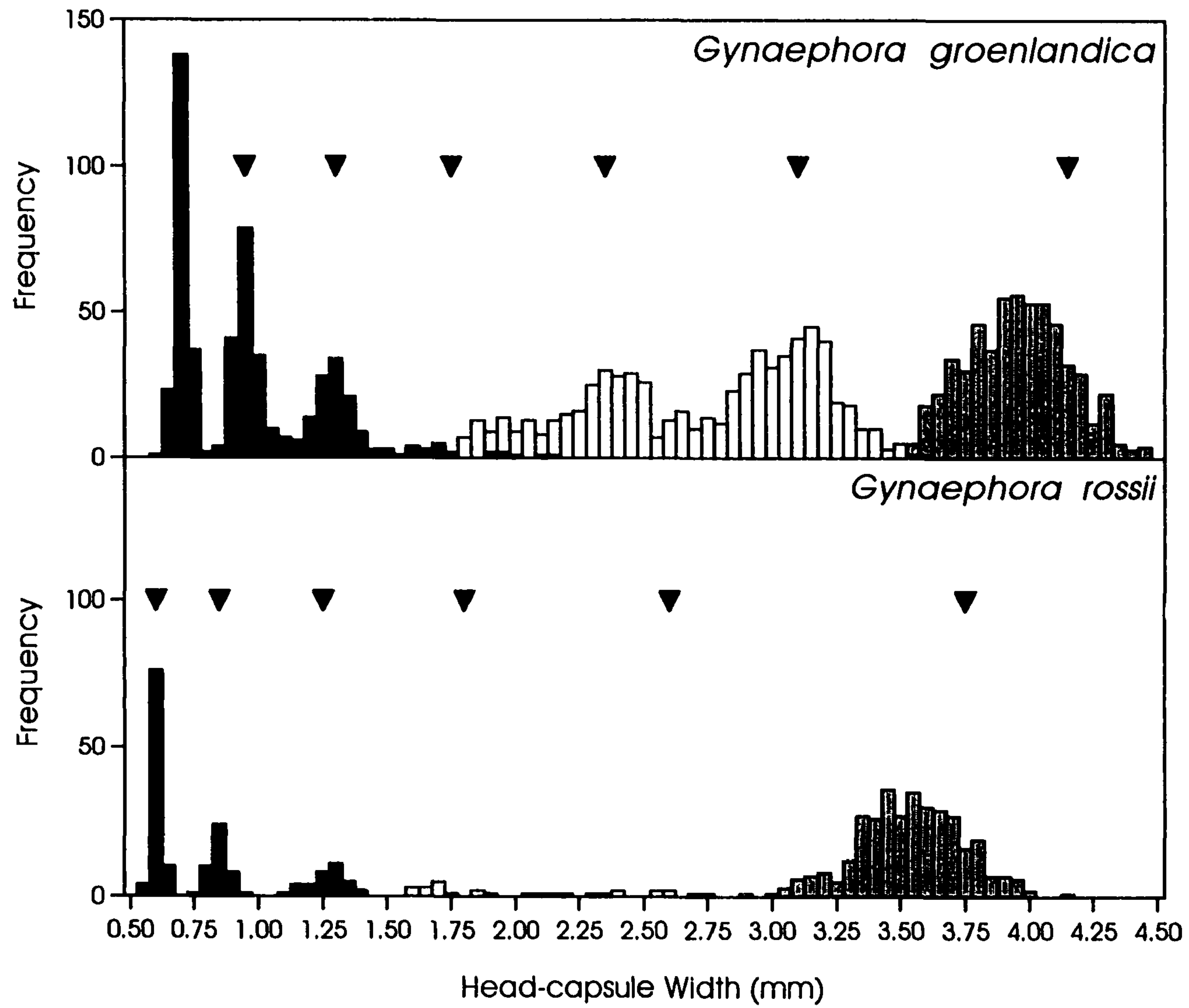

Gynaephora groenlandica
Gynaephora rossii
Frequency
Frequency
150
100
50
0
100
50
0
0.50 0.75 1.00 1.25 1.50 1.75 2.00 2.25 2.50 2.75 3.00 3.25 3.50 3.75 4.00 4.25 4.50
Head-capsule Width (mm)

Figure 15. Frequency distribution of measured head capsule widths of *Gynaephora groenlandica* with the fitted function representing six (above) or seven (below) larval instars. Parameters for the fitted function, estimated through the EM algorithm, are given as mean ± standard deviation, with the proportion in parentheses, for each instar.

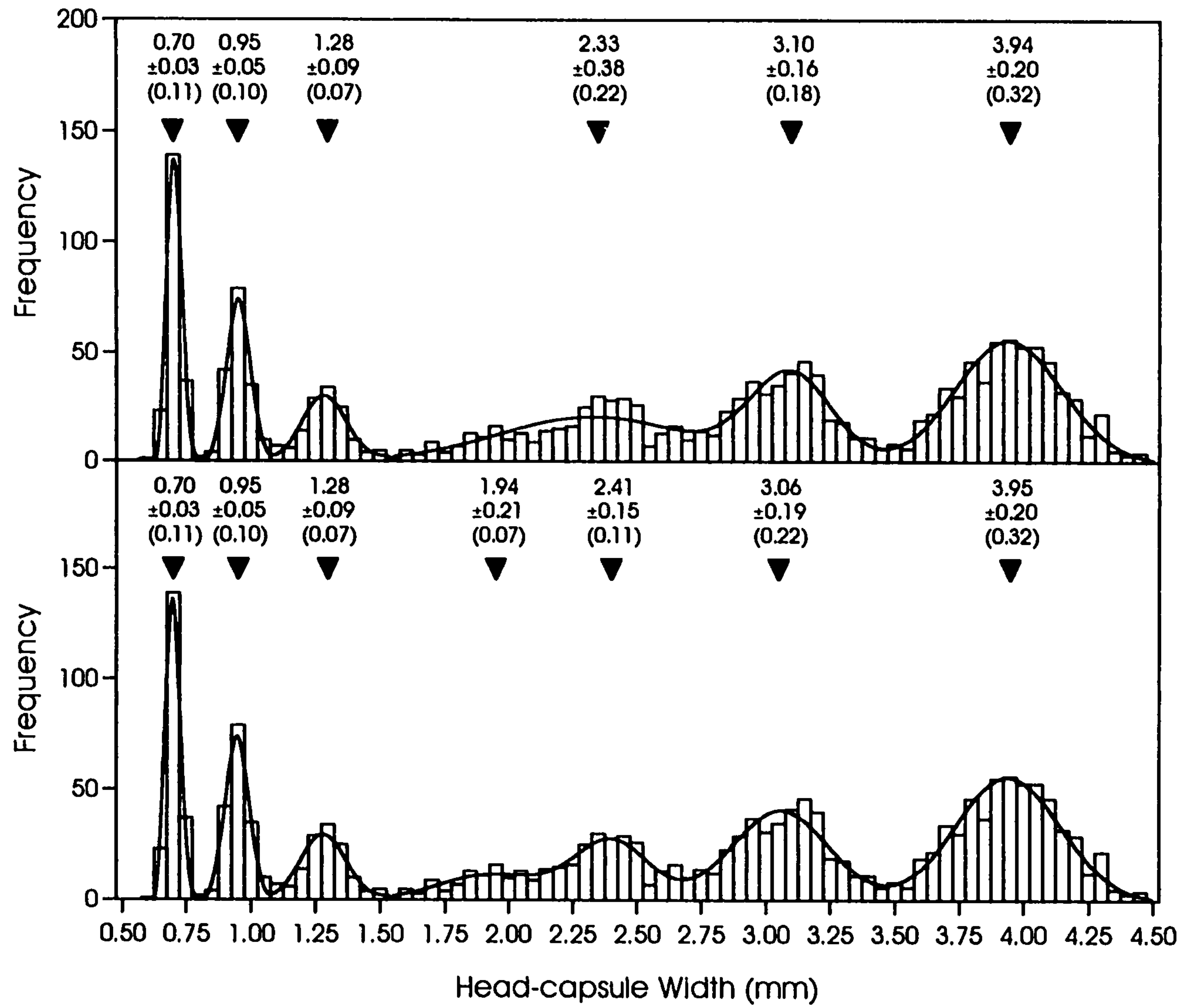

0.70
±0.03
(0.11)
0.95
±0.05
(0.10)
1.28
±0.09
(0.07)
2.33
±0.38
(0.22)
3.10
±0.16
(0.18)
3.94
±0.20
(0.32)
0.70
±0.03
(0.11)
0.95
±0.05
(0.10)
1.28
±0.09
(0.07)
1.94
±0.21
(0.07)
2.41
±0.15
(0.11)
3.06
±0.19
(0.22)
3.95
±0.20
(0.32)
Frequency
0
50
100
150
200
0.50 0.75 1.00 1.25 1.50 1.75 2.00 2.25 2.50 2.75 3.00 3.25 3.50 3.75 4.00 4.25 4.50
Head-capsule Width (mm)

Table 3. Comparison of previously reported mean larval head capsule widths (HCW) of *Gynaephora groenlandica* to expected and observed mean HCW determined in this study, with corresponding growth ratios and boundary points between observed means. Reported means are from Kukal and Kevan (1987), expected means were predicted by the Brooks-Dyar Rule, observed means were estimated from measured data through the EM algorithm, and boundary points between instars were determined by the likelihood ratio method of Beaver and Sanderson (1989).

Instar:	I		II		III		IV		V		VI		VII
Reported mean (mm)	0.7		1.4		2.4		2.8		3.2		3.8		n/a
Growth ratio		**2.00**		**1.71**		**1.17**		**1.14**		**1.19**		**n/a**	
Expected mean (mm)	0.73		0.97		1.30		1.74		2.33		3.11		4.16
Growth ratio		**1.34**		**1.34**		**1.34**		**1.34**		**1.34**		**1.34**	
Observed mean (mm)	0.70		0.95		1.28		1.94		2.41		3.06		3.95
Growth ratio		**1.35**		**1.35**		**1.51**		**1.24**		**1.27**		**1.29**	
Boundary point (mm)		0.80		1.08		1.50		2.16		2.68		3.47	

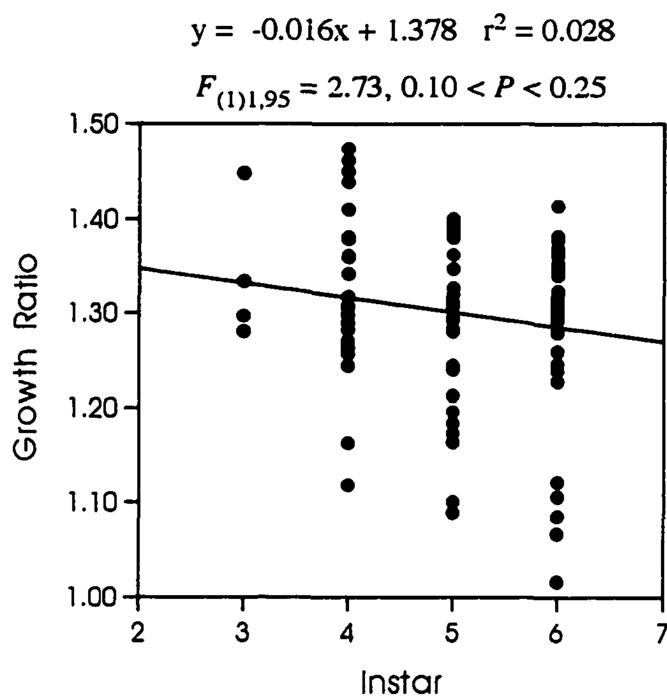


Figure 16. Regression of individual growth ratios of *Gynaephora groenlandica* by instar, with instars classified according to the head-capsule width of exuviae using the boundary points in Table 3.

Larval activity and moulting frequency

Most *Gynaephora* larvae obtained from eggs hatched indoors and subsequently reared indoors did not develop beyond the first instar before the end of the field season. Of 589 and 785 larvae of *G. groenlandica* reared in this way in 1994 and 1995, respectively, only 123 (21%) and 241 (31%) moulted to the second instar before the end of the field season, while a single individual developed as far as the third instar each year. Of the 100 first-instar and 100 second-instar larvae of *G. groenlandica* placed in corrals in August of 1994, 79 and 46, respectively, were recovered alive in June of 1995 and all were the same instar as when they had been placed in the corrals. Similarly, 35 larvae were recovered in June of 1995 from six different egg masses of *G. groenlandica* that had hatched in corrals in the field during the summer of 1994, and all of these were still first instars. These larvae were left in the corrals to develop under field conditions until the end of the field season in 1996, at which time 11 larvae were recovered. All of these larvae were judged to be third instars when they were collected and this was confirmed by measurements of their head capsules moulted in the laboratory in the spring of 1997. Of 38 larvae of *G. rossii* reared indoors from eggs hatched in 1995, only four moulted to the second instar before the end of the field season and of these 34 first-instar and four second-instar larvae placed in a small corral in August of 1995, 20 and one, respectively, were recovered alive in July of 1996.

In the spring of 1996, each of the larvae of *G. groenlandica* held in larger corrals emerged from its hibernaculum on the day that the location of its hibernaculum became snow-free (Figure 17) and these larvae remained active for only 19 ± 3 d ($n = 17$) (Figure 18). Standardized surveys indicated that the bulk of the larval population was active only until the third week of June in 1994, the fourth week of June in 1995, and the second week of July in 1996 due to an extremely late and prolonged snowmelt (Figure 19). These data were corroborated by more wide-ranging observations; very few *G. groenlandica* larvae were found active on the tundra after 1 July 1994, 15 July 1995, and 19 July 1996, and none were found after 1 August 1994, 31 July 1995, and 4 August 1996, except neonates (see "Metamorphosis and reproduction" below). In contrast, larvae

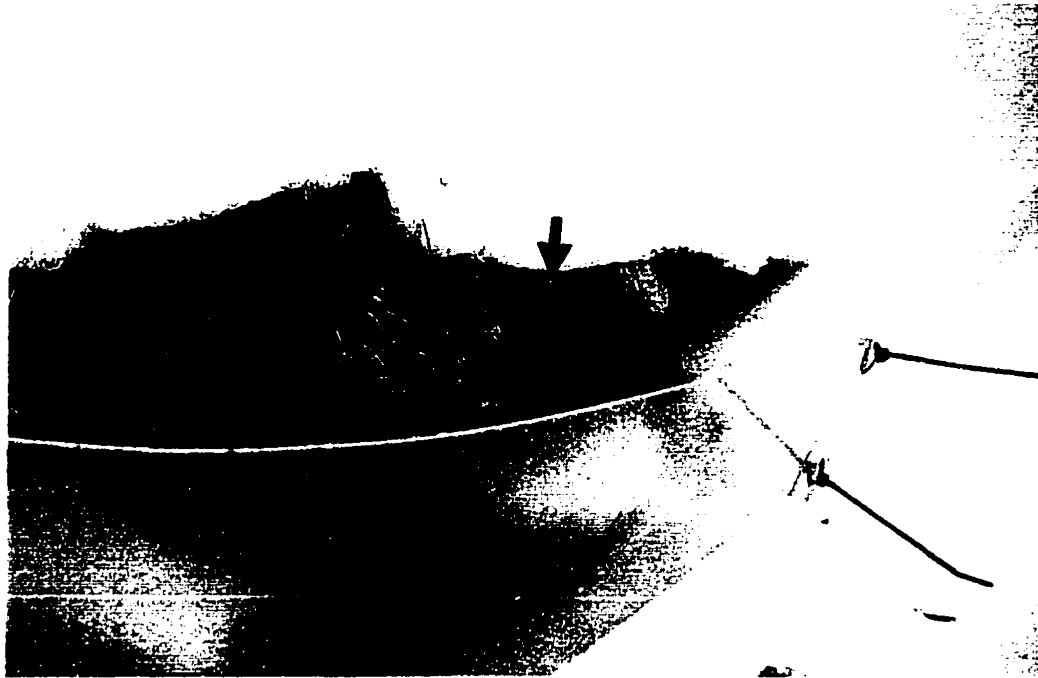


Figure 17. An active *Gynaephora groenlandica* larva (arrow) in a very small patch of snow-free ground in a corral within a small open-top chamber.

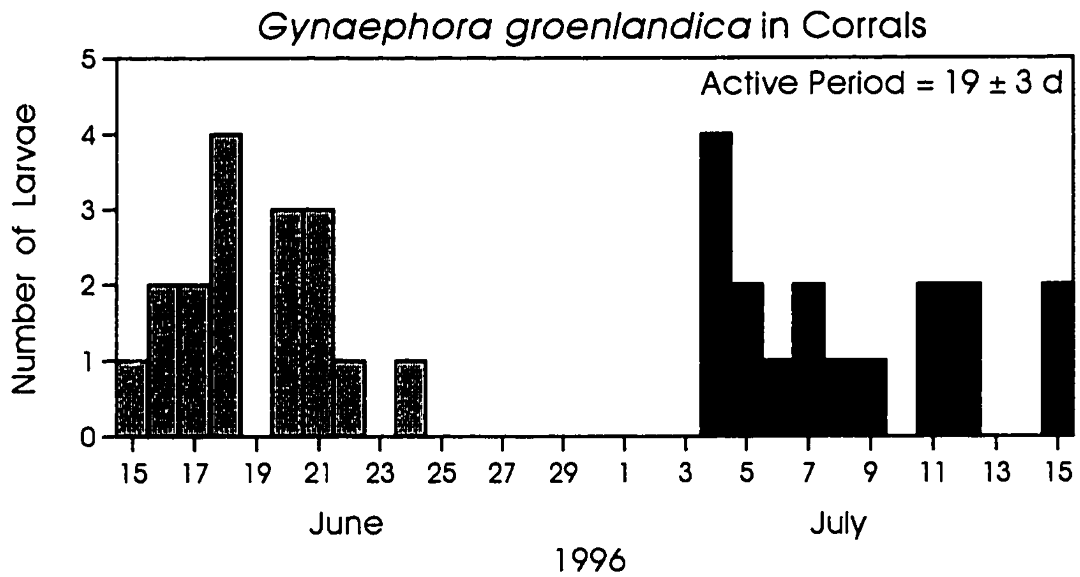


Figure 18. Spring emergence from hibernacula (stippled columns), and spinning of new hibernacula (solid columns), by *Gynaephora groenlandica* larvae held in corrals in the field in 1996. "Active period" was calculated from the dates of emergence and hibernaculum-spinning for each larva individually.

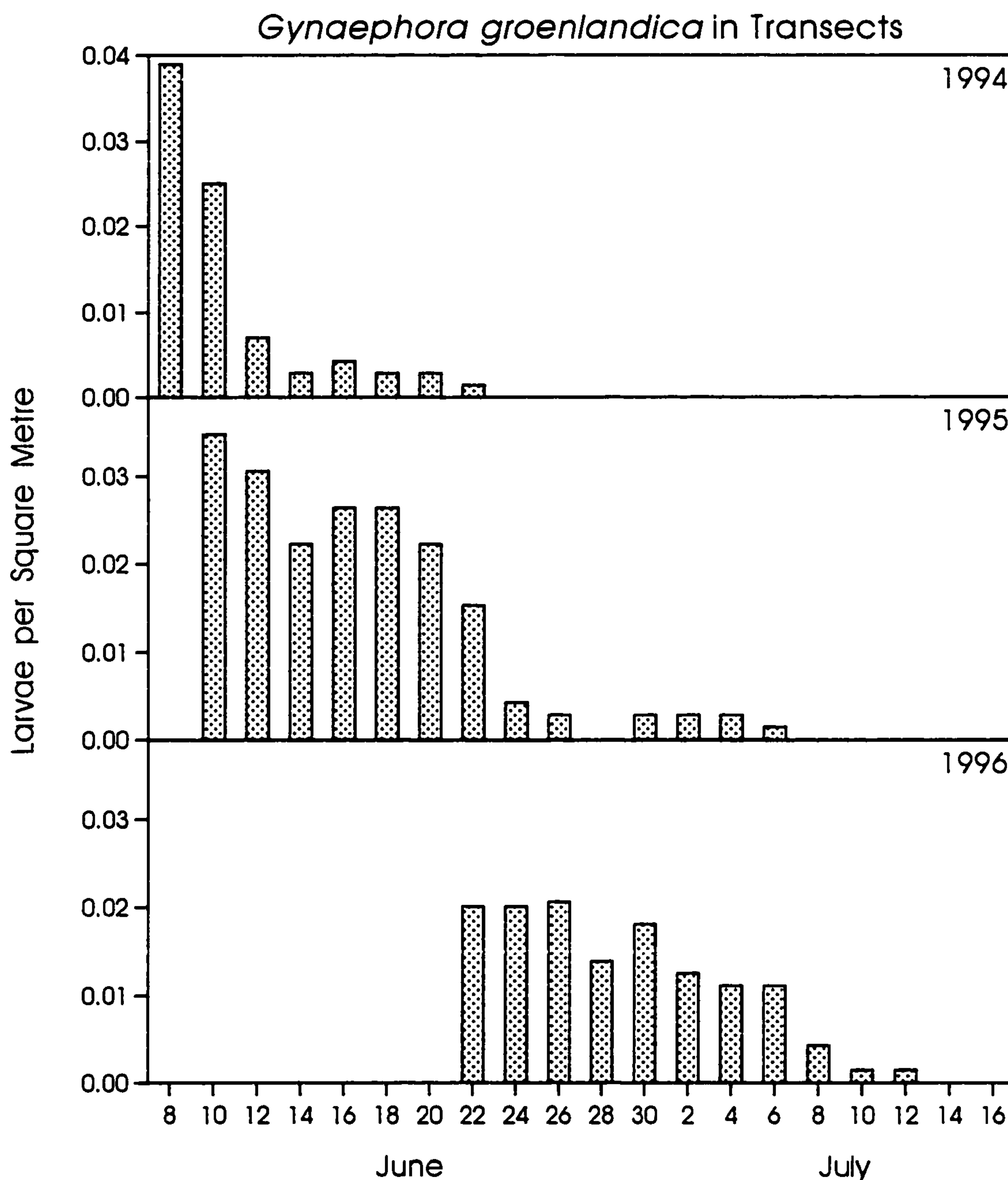


Figure 19. Seasonal decline in larval activity of *Gynaephora groenlandica* as recorded in standardized transect surveys. Later declines reflect later onsets of the growing season caused by heavier snowpacks and later snowmelts. Earlier portions of the period of larval activity in 1995 and 1996 were not recorded due to lingering snow cover on the transects.

Table 4. Numbers of *Gynaephora rossii* larvae found active on the tundra during each month of each year of the study, excluding fully grown larvae spinning cocoons in June.

	June	July	August	Total
1994	3	5	11	19
1995	2	3	7	12
1996	0	2	11	13
Total	5	10	29	44

of *G. rossii* remained active late in the growing season, with active larvae observed regularly on the tundra until and including 15 August 1994, 17 August 1995, and 13 August 1996, the last day of the field season each year. In all three years, with the exception of fully grown larvae that were spinning cocoons in June, more *G. rossii* larvae were found active in August than in June and July combined (Table 4), even though the number of days of fieldwork in August was only half that in either June or July.

Of the 24 *G. groenlandica* larvae placed in corrals on 13 June 1995, 17 moulted that year, one was killed by the parasitoid *H. pectinatus*, and the remaining six did not moult during the time they were monitored, but may have done so before they were placed in the corrals. Of the 48 larvae monitored throughout the field season in 1996, 15 were killed by parasitoids, three died of other causes, and all of the remaining 30 either moulted or spun cocoons. Furthermore, of 11 larvae that had been observed to moult in 1995 and that survived to be monitored throughout a second field season, one moulted again and the other 10 all spun cocoons in 1996 despite the extremely late snowmelt and poor summer weather. Similarly, of the 17 larvae collected from these corrals at the end of the field season in 1996 and reared in the laboratory in the spring of 1997, all of which had moulted in the field in 1996, eight were killed by parasitoids, one moulted again, and the remaining eight all spun cocoons.

Laboratory-reared larvae became active within hours of being brought out of

Table 5. Numbers of individual *Gynaephora groenlandica* larvae (fourth to seventh instars) reared individually in the field (1996) or in the laboratory under continuous light at a constant temperature of 15°C, 20°C, or 25°C (1996 & 1997) showing the developmental pattern specified.

	Field	15°C	20°C	25°C	Total
Spun cocoon	12	3	22	4	41
Moulted once	18	8	15	11	52
Moulted twice	0	0	1	0	1
Moulted then spun cocoon	0	0	1	1	2
Did not moult or spin cocoon	0	1	0	0	1
Total	30	12	39	16	97

subzero temperatures, and most began feeding within a day or two. The majority (almost 75%) of the *G. groenlandica* larvae collected in the field in 1996 for laboratory rearing in the spring of 1997 were parasitized and were killed by the parasitoids during laboratory rearing. Of the 45 remaining larvae (excluding the nine already reported above), 13 spun cocoons and pupated, 27 moulted once and later spun hibernacula and became dormant, one did not moult before spinning a hibernaculum, one moulted twice before spinning a hibernaculum, two moulted and later spun cocoons and pupated, and one moulted once but did not spin a hibernaculum (this last larva simply ceased feeding and hid in the leaf litter). Overall, laboratory-reared larvae of *G. groenlandica* showed a pattern of development strikingly similar to that observed in the field (Table 5), the larvae becoming active as soon as conditions allowed, moulting once (with very few exceptions), and later spinning hibernacula and becoming dormant even under unchanging rearing conditions.

In contrast, larvae of *G. rossii* remained active late in the growing season, as noted above, and were not limited to a single moult each year (except for most neonates, which did not eclose from eggs until late in the growing season). Unfortunately, too few larvae of *G. rossii* were found in the field to monitor moulting frequency as was done with

G. groenlandica; however, larvae that were found relatively early in the growing season (late June or early July) and reared indoors at the field site until the end of the field season developed through two or three moults ($n = 2$ and 1, respectively) during that time. Furthermore, of 11 larvae from eggs hatched in 1995 that survived to be reared in the laboratory in 1997, four were third instars, four were fourth instars, and three were fifth instars by the end of the growing season in 1996, based on measurements of head capsules moulted in the laboratory in the spring of 1997. Similarly, larvae from eggs hatched in 1996 developed as far as the sixth (final) instar before becoming dormant during laboratory rearing at 20°C in 1997.

Larvae of *G. groenlandica* always moulted out in the open and usually spun a thin silk platform on which to anchor themselves during the moult. The early-instar larvae of *G. rossii* reared indoors also moulted out in the open; however, older larvae of *G. rossii* spun silk shelters, similar to hibernacula in structure and location, in which to moult. After moulting, these larvae emerged from the shelters to resume their activity, leaving their exuviae within. This difference in moulting behaviour between *G. groenlandica* and *G. rossii* was observed both in the field and in laboratory-reared larvae.

Gynaephora larvae were observed feeding on 11 different species of plants, representing seven different plant families (Table 6). For *G. groenlandica*, *Salix arctica* represented 87% of the feeding observations, most of these being buds and expanding leaves, with *Dryas integrifolia* representing 7%, *Saxifraga oppositifolia* 3%, and the remainder represented by single or very few observations. The few feeding observations for *G. rossii* were almost evenly split between *S. arctica* and *D. integrifolia*, with a single observation of a larva feeding on developing fruits of *Cassiope tetragona* on the tundra (Table 6).

Gynaephora larvae apparently suffered very little predation, with only two instances of predation on *Gynaephora* larvae being observed during the course of this study. In both cases, syrphid larvae (Diptera: Syrphidae) were found feeding on small larvae of *G. groenlandica*.

Table 6. Plants on which *Gynaephora* larvac were observed feeding at Alexandra Fiord, Ellesmere Island, during the spring and summer of 1995 and 1996.

Plant species Part eaten	Number of observations *G. groenlandica*	 *G. rossii*
Salix arctica Pallas (Salicaceae)		
Buds (unopened)	99	0
Expanding leaves	166	1
Developing catkins	48	0
Mature leaves	6	2
Senescent leaves	0	3
Dryas integrifolia M. Vahl (Rosaceae)		
Leaves	24	5
Flower petals	1	0
Saxifraga oppositifolia Linnaeus (Saxifragaceae)		
Flowers	9	0
Leaves	3	0
Oxyria digyna (Linnaeus) Hill (Polygonaceae)		
Leaves	1	0
Arctagrostis latifolia (R. Brown) Grisebach (Gramineae)		
Leaves	1	0
Festuca brachyphylla Schultes (Gramineae)		
New shoots	1	0
Luzula confusa Lindeberg (Juncaceae)		
Leaves	2	0
Flower head	1	0
Luzula arctica Blytt (Juncaceae)		
Leaves	1	0
Flower stalk	1	0
Potentilla hyparctica Malte (Rosaceae)		
Flower	1	0
Vaccinium uliginosum Linnaeus (Ericaceae)		
Leaves	1	0
Cassiope tetragona (Linnaeus) D. Don (Ericaceae)		
Developing fruits*	0	1

*Developing fruits were also accepted as food by *G. rossii* larvae held in the laboratory; foliage and mature fruits were not.

Metamorphosis and reproduction

Fully grown larvae began spinning cocoons very soon after becoming active in the spring. Larvae of *G. groenlandica* held in corrals began spinning cocoons 5 ± 2 d (range: 0-7 d; n = 13) after emerging from their overwintering hibernacula, and larvae of both species were commonly seen spinning cocoons in small patches of snow-free ground where they could not have been active for more than a few days. Cocoons were either completed within one day or required two or three days for completion. Similarly, pupation either occurred within one day of the cocoon being completed or was delayed for two or three days. Pupal development in the field, from pupation to adult emergence, required 15 ± 4 d for both *G. groenlandica* (n = 55) and *G. rossii* (n = 3). The variation in time required to complete these developmental stages was due, at least in part, to variations in weather conditions, with cool and/or cloudy weather retarding activity and development.

Pupae and occasionally prepupae, mainly those of *G. groenlandica*, were subject to extensive predation by birds, probably due to the conspicuous nature of their cocoons. Jaegers (*Stercorarius* spp.), both parasitic (*S. parasiticus* L.), which breed on the Alexandra Fiord lowland, and long-tailed (*S. longicaudatus* Vieillot), which do not breed at Alexandra Fiord but often forage there, were seen to tear open cocoons and consume the contents. Smaller birds preyed on *Gynaephora* pupae by pecking through the cocoon and into the pupa. In 1995, 248 cocoons of *G. groenlandica* and six of *G. rossii* were attacked by birds, compared to 400 and 39, respectively, from which adults emerged. Jaegers were the most important bird predators, as indicated by a subsample of cocoons in which 10 of *G. groenlandica* and one of *G. rossii* were pecked and 66 of *G. groenlandica* and four of *G. rossii* were torn open and empty. Similarly in 1996, 86 cocoons of *G. groenlandica* and six of *G. rossii* were attacked by birds, of which 70 of *G. groenlandica* and all six of *G. rossii* were torn open and empty, compared to 152 and 21, respectively, from which adults emerged. The proportions of cocoons attacked in different ways (*i.e.* torn open *vs.* pecked) was independent of the species of cocoon and did not differ significantly between years (G_3 = 1.513, $0.50 < P < 0.75$). Similarly, the overall rate of predation on cocoons by birds did not differ significantly between years for either *G. groenlandica*

($\chi^2_{c'}$ = 0.300, 0.50 < P < 0.75) or *G. rossii* ($\chi^2_{c'}$ = 0.445, 0.50 < P < 0.75); however, the rate of predation was not independent of the species of prey ($\chi^2_{c'}$ = 12.757, P < 0.001), with a larger proportion of the cocoons of *G. groenlandica* than those of *G. rossii* being attacked.

Gynaephora adults also suffered predation by birds, with snow buntings (*Plectrophenax nivalis* L.) attacking recently emerged adults on cocoons and chasing males in flight, but no attempt was made to quantify this type of predation. The adult population, as determined from total numbers of pupal exuviae collected throughout the field season, of *G. groenlandica* declined markedly from 1994 to 1996, with a large difference between 1994 and 1995 and a smaller difference between 1995 and 1996; the adult population of *G. rossii* also varied from year to year but was larger in 1995 than in 1994 and smaller in 1996 than in the previous two years (Figure 20).

Adults of both sexes have fully developed wings and males were seen to be strong fliers; however, females flew very little and when they did, scarcely got off the ground. These females apparently relied on pheromones to attract mates. Calling females of both species repeatedly extended and retracted their ovipositors but did not flutter their wings as described for *G. groenlandica* by Kukal and Kevan (1987); this behaviour was observed in the field as well as in cages both at the field site and at the University of Victoria. In 1995, none of the males of *G. rossii* made any attempt to mate after being placed in the cage with virgin females of *G. groenlandica*, even when they came into direct contact with the females; however, the two males of *G. groenlandica* that were later added to the same cage each mated with one of the females within one minute of being placed in the cage. In 1996, statistically equal numbers of males of each species were attracted by calling females of *G. groenlandica* (χ^2_c = 0.817, 0.25 < P < 0.50); however, attraction of the different species of males was not independent of the species of calling female (χ^2_c = 22.825, P < 0.001), with many more males of *G. rossii* than of *G. groenlandica* attracted to the female of *G. rossii* (Table 7). In no case did an interspecific mating occur; however, all

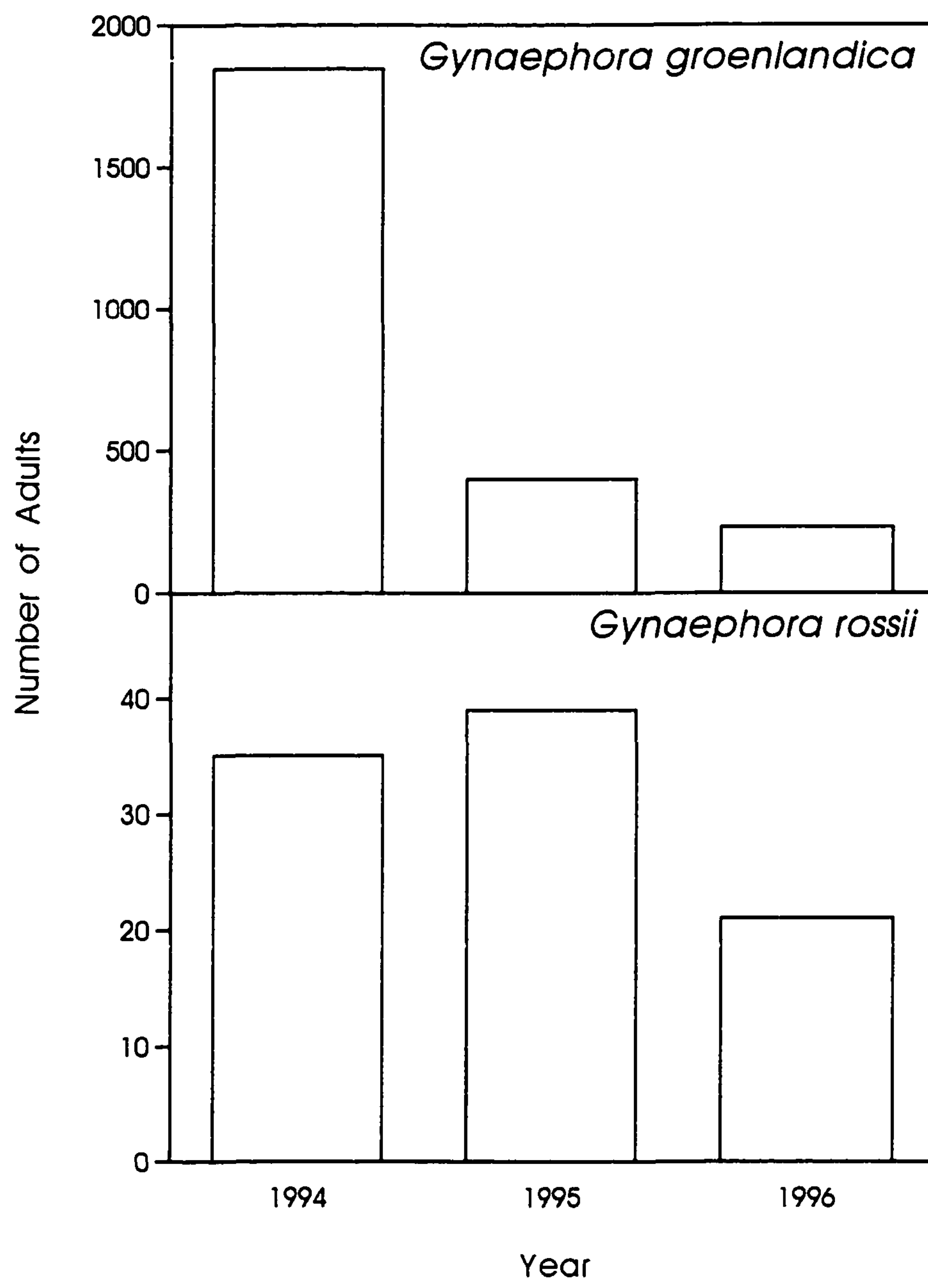


Figure 20. Adult populations of *Gynaephora groenlandica* and *Gynaephora rossii* in the study area each year, as indicated by total numbers of empty pupal exuviae collected throughout the field season each year.

Table 7. Number of male *Gynaephora* attracted to caged virgin females of either *Gynaephora groenlandica* or *Gynaephora rossii* during three 3-h periods in 1996, and females mated when heterospecific followed later by conspecific males were introduced.

Date	Species of female (n)	Males attracted		Females mated	
		G. groenlandica	*G. rossii*	Interspecific	Conspecific
8 July	*G. groenlandica* (2)	3	4	0	2
13 July	*G. groenlandica* (4)	31	22	0	4
14 July	*G. rossii* (1)	3	37	0	1

females mated when conspecific males were later introduced into the cage (Table 7) and did so within three minutes of the introduction of the males, with the exception of a single female on 13 July which remained unpaired for almost an hour. Males that mated did so from alongside the female and then usually turned around to assume an end-to-end position rather than remaining in the side-by-side position as do other lymantriid moths (Charlton and Cardé 1990a).

In the field, a female normally remained on her cocoon until she attracted a male and, once mated, often laid a mass of eggs there (Figure 10A). Additional eggs were laid nearby on vegetation or on the ground, with no apparent discrimination among potential oviposition sites, and some females left their cocoons even before laying their initial egg masses (Figure 10B). Of nine initial egg masses laid in the field in 1996, four were laid on cocoons whereas five were not. Eggs of *G. groenlandica* laid on cocoons were very conspicuous and suffered heavy predation by birds (Figure 10C), primarily snow buntings. Of 39 egg masses found on cocoons during the summer of 1994, 26 showed signs of predation and a further 11 were completely removed before they could be protected with netting; only two egg masses were protected before apparently suffering any predation. In contrast, egg masses laid on the ground were quite cryptic (Figure 10D) and none of these egg masses were found to suffer any predation. No evidence of predation

on eggs of *G. rossii* was seen; however, very few egg masses of this species were found in the field.

Embryonic development in the field, measured from the day an initial egg mass was laid to the day the first larvae eclosed, required 27 ± 5 d (n = 13) for *G. groenlandica*; only one *G. rossii* was observed to lay an egg mass in the field and this required 31 d to begin hatching. Upon hatching, neonates usually ate a portion, often most but rarely all, of the chorion from which they emerged. Most of the field data for embryonic development was obtained in 1995; due to the delayed and prolonged snowmelt and poor summer weather in 1996, only 4 of 12 egg masses that were being monitored in the field began hatching before the end of the field season (13 August). Some of the unhatched egg masses were collected and transported to the University of Victoria, where most of the eggs hatched within several days at room temperature.

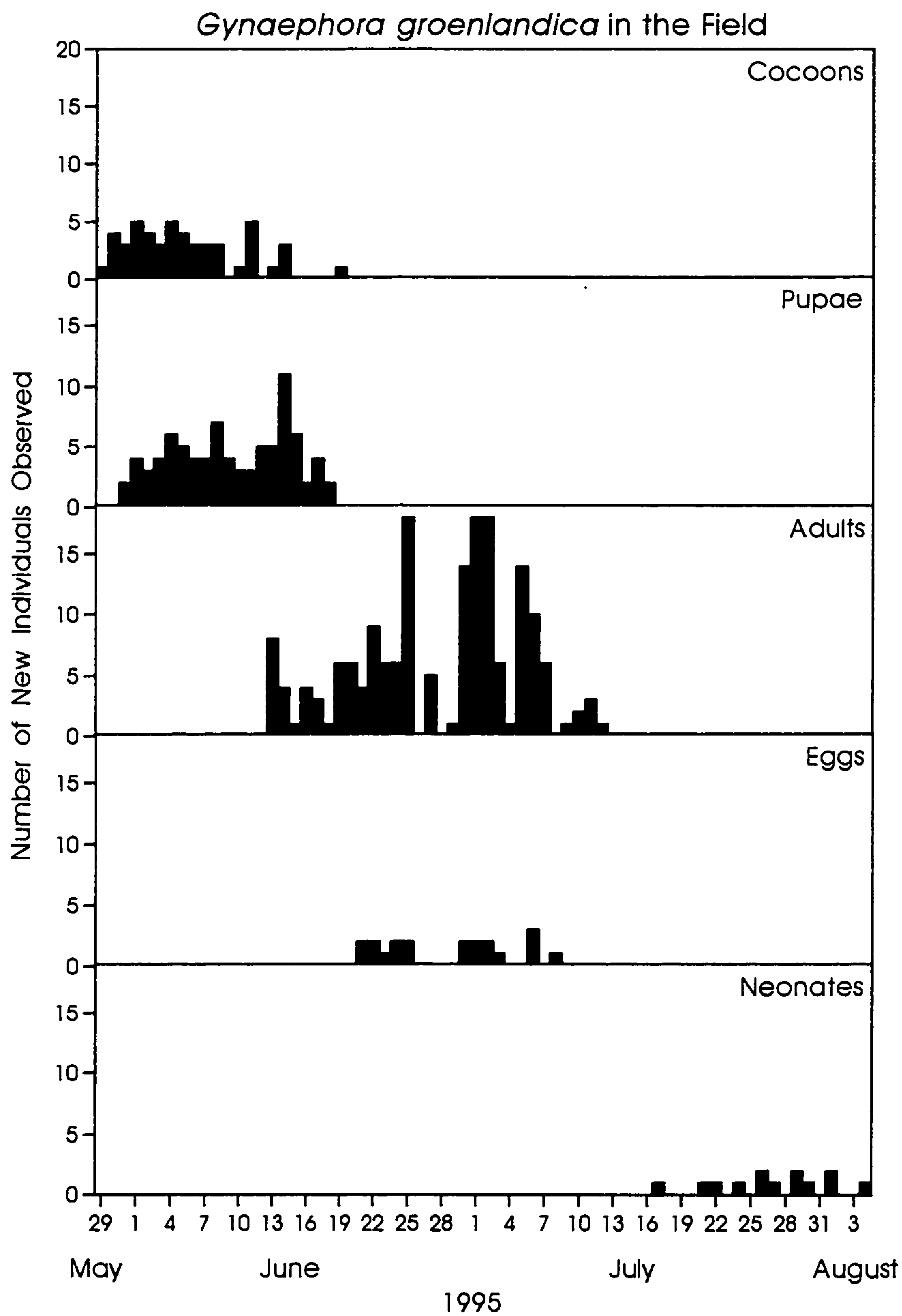
Combined pupal and embryonic development for *G. groenlandica*, from the pupation date of a female to the initial hatching date of her eggs, required 44 ± 6 d (n = 4) in the field. Overall, metamorphosis and reproduction required a minimum of 49 d on average in the field, combining days to begin cocoon-spinning with days required to complete cocoon-spinning, pupation, pupal development, and embryonic development. As a result, eggs did not hatch until quite late in the growing season (Figure 21).

Parasitoids of *Gynaephora* Species

Only four species of parasitoids were found to use *Gynaephora* species, directly or indirectly, as hosts at Alexandra Fiord, three of these being primary parasitoids that attack *Gynaephora* larvae and one being a hyperparasitoid that attacks the primary parasitoids during their metamorphosis (Figure 22).

No attempt was made to evaluate the extent of superparasitism or multiparasitism; however, instances of both were noted (see the following species accounts for evidence of superparasitism). Multiparasitism occurred only in the case of tachinid flies attacking the same individual hosts as the ichneumonid wasp *Hyposoter pectinatus* and was never completely successful. Tachinid eggs were sometimes found on *Gynaephora* larvae that

Figure 21. Phenology of metamorphosis and reproduction of *Gynaephora groenlandica* in 1995, the year in which the most complete data were collected. Data for eggs and neonates are individual egg masses.


Gynaephora groenlandica in the Field
Cocoons
Pupae
Adults
Eggs
Neonates
Number of New Individuals Observed
0
5
10
15
20
29 1 4 7 10 13 16 19 22 25 28 1 4 7 10 13 16 19 22 25 28 31 3
May
June
July
August
1995

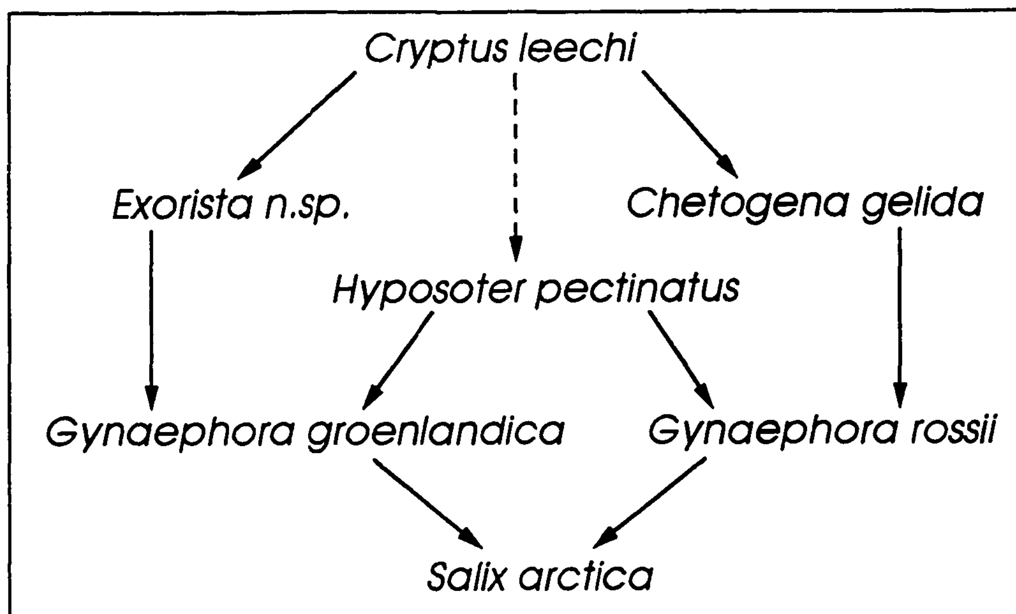


Figure 22. Simplified trophic relationships of *Gynaephora* species and their insect parasitoids at Alexandra Fiord. The arrow with a dashed line represents an infrequent relationship.

were killed by *H. pectinatus* and in one instance a dead pharate adult of *H. pectinatus* was found to be sharing a seventh-instar larva of *G. groenlandica* with a single puparium of the tachinid *Exorista* n.sp. from which the adult fly had emerged.

Unhatched eggs from a total of 29 egg masses of *Gynaephora* species, one of *G. rossii* and 12 of *G. groenlandica* laid in 1994 and 16 of *G. groenlandica* laid in 1995, were screened for parasitoids. No parasitoids emerged from these eggs in either the year they were laid or the following year.

<u>*Hyposoter pectinatus* (Hymenoptera: Ichneumonidae)</u>

Adults of *H. pectinatus* emerged from larvae of both species of *Gynaephora*, predominantly from the fifth and/or sixth, but also occasionally from the seventh, instar of *G. groenlandica* and from the fifth, and occasionally sixth, instar of *G. rossii* (Figure 23). In no case did more than one adult *H. pectinatus* emerge from a single host, confirming that this ichneumonid is strictly a solitary parasitoid, and no evidence of superparasitism was detected for this species. The size of host from which adults of *H. pectinatus* emerged was fairly consistent among years (Figure 24) but not entirely so. Mean HCW differed slightly, but significantly, among years for *G. groenlandica* killed by *H. pectinatus* ($F_{(1)2,1300} = 22.690$, $P < 0.0005$), being larger in 1994 than in the other two years (SNK, $P < 0.05$), and the proportion of host larvae that were seventh instars differed significantly among years ($\chi^2_2 = 20.330$, $P < 0.001$), being similar in 1995 and 1996 ($\chi^2_{c'} = 2.880$, $0.05 < P < 0.10$) but significantly larger in 1994 ($\chi^2_{c'} = 18.564$, $P < 0.001$). Too few *G. rossii* parasitized by *H. pectinatus* were found to compare among years.

Oviposition behaviour of *H. pectinatus* was observed indoors at the field site. Upon encountering larvae of *G. groenlandica*, females of *H. pectinatus* probed the larvae with their antennae and then extended their abdomens between their legs to oviposit, this process usually taking no more than a few seconds. These females readily accepted all instars of *G. groenlandica* for oviposition but usually were unable to oviposit into seventh-instar larvae because they could not reach through the long hairs of these larvae to penetrate

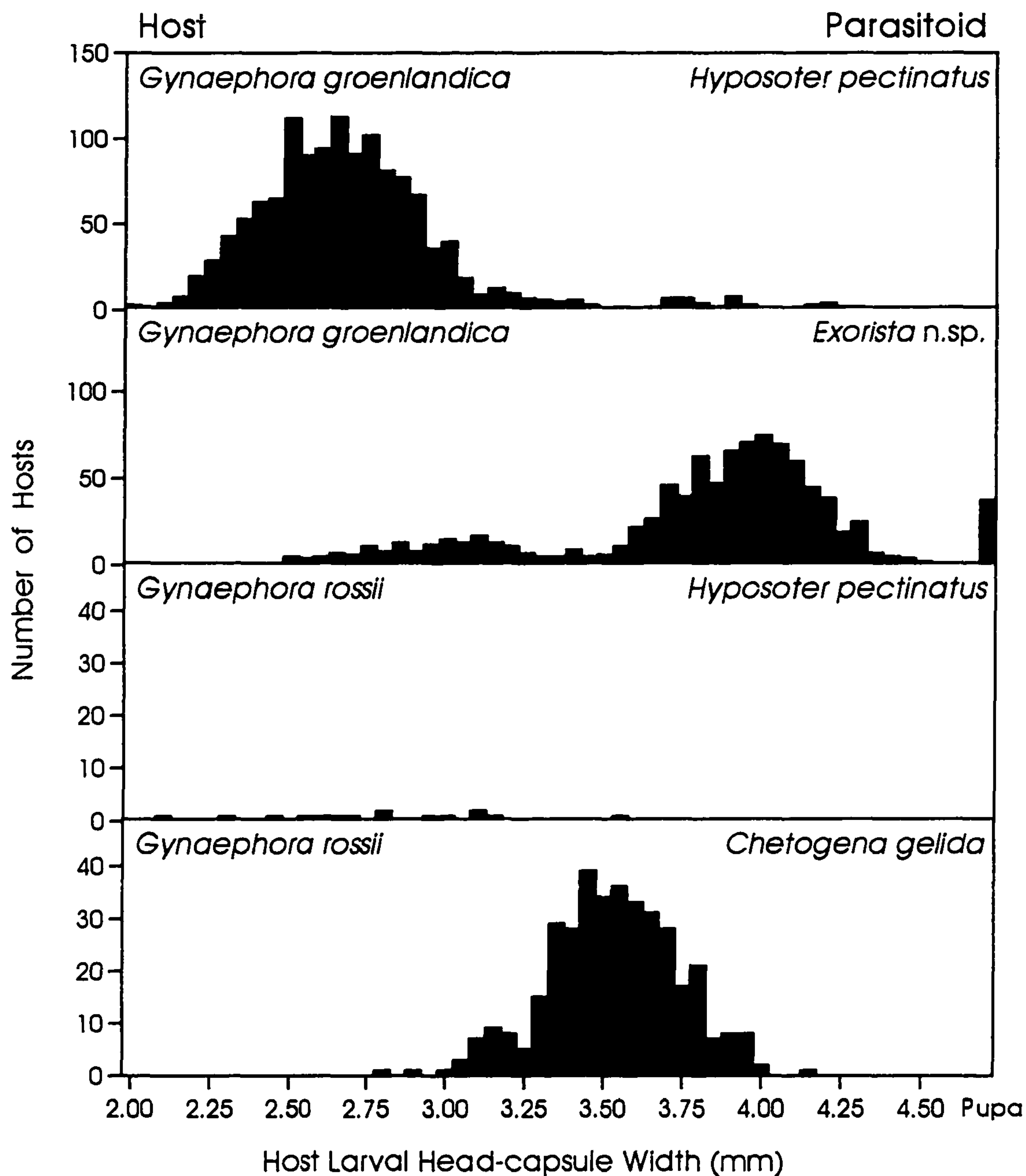


Figure 23. Frequency distributions of head-capsule widths of each species of *Gynaephora* killed by each species of primary parasitoid.

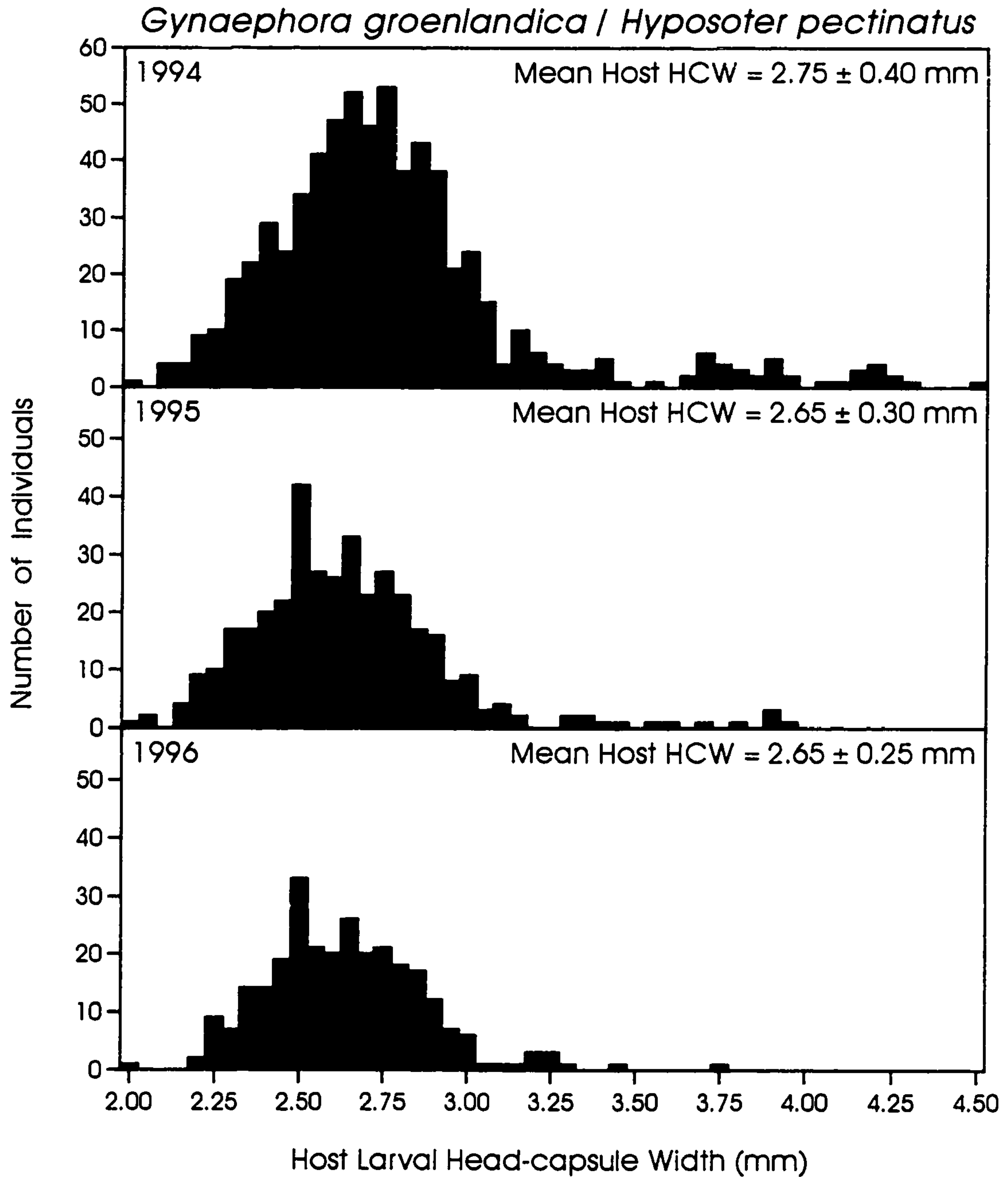


Figure 24. Frequency distributions of head-capsule widths of *Gynaephora groenlandica* killed by *Hyposoter pectinatus* during each year of the study.

the cuticle. Of the larvae that were stung in 1995, four fifth instars and one sixth instar were found to contain fully grown larvae of *H. pectinatus* which spun cocoons in the spring of 1996, although an adult *H. pectinatus* emerged only from one of the fifth instars. None of the earlier instars that were stung survived the subsequent winter. On the other hand, a fifth-instar larva of *G. groenlandica* collected in the field in 1996, which moulted and later spun a hibernaculum during laboratory rearing in 1997, was overwintered in the laboratory a second time and found to contain a fully grown larva of *H. pectinatus* in the spring of 1998 (this parasitoid larva spun a cocoon but failed to complete its metamorphosis).

Hyposoter pectinatus overwintered as larvae within their hosts, killing their hosts and initiating their own metamorphosis soon after their hosts became active in the spring. *Gynaephora* larvae parasitized by *H. pectinatus* spun silk platforms like those spun for moulting except that these were spun usually at the highest point available, such as the upper end of a plant shoot or flower stalk or the top of a rock. Once the host had spun its silk platform, the larva of *H. pectinatus* tore open the venter of the host larva and spun a false cocoon attaching the host remains to the substrate. A pupal cocoon was then spun entirely within the host remains, which almost always consisted of nothing more than cuticle. Initiation of metamorphosis was delayed in 1996, relative to 1995, by the late and prolonged snowmelt that year (Figure 25). A few individuals of *H. pectinatus* initiated their metamorphosis before the onset of snowmelt in 1996 because their hosts had become active on ridgetops that had blown free of snow; however, these insects failed to complete their development due to repeated formation of ice crusts over the exposed ridgetops from blowing snow during storms. Metamorphosis of *H. pectinatus*, measured from the day a parasitoid larva spun its cocoon to the day the adult parasitoid emerged, required approximately two weeks in the field and was prolonged in 1996, compared to 1995 (Table 8), but not significantly so ($t_{(1)32} = 1.661$, $0.05 < P < 0.10$).

The number of *G. groenlandica* killed by *H. pectinatus* declined from 1994 to 1996 (Figure 26) and was proportional to the number of *G. groenlandica* adults found in the following year ($\chi^2_{c'} = 0.068$, $0.75 < P < 0.90$). Adults of *H. pectinatus* did not always

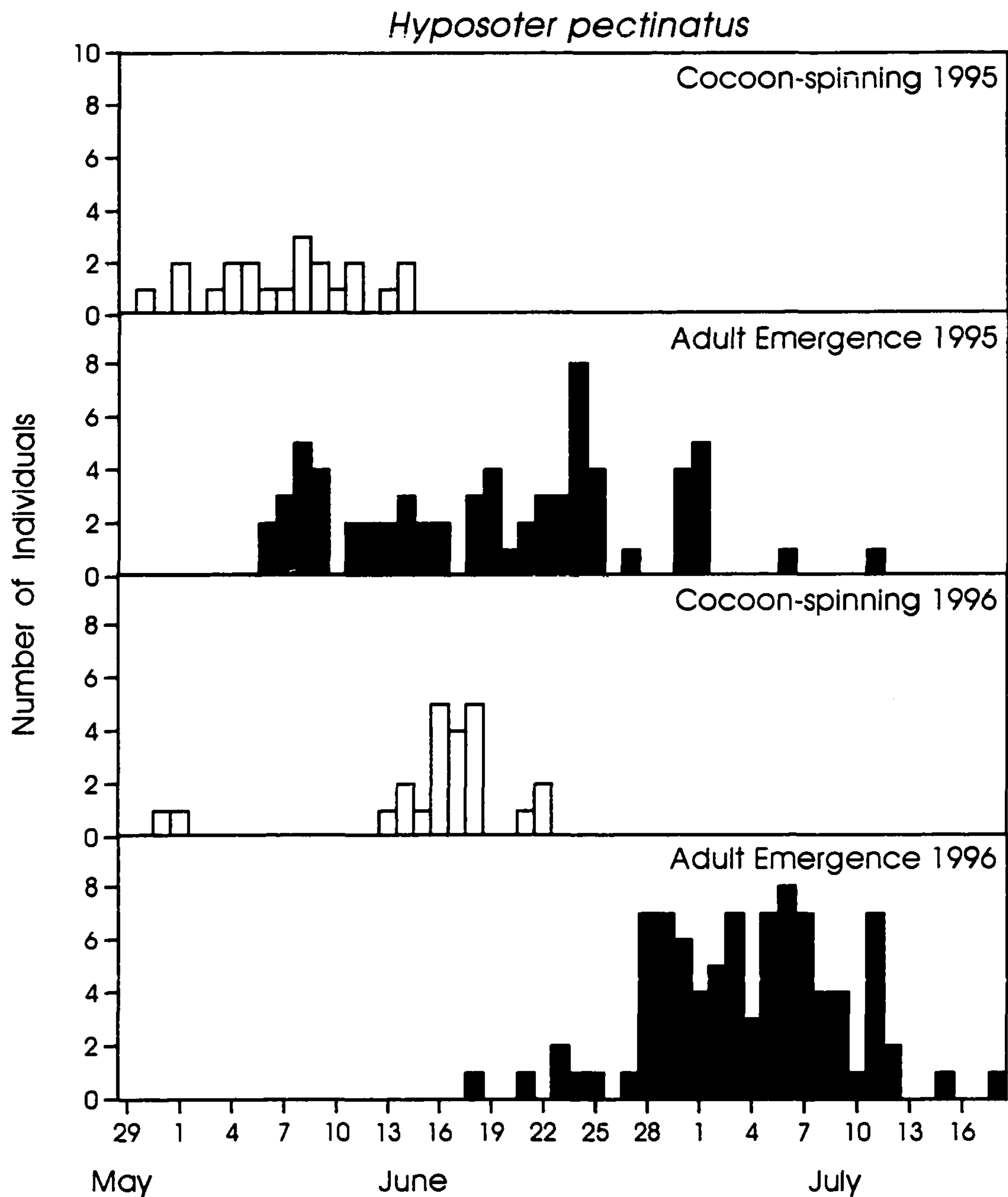


Figure 25. Phenology of metamorphosis of *Hyposoter pectinatus* in 1995 and 1996. Cocoon-spinning and subsequent adult emergence were delayed in 1996 by the prolonged snowmelt that year. The two individuals that spun cocoons on 31 May and 1 June 1996 failed to emerge as adults.

Table 8. Mean dates of cocoon-spinning (*Hyposoter pectinatus*) or pupariation (*Exorista* n.sp. and *Chetogena gelida*) and adult emergence, and time required for the primary parasitoids of *Gynaephora* species to complete metamorphosis in the field.

Parasitoid species	1995	1996
Mean ± standard deviation (*n*) date (Year Day) of cocoon-spinning or pupariation		
Hyposoter pectinatus	158 ± 4 (21)	169 ± 3 (21)
Exorista n.sp.	158 ± 4 (39)	171 ± 3 (47)
Chetogena gelida	155 ± 4 (27)	178 ± 6 (9)
Mean ± standard deviation (*n*) date (Year Day) of adult emergence		
Hyposoter pectinatus	171 ± 8 (64)	186 ± 5 (88)
Exorista n.sp.	170 ± 7 (49)	185 ± 5 (51)
Chetogena gelida	167 ± 8 (39)	190 ± 4 (17)
Mean ± standard deviation (*n*) days to complete metamorphosis		
Hyposoter pectinatus	13 ± 4 (15)	15 ± 2 (19)
Exorista n.sp.	10 ± 1 (16)	13 ± 2 (25)
Chetogena gelida	10 ± 2 (12)	14 ± 4 (4)

emerge from *G. groenlandica* killed by these parasitoids, however, and the proportion of parasitoid-killed hosts from which adults emerged did not differ significantly between years ($\chi^2_{c'} = 0.018$, $0.75 < P < 0.90$) for those that were not subject to any temperature manipulation in 1995 and 1996.

Exorista n.sp. (Diptera: Tachinidae)

Adults of *Exorista* n.sp. emerged only from *G. groenlandica*. Of 1570 tachinid flies reared from 701 *G. groenlandica* and identified to genus during the course of this study, all were *Exorista*. Adults of *Exorista* emerged predominantly from seventh-instar

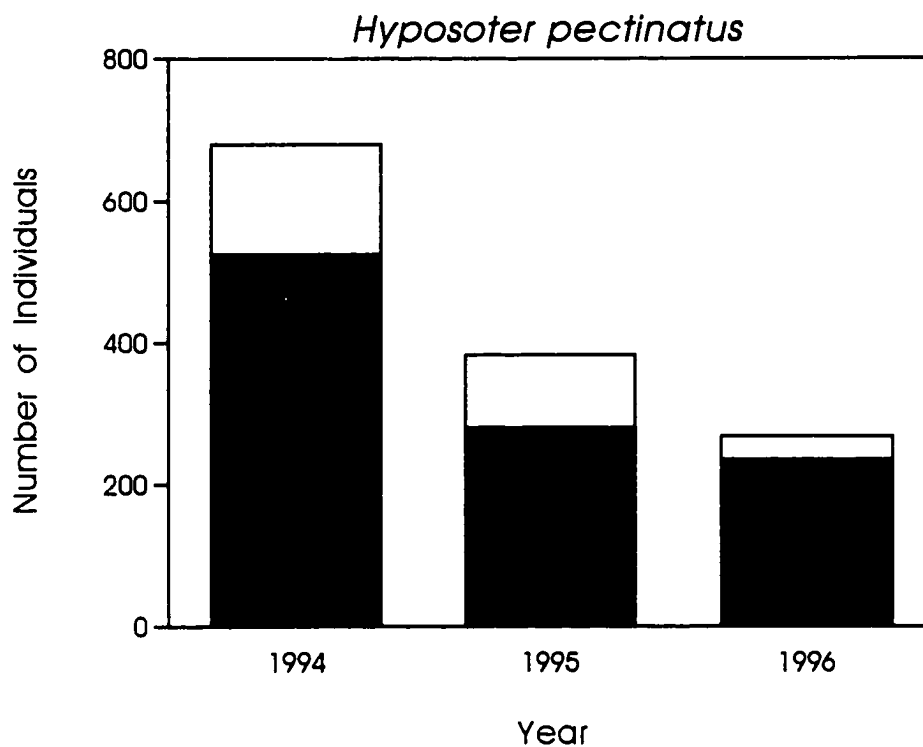


Figure 26. Total numbers of *Gynaephora groenlandica* found killed by *Hyposoter pectinatus* during each year of the study. The solid portion of each column represents the number of hosts from which adult parasitoids emerged.

larvae (including prepupae, larvae that had spun cocoons but not yet pupated) but some emerged from sixth-instar larvae or from pupae (Figure 23). Of 907 *G. groenlandica* parasitized by *Exorista* for which this information was recorded, 699 had spun cocoons before being killed by the parasitoids, but of 1130 *G. groenlandica* killed by *Exorista* in the field during this study, only 38 had pupated and the proportion that had pupated before being killed did not differ significantly among years ($\chi^2_2 = 2.276$, $0.25 < P < 0.50$). The size of larval host from which adults of *Exorista* emerged was fairly consistent among years (Figure 27) but not entirely so. Mean host HCW differed slightly, but significantly, among years ($F_{(1)2,842} = 6.933$, $0.0005 < P < 0.001$), being larger in 1994 than in the other two years (SNK, $P < 0.05$), and the proportion of host larvae that were seventh instars differed significantly among years ($\chi^2_2 = 14.990$, $P < 0.001$), being similar in 1995 and 1996 ($\chi^2_{c'} = 0.104$, $0.50 < P < 0.75$) but significantly larger in 1994 ($\chi^2_{c'} = 17.519$, $P < 0.001$). Greater numbers of *Exorista* developed on larger hosts, with significant increases in both mean and maximum numbers of puparia per host with increasing host HCW (Figure 28) and superparasitism was not uncommon, as evidenced by the presence of well over 30 eggs on individual hosts, compared to the maximum of 17 puparia produced from a single host. However, pupae of *G. groenlandica* killed by *Exorista* were found to contain fewer puparia than final-instar larval hosts, with only four of 38 pupae containing more than five puparia. Overall, 3 ± 2 ($n = 1029$) *Exorista* puparia were produced per host in the field, but the frequency distribution of numbers of puparia per host differed significantly among years ($\chi^2_{16} = 35.846$, $0.001 < P < 0.005$), being similar in 1995 and 1996 ($\chi^2_8 = 8.301$, $0.25 < P < 0.50$), but with greater numbers of puparia produced per host in 1994 ($\chi^2_8 = 27.249$, $P < 0.001$).

Females of *Exorista* were observed ovipositing on *G. groenlandica* held in one of the large stock corrals in the field. These females were seen perched on vegetation within several centimetres of *G. groenlandica* larvae and if undisturbed they remained there as

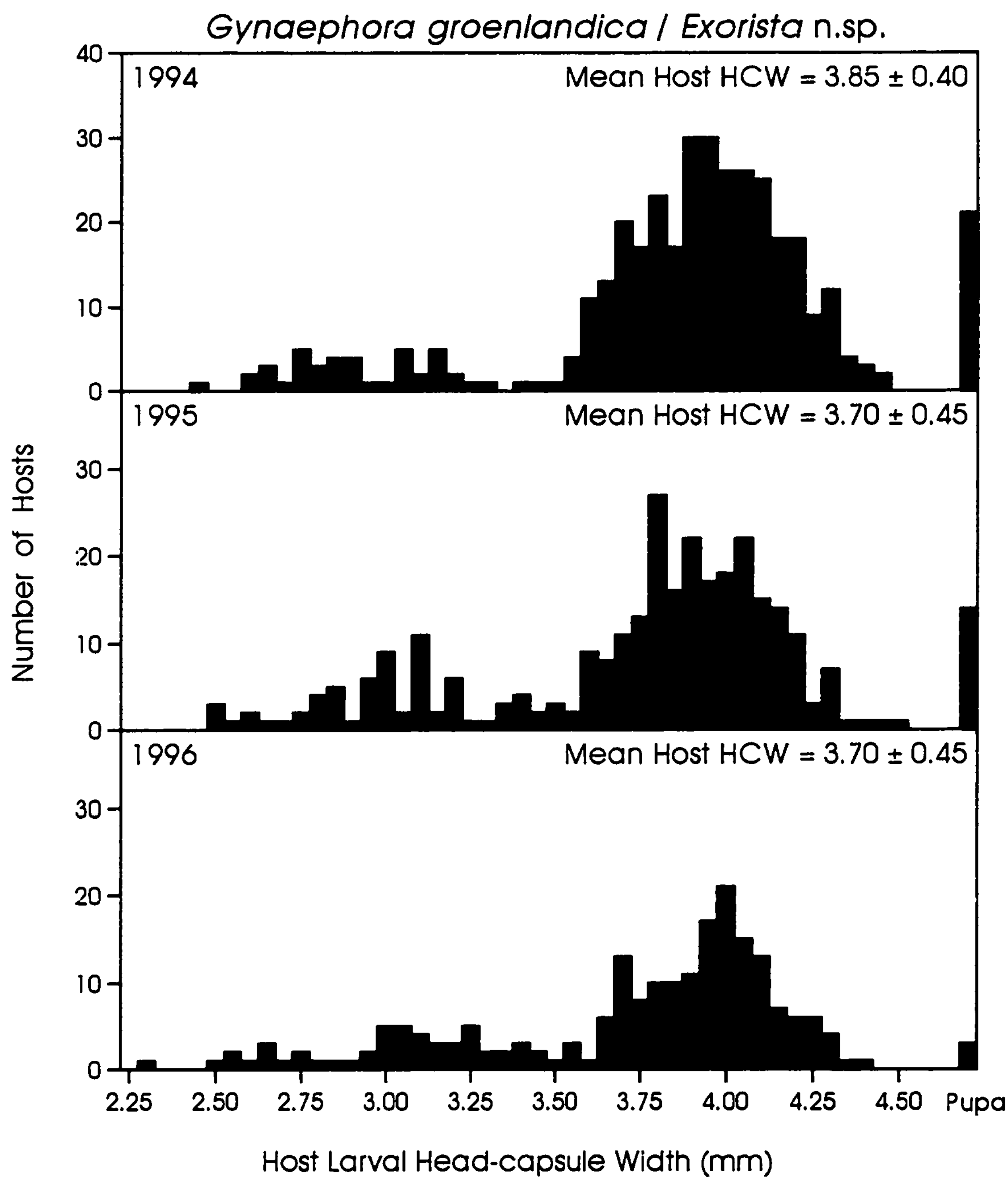


Figure 27. Frequency distributions of head-capsule widths of *Gynaephora groenlandica* killed by *Exorista* n.sp. during each year of the study.

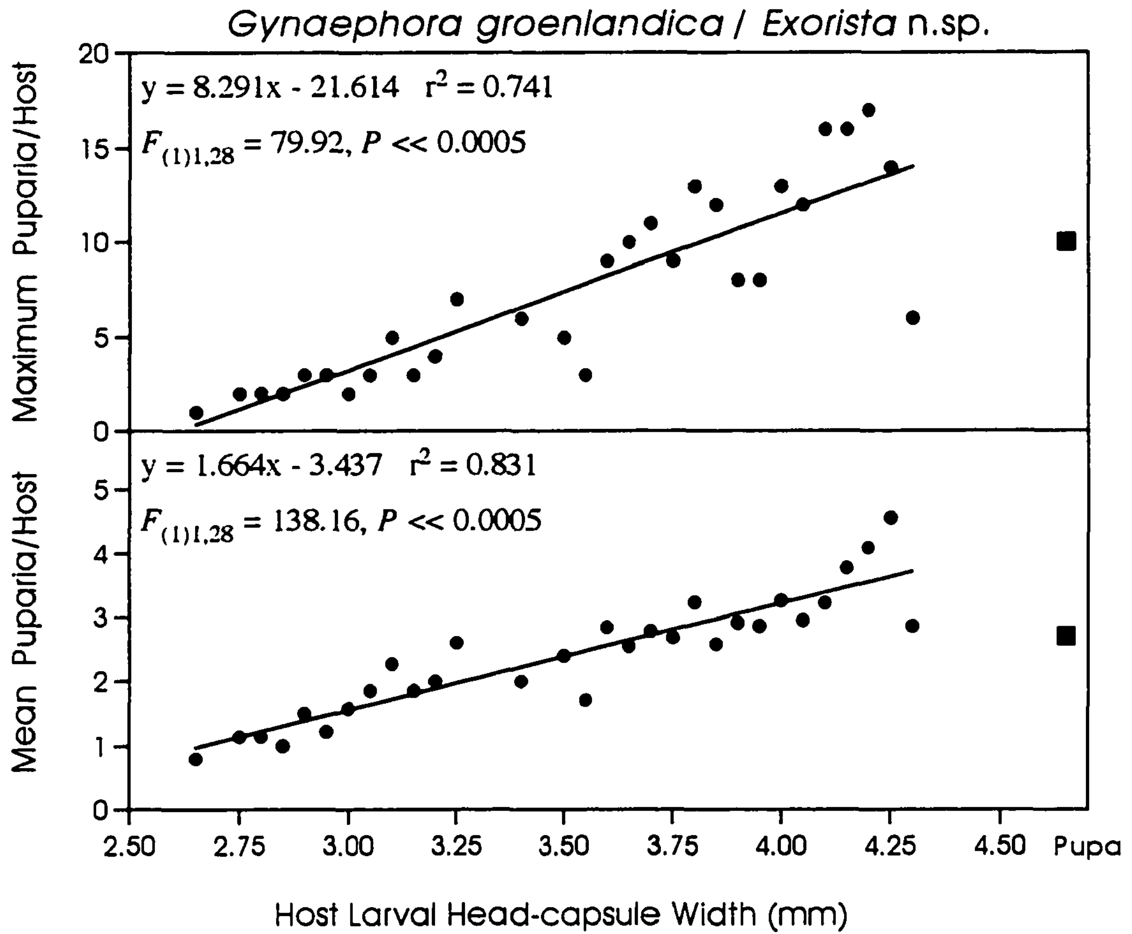


Figure 28. Relationships between host head-capsule width (HCW) and mean and maximum numbers of *Exorista* n.sp. puparia produced per host. HCW categories with sample sizes smaller than five were excluded from the analysis. Data for host pupae are included for comparison but were not included in the regression.

long as the larvae remained motionless. When the *G. groenlandica* larvae began to move, however, the *Exorista* females took flight and landed just ahead and to the side of the moving larvae, extending their abdomens between their legs to oviposit as the larvae passed by. This process was repeated several times if the *G. groenlandica* larvae kept moving and, as a result of this behaviour, most *Exorista* eggs were affixed to the cuticle of the host ventrally and laterally on the thoracic and first few abdominal segments. Of the *G. groenlandica* larvae collected in the field for laboratory rearing that were parasitized by *Exorista* when they were collected, all were killed by the parasitoids during laboratory rearing the following spring. In addition, of the *G. groenlandica* larvae that were not parasitized by *Exorista* when they were collected but were held in an uncovered corral and thus exposed to attack by parasitoids late in their active season, most (43 of 49 in 1995 and 29 of 33 in 1996) were attacked by *Exorista* in the field and all of these were killed by the parasitoids during laboratory rearing the following spring.

Exorista overwintered as larvae within their hosts, killing their hosts and initiating their own metamorphosis soon after their hosts became active in the spring. Larvae of *Exorista* pupariated within the remains of their hosts, sometimes with portions of puparia protruding through the host cuticle, especially in cases where many *Exorista* had developed within a single host. In these cases, the host remains consisted of nothing more than cuticle; however, substantial amounts of host tissue remained in most *G. groenlandica* killed by *Exorista*. Initiation of metamorphosis was delayed in 1996, relative to 1995, by the late and prolonged snowmelt that year (Figure 29). A few individuals of *Exorista* initiated their metamorphosis before the onset of snowmelt in 1996 because their hosts had become active on ridgetops that had blown free of snow; however, these insects failed to complete their development due to repeated formation of ice crusts over the exposed ridgetops from blowing snow during storms. Metamorphosis of *Exorista* in the field, measured from the day the parasitoid larvae in a given host began pupariating to the day the first adult parasitoids emerged from that host, required approximately ten days in 1995 and almost two weeks in 1996 (Table 8), the difference between years being statistically significant ($t_{(1)39} = 5.226$, $P < 0.0005$).

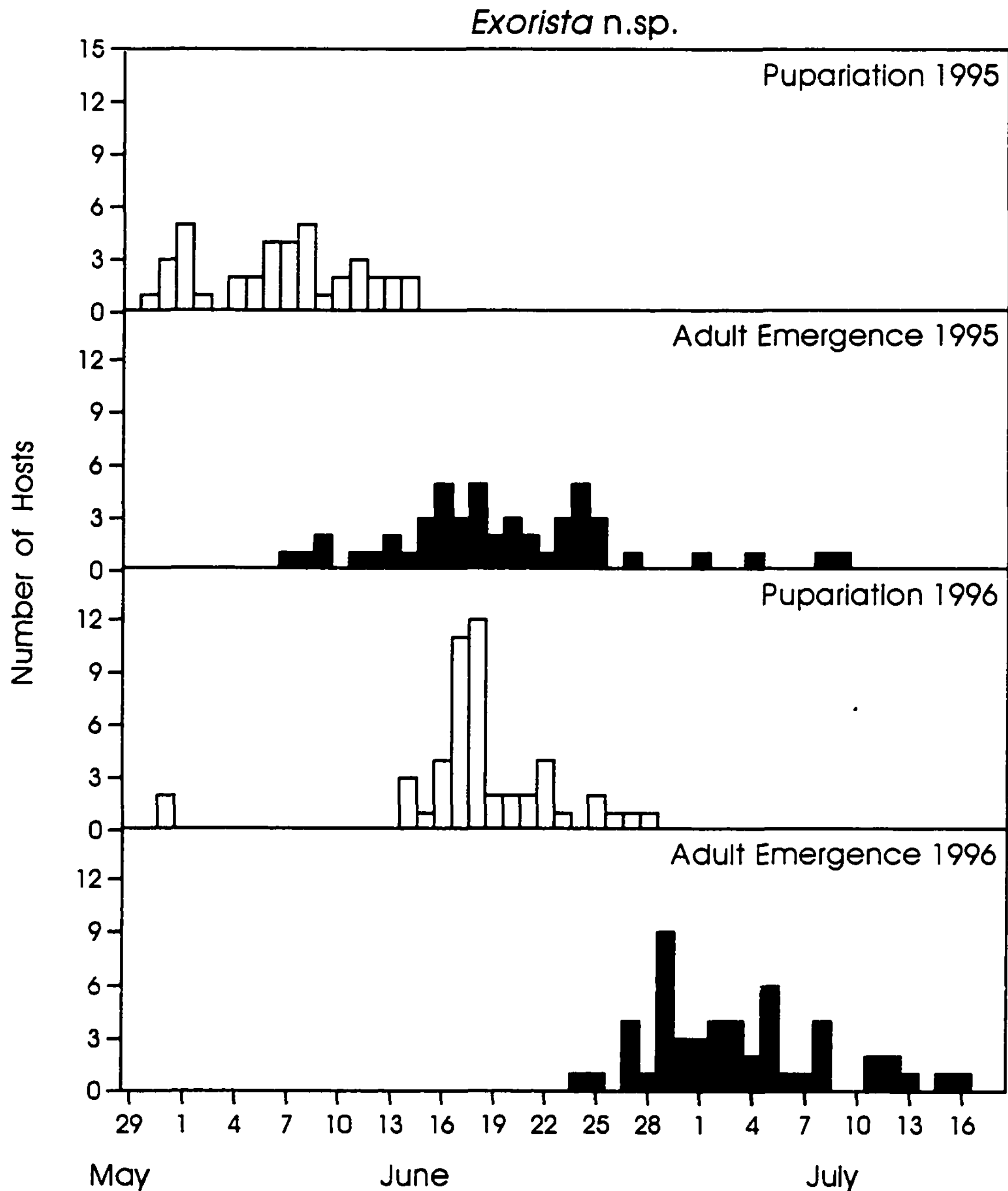


Figure 29. Phenology of metamorphosis of *Exorista* n.sp. in 1995 and 1996. Pupariation and subsequent adult emergence were delayed in 1996 by the prolonged snowmelt that year; the individuals that pupariated on 31 May 1996 failed to emerge as adults. For a given host, only the dates that the first puparium formed and the first adult emerged were recorded.

The number of *G. groenlandica* killed by *Exorista* declined from 1994 to 1996 (Figure 30) and was proportional to the number of *G. groenlandica* adults found in the same year in 1995 and 1996 ($\chi^2_{c'} = 0.012$, $0.90 < P < 0.95$) but disproportionately smaller in 1994 ($\chi^2_{c'} = 356.748$, $P << 0.001$). The total number of *Exorista* puparia produced was proportional to the number of hosts killed and this proportion did not differ significantly among years ($\chi^2_2 = 5.101$, $0.05 < P < 0.10$). Adults did not always emerge from *Exorista* puparia, however, and the proportion of puparia from which adults emerged did not differ significantly between years ($\chi^2_{c'} = 2.324$, $0.10 < P < 0.25$) for those that were not subject to any temperature manipulation in 1995 and 1996.

Chetogena gelida (Diptera: Tachinidae)

Adults of *C. gelida* emerged only from *G. rossii*. Of 545 tachinid flies reared from 239 *G. rossii* and identified to genus during the course of this study, all were *Chetogena*. Adults of *C. gelida* emerged almost exclusively from sixth-instar larvae, including prepupae, and 338 of 371 *G. rossii* parasitized by *C. gelida* for which this information was recorded had spun cocoons before being killed by the parasitoids but all were killed before pupating (Figure 23). The size of host from which adults of *C. gelida* emerged was consistent among years (Figure 31), with no significant differences in mean host HCW ($F_{(1)2,363} = 0.326$, $P > 0.25$). Greater numbers of *C. gelida* developed on larger hosts, with significant increases in both mean and maximum numbers of puparia per host with increasing host HCW (Figure 32) and superparasitism was not uncommon, as evidenced by the presence of well over 30 eggs on individual hosts, compared to the maximum of 19 puparia produced from a single host. Overall, 5 ± 3 ($n = 399$) *C. gelida* puparia were produced per host, and the frequency distribution of numbers of puparia per host did not differ significantly among years ($\chi^2_{33} = 41.104$, $0.10 < P < 0.25$).

The relationship between mean numbers of puparia per host and host HCW

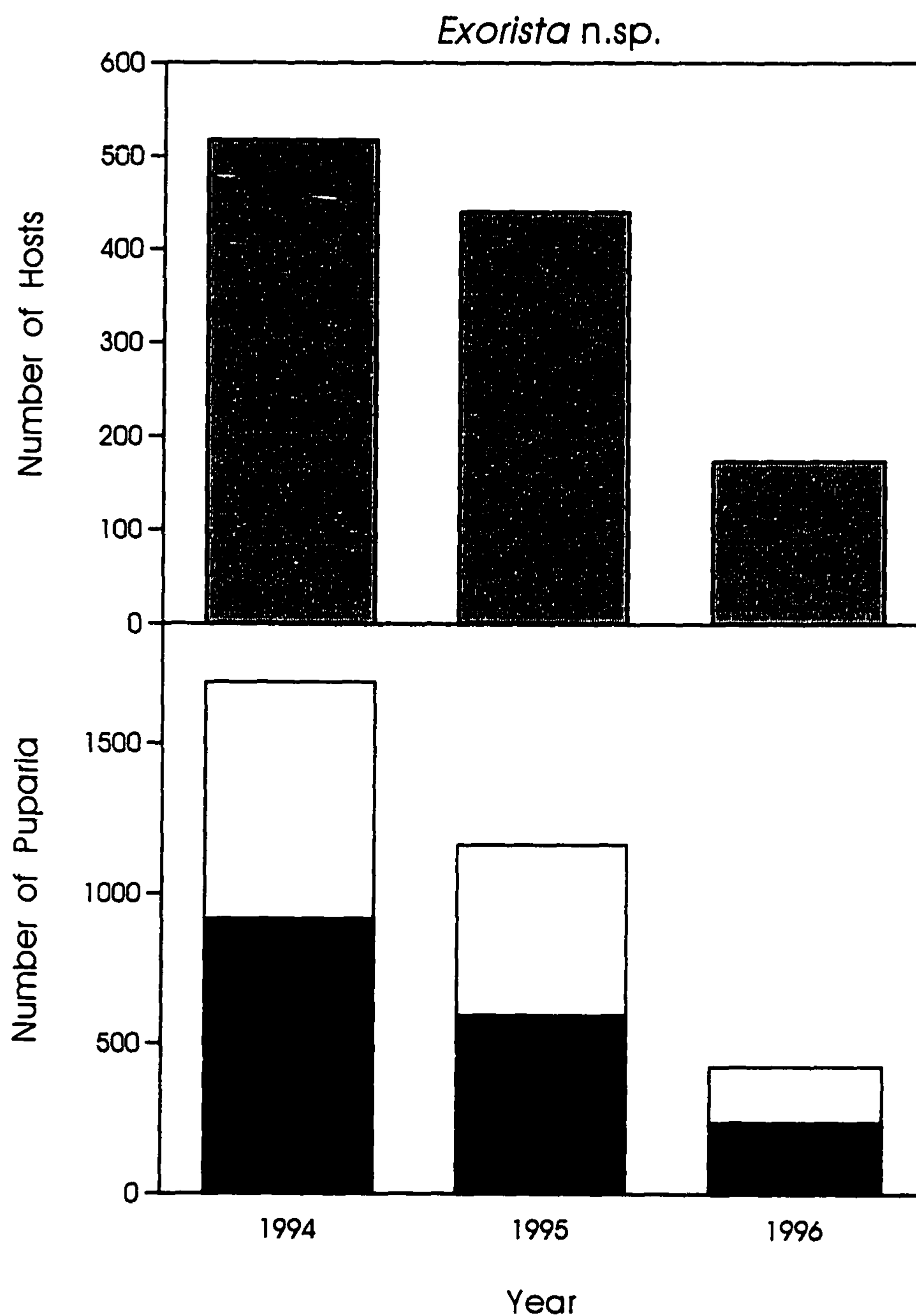


Figure 30. Total numbers of *Gynaephora groenlandica* found killed by *Exorista* n.sp. (above) and total numbers of *Exorista* puparia produced (below) during each year of the study. The solid portion of each column below represents the number of puparia from which adult parasitoids emerged.

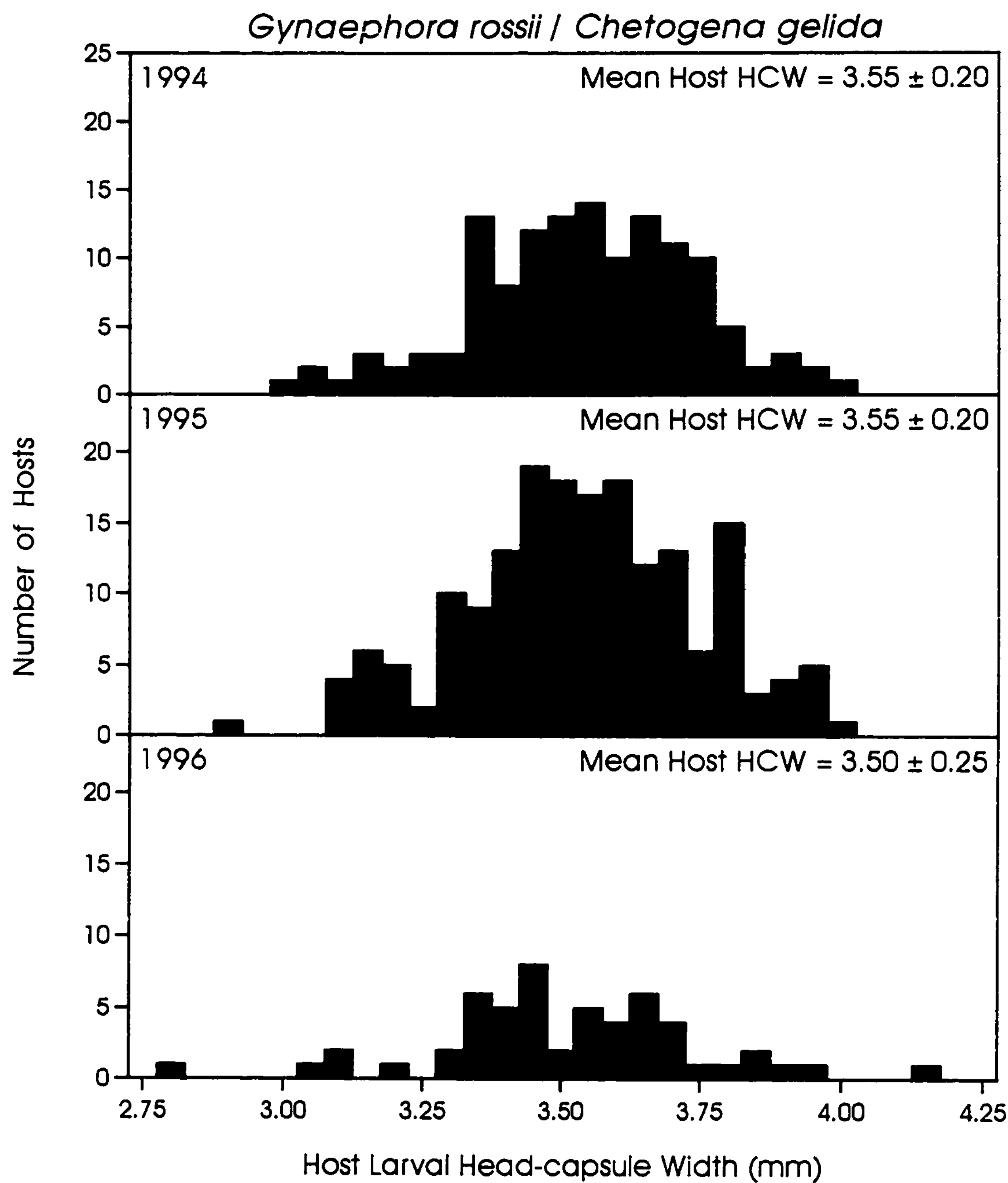


Figure 31. Frequency distributions of head-capsule widths of *Gynaephora rossii* killed by *Chetogena gelida* during each year of the study.

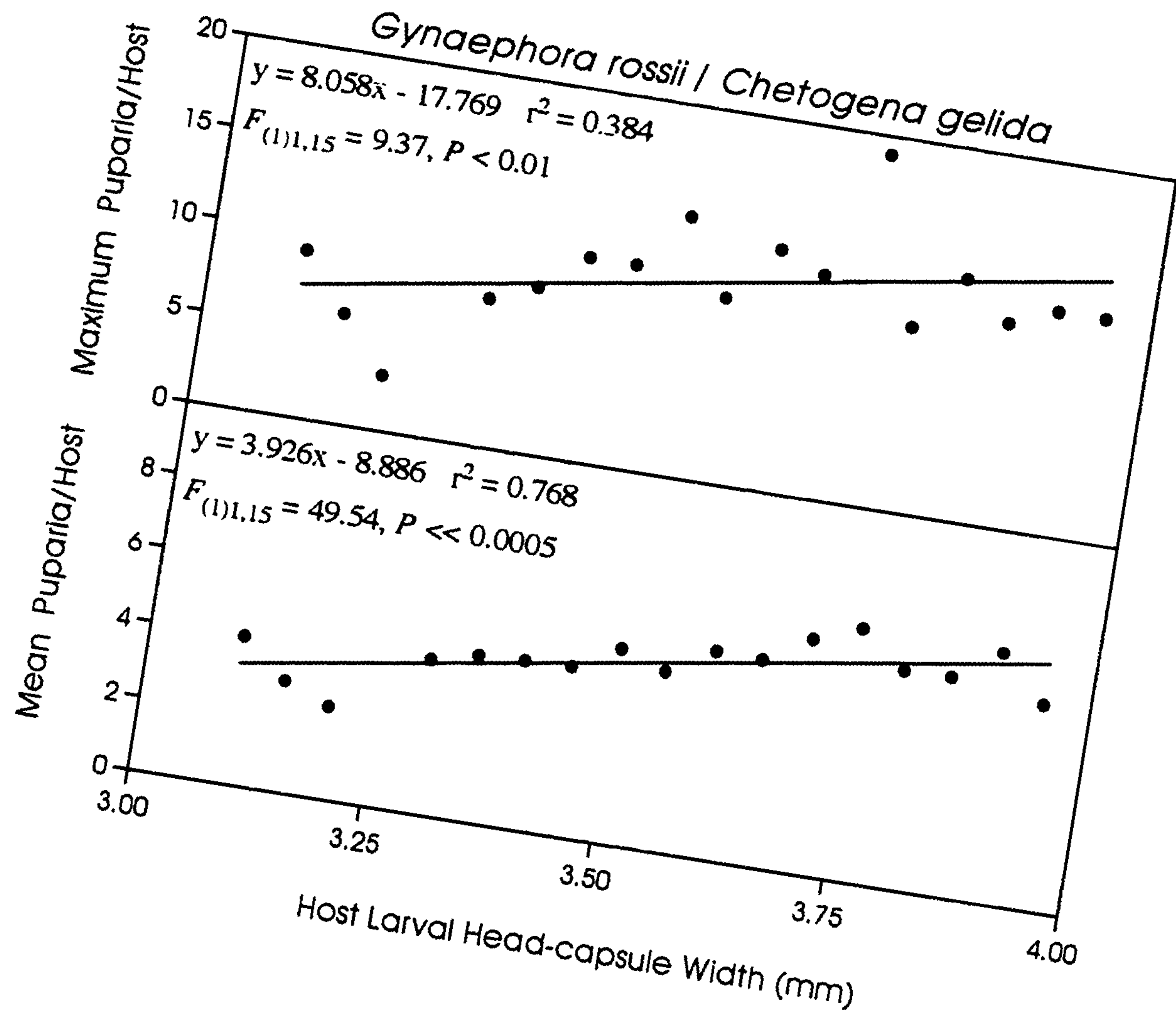


Figure 32. Relationships between host head-capsule width and mean and maximum numbers of *Chetogena gelida* puparia produced per host. Head-capsule-width categories with sample sizes smaller than five were excluded from the analysis.

differed significantly between tachinid species ($t_{(2)43} = 4.773$, $P < 0.001$), with *C. gelida* showing a greater increase than *Exorista* in mean numbers of puparia per host with increasing host HCW. The increase in maximum numbers of puparia per host with increasing host HCW did not differ significantly between tachinid species ($t_{(2)43} = 0.088$, $P > 0.50$) but maximum numbers of puparia produced from hosts of any given size did ($t_{(2)44} = 3.821$, $P < 0.001$), with greater maximum numbers of puparia of *C. gelida* than of *Exorista* produced per host.

Oviposition by *C. gelida* was never observed directly; however, most *C. gelida* eggs were found dorsally and laterally on *G. rossii* larvae and were often affixed to the larval hairs rather than directly to the cuticle, suggesting oviposition behaviour different from that of *Exorista*. Of the *G. rossii* larvae collected in the field for laboratory rearing that were parasitized by *C. gelida* when they were collected, all were killed by the parasitoids during laboratory rearing the following spring. In addition, the *G. rossii* larva on which four eggs were laid by a mated female of *C. gelida* in the summer of 1995 produced four adults of *C. gelida* in the summer of 1996.

Chetogena gelida overwintered as larvae within their hosts, killing their hosts and initiating their own metamorphosis soon after their hosts became active in the spring. Larvae of *C. gelida* almost always emerged from their hosts prior to pupariation and pupariated within the cocoons of hosts that had spun cocoons or simply on the ground within a few centimetres of hosts that were killed before spinning cocoons. Only rarely did the host remains consist of anything more than cuticle by the time *C. gelida* larvae emerged to pupariate. Initiation of metamorphosis was delayed in 1996, relative to 1995, by the late and prolonged snowmelt that year (Figure 33). Metamorphosis of *C. gelida* in the field, measured from the day the parasitoid larvae began pupariating to the day the first adult parasitoids emerged from a given host, required approximately ten days in 1995 and two weeks in 1996 (Table 8), the difference between years being statistically significant ($t_{(1)14} = 2.716$, $0.005 < P < 0.01$).

Mean date of initiation of metamorphosis (cocoon-spinning for *H. pectinatus* or pupariation for *Exorista* and *C. gelida*) differed significantly among the three primary

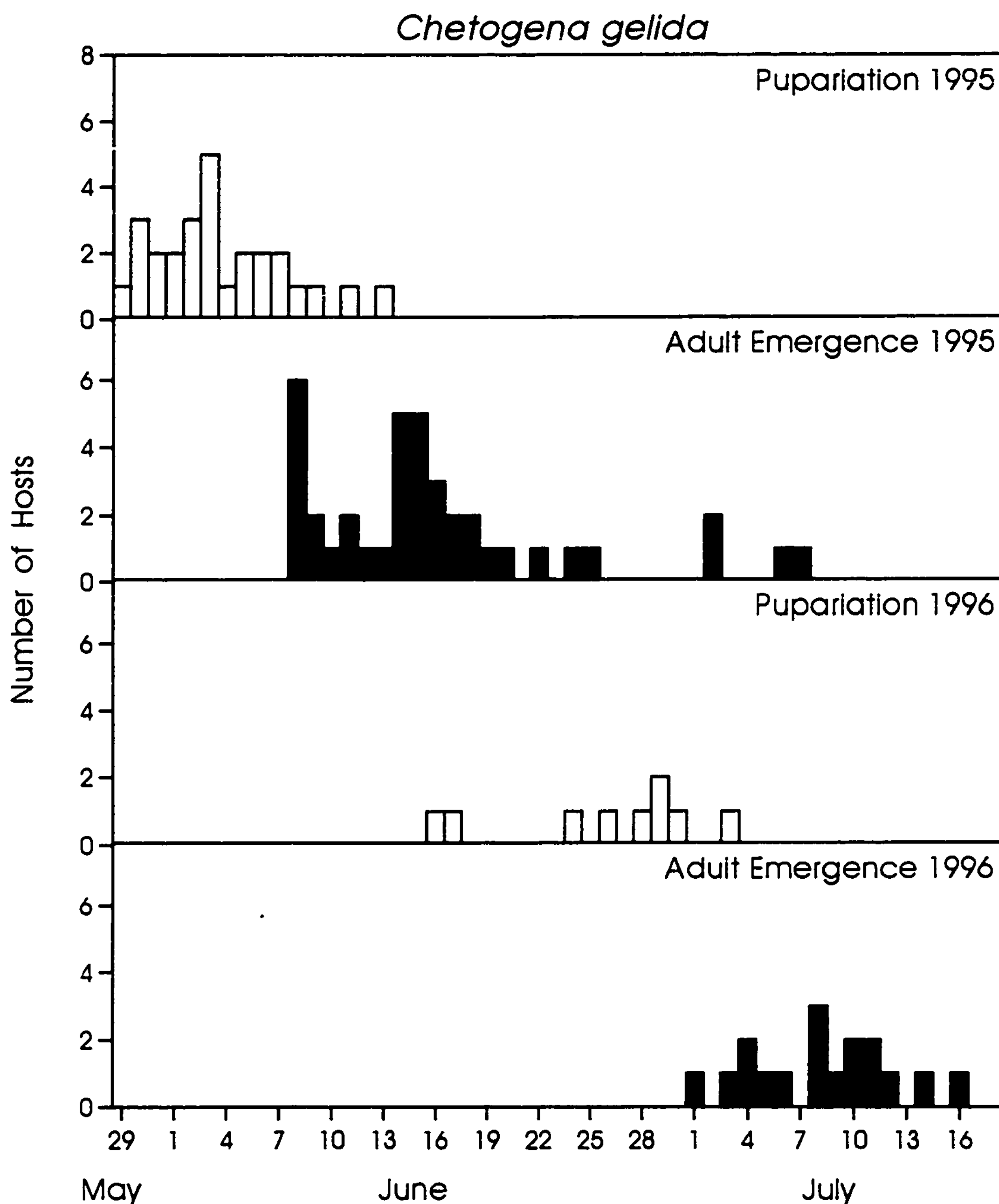


Figure 33. Phenology of metamorphosis of *Chetogena gelida* in 1995 and 1996. Pupariation and subsequent adult emergence were delayed in 1996 by the prolonged snowmelt that year. For a given host, only the dates that the first puparium formed and the first adult emerged were recorded.

parasitoid species in 1995 ($F_{(1)2,84} = 5.50$, $0.005 < P < 0.01$), being earlier for *C. gelida* than for *H. pectinatus* and *Exorista* (SNK, $P < 0.05$). Mean date of adult emergence also was earlier in 1995 for *C. gelida* than for the other two species (Table 8), although the difference was not statistically significant ($F_{(1)2,149} = 2.74$, $0.05 < P < 0.10$). Mean date of initiation of metamorphosis again differed significantly among the three primary parasitoid species in 1996 ($F_{(1)2,74} = 12.04$, $P < 0.0005$), but was later for *C. gelida* than for *H. pectinatus* and *Exorista* (SNK, $P < 0.05$). Mean date of adult emergence in 1996 also differed significantly among the three primary parasitoid species ($F_{(1)2,153} = 6.53$, $0.001 < P < 0.0025$), being later for *C. gelida* than for the other two species (SNK, $P < 0.05$). Metamorphosis under field conditions of both species of tachinid flies was generally more rapid than that of *H. pectinatus*, significantly so in 1995 ($F_{(1)2,40} = 6.55$, $0.0025 < P < 0.005$) but not in 1996 ($F_{(1)2,45} = 2.84$, $0.05 < P < 0.10$), in the individuals for which both initiation of metamorphosis and adult emergence were recorded (Table 8).

The number of *G. rossii* killed by *C. gelida* was larger in 1995 than in 1994 and smaller in 1996 than in the previous two years (Figure 34) and was equally proportional to the number of *G. rossii* adults found each year ($\chi^2_2 = 5.549$, $0.05 < P < 0.10$). The total number of *C. gelida* puparia produced was proportional to the number of hosts killed and this proportion did not differ significantly among years ($\chi^2_2 = 0.492$, $0.25 < P < 0.50$). Adults did not always emerge from *C. gelida* puparia, however, and the proportion of puparia from which adults emerged differed significantly between years ($\chi^2_{c'} = 21.246$, $P < 0.001$) for those that were not subject to any temperature manipulation in 1995 and 1996, being larger in 1995.

<u>*Cryptus leechi* (Hymenoptera: Ichneumonidae)</u>

Adults of *C. leechi* emerged from puparia of both *Exorista* n.sp. and *C. gelida*, and occasionally from cocoons of *H. pectinatus* that had parasitized *G. groenlandica*. Of 97 parasitized puparia in which host remains were identified with respect to developmental

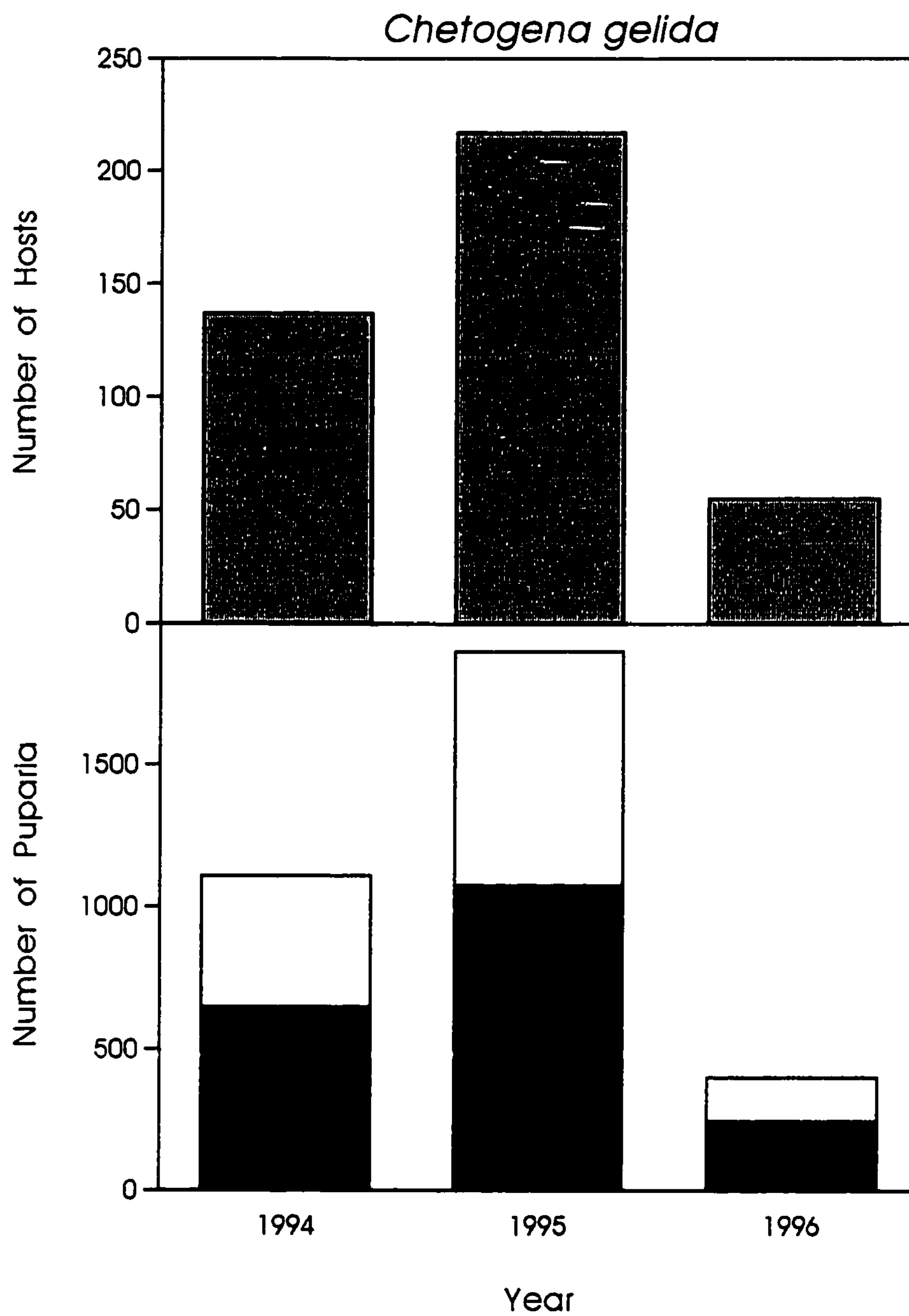


Figure 34. Total numbers of *Gynaephora rossii* found killed by *Chetogena gelida* (above) and total numbers of *C. gelida* puparia produced (below) during each year of the study. The solid portion of each column below represents the number of puparia from which adult parasitoids emerged.

stage, 48 contained immatures and 49 contained pharate adults. Routine dissections of host remains frequently revealed two or more eggs or larvae of *C. leechi* within a single puparium, always on rather than in the actual host, but no more than one living larva was found and no more than one adult emerged from a given host, indicating that this ichneumonid is also strictly a solitary parasitoid.

Only rarely did *C. leechi* attack *H. pectinatus*; less than 1% (n = 1193) of *H. pectinatus* were found to be parasitized by *C. leechi* (Table 9) and the proportion did not vary significantly among years ($\chi^2_2 = 0.533$, $0.25 < P < 0.50$). In contrast, tachinid puparia were found to have been attacked by *C. leechi* in 38% of *G. groenlandica* (n = 889) killed by *Exorista* and 26% of *G. rossii* (n = 350) killed by *C. gelida* (Table 9), the proportion of primary hosts with puparia attacked by *C. leechi* being significantly larger for *G. groenlandica* than for *G. rossii* ($\chi^2_{c'} = 16.861$, $P < 0.001$). Of the primary hosts for which this information was recorded, a larger proportion of those that had spun cocoons than those that had not were found to have been attacked by *C. leechi*; however, the difference was not statistically significant for either *G. groenlandica* ($\chi^2_{c'} = 3.412$, $0.05 < P < 0.10$) or *G. rossii* ($\chi^2_{c'} = 1.170$, $0.25 < P < 0.50$). Only rarely were all of the puparia associated with a given primary host attacked by *C. leechi*, the total number of puparia attacked being consistently proportional to the total number of primary hosts attacked each year for both *G. groenlandica* ($\chi^2_2 = 3.611$, $0.10 < P < 0.25$) and *G. rossii* ($\chi^2_2 = 0.790$, $0.50 < P < 0.75$). However, the proportion of the puparia produced each year that was attacked by *C. leechi* varied significantly for both primary hosts ($\chi^2_2 = 33.376$ for *G. groenlandica*, 25.356 for *G. rossii*; $P < 0.001$ in both cases). Similar proportions of *Exorista* puparia associated with *G. groenlandica* were attacked by *C. leechi* in 1995 and 1996 ($\chi^2_{c'} = 0.716$, $0.25 < P < 0.50$) but a significantly larger proportion was attacked in 1994 ($\chi^2_{c'} = 32.607$, $P < 0.001$). In contrast, identical

Table 9. Numbers and percentages of parasitized primary hosts (*Gynaephora* spp.) and tachinid puparia attacked by *Cryptus leechi* in each year of the study, excluding primary hosts held in cages to monitor the emergence of adult primary parasitoids in 1995.

Host species	Primary hosts			Tachinid puparia		
Year	Attacked	Total	%	Attacked	Total	%
Gynaephora groenlandica killed by *Hyposoter pectinatus* (Ichneumonidae)						
1994	6	681	< 1		N/A	
1995	1	244	< 1		N/A	
1996	2	268	< 1		N/A	
Gynaephora groenlandica killed by *Exorista* n.sp. (Tachinidae)						
1994	220	505	44	415	1618	26
1995	71	235	30	101	651	16
1996	51	149	34	74	421	18
Gynaephora rossii killed by *Chetogena gelida* (Tachinidae)						
1994	40	133	30	96	648	15
1995	33	162	20	62	856	7
1996	18	55	33	36	243	15

proportions of puparia associated with *G. rossii* were attacked by *C. leechi* in 1994 and 1996 but a significantly smaller proportion was attacked in 1995 ($\chi^2_{c'} = 25.269$, $P < 0.001$). All of these estimated rates of hyperparasitism (Table 9) are conservative in that only hosts in which eggs, larvae, or cocoons of *C. leechi* could be positively identified were counted as having been attacked by *C. leechi*.

Females of *C. leechi* were sometimes found within cocoons containing the remains of *Gynaephora* parasitized by tachinid flies, where they were presumably searching for hosts, but oviposition was observed only once in the field. In this case, a female was

found ovipositing into puparia of *C. gelida* and this female took several minutes to oviposit into each puparium; eight of the ten puparia associated with the primary host were later found to have been parasitized.

Cryptus leechi overwintered as larvae within the puparia or cocoons of their hosts. In the course of routine dissections of host remains in the fall of each year, no living larvae of *C. leechi* were found that had not spun cocoons in preparation to pupate. These cocoons were spun within host puparia or cocoons, alongside the remains of the host, in the fall but pupation did not occur until spring. Because *C. leechi* developed entirely within host puparia or cocoons and showed no evidence of their presence prior to adult emergence, metamorphosis of these parasitoids was not monitored in the field and very few adults were reared from their hosts in the field.

Temperature/Development Relationships

Field Studies

Shaded ground-level air temperature averaged 14.1°C in the OTC and 10.0°C in the control corral during the afternoons when temperatures were recorded for behavioural observations (Figure 35). There was no difference between larvae of *G. groenlandica* held within OTCs and those held in control corrals with respect to either moulting frequency (once for each larva) or the number of days they were active [19 ± 2 d in OTCs (n = 10) *vs*. 20 ± 3 d in control corrals (n = 7); $t_{(1)15} = 0.4175$, $P > 0.25$], although the active period for larvae in OTCs began (and ended) three days earlier, on average, due to a more rapid snowmelt within the OTCs (Figure 36) than in the control corrals. Larvae of *G. groenlandica* showed an apparently exponential pattern of growth interrupted by declines in mass associated with moulting and with the cessation of feeding in preparation for dormancy (Figure 37). Mean RGR based on peak larval mass was significantly greater (Table 10) for larvae held within OTCs than those held in control corrals ($t_{(1)15} = 2.934$, $0.005 < P < 0.01$) but mean RGR based on final larval mass did not differ significantly ($t_{(1)15} = 1.219$, $0.10 < P < 0.25$).

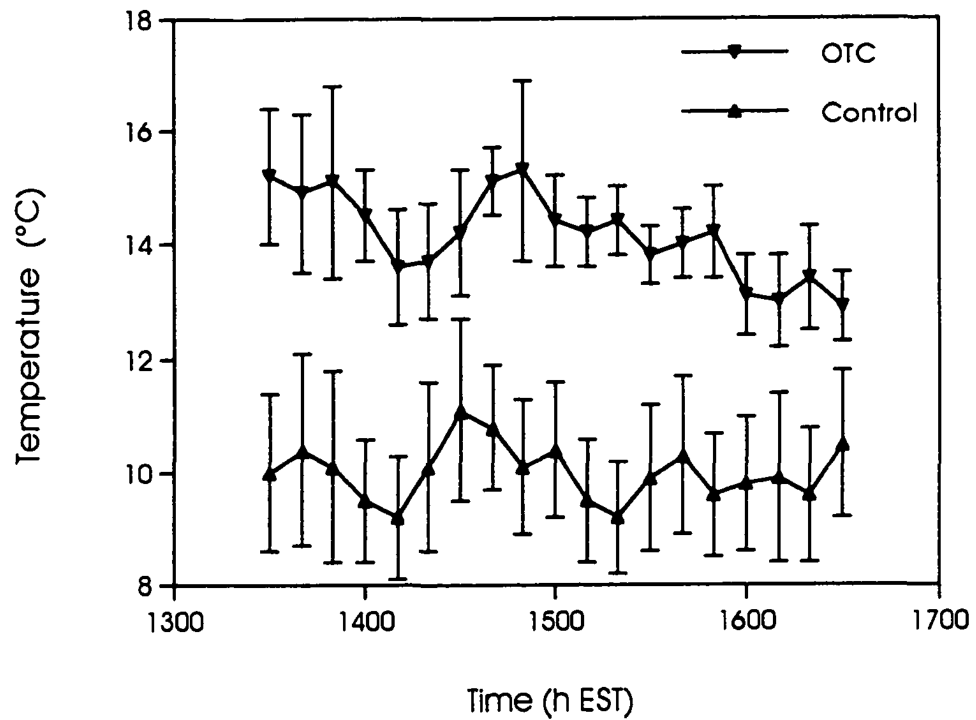


Figure 35. Shaded ground-level (*ca.* 1 cm) air temperatures measured within an open-top chamber (OTC) and a control corral (Control). Data are means ± standard errors of temperatures measured at the same times on five different days between 23 June and 1 July 1996.

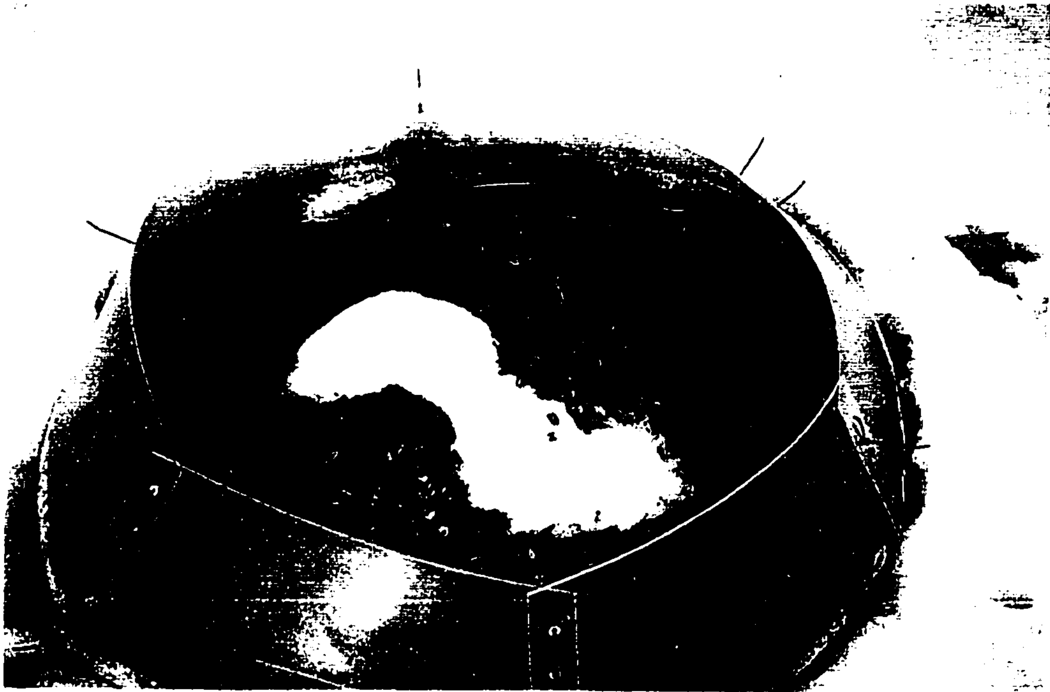


Figure 36. Small open-top chamber showing evidence of the more rapid snowmelt within, compared to without, the chamber.

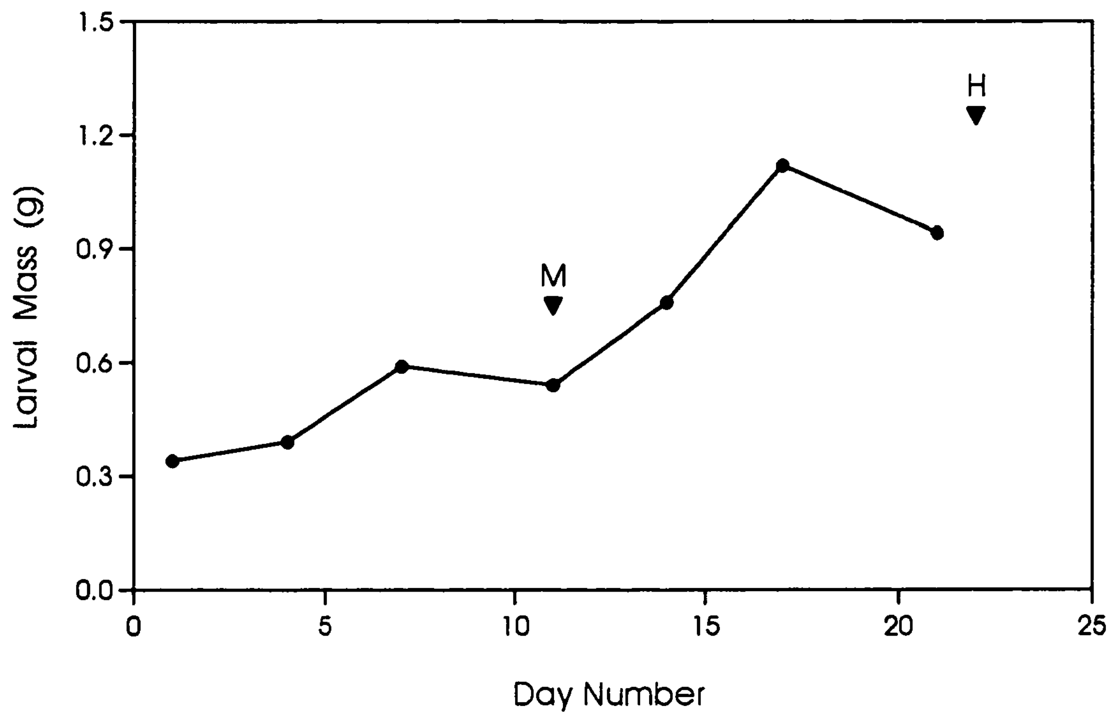


Figure 37. Typical pattern of mass increase for larvae of *Gynaephora groenlandica* in the field, showing exponential increases in mass interrupted by declines associated with moulting and with cessation of feeding in preparation for dormancy. This larva emerged from its overwintering hibernaculum on Day 0, moulted on Day 11 (M), and spun a new hibernaculum on Day 22 (H).

Table 10. Relative growth rates for larvae of *Gynaephora groenlandica* reared under different conditions and for other leaf-feeding larvae of Lepidoptera.

Rearing conditions (n)	Peak	Relative growth rate (RGR) (g)(g body mass^{-1})(d^{-1})	Final
G. groenlandica reared during this study		(mean ± standard deviation)	
Field: Open-top chambers (10)	0.21 ± 0.05		0.15 ± 0.04
Control corrals (7)	0.14 ± 0.05		0.12 ± 0.06
Lab: 15°C (8)	0.07 ± 0.02		0.05 ± 0.03
20°C (9)	0.17 ± 0.06		0.13 ± 0.06
25°C (10)	0.20 ± 0.07		0.20 ± 0.07
G. groenlandica reared by Kukal and Dawson (1989)		(mean ± standard error)	
Lab: 5°C (30)		0.001 ± 0.0005	
15°C (30)		0.016 ± 0.007	
30°C (30)		0.017 ± 0.007	
Other Lepidoptera (Slansky and Scriber 1985)		(mean / range)	
Forb feeders (444 from 29 species)		0.38 / 0.03–1.50	
Tree feeders (810 from 90 species)		0.17 / 0.03–0.80	

Larvae of *G. groenlandica* for which behavioural observations were recorded spent most of their time basking, with the remaining time divided between feeding and moving (Figure 38). The proportions of time spent in these three activities differed significantly between larvae held within the OTC and those held in the control corral ($\chi^2_2 = 39.701$, $P < 0.001$), with larvae in the OTC spending less time basking and less time feeding (but not significantly so; $\chi^2_{c'} = 1.482$, $0.10 < P < 0.25$) and significantly more time moving ($\chi^2_{c'} = 38.152$, $P < 0.001$) than those in the control corral.

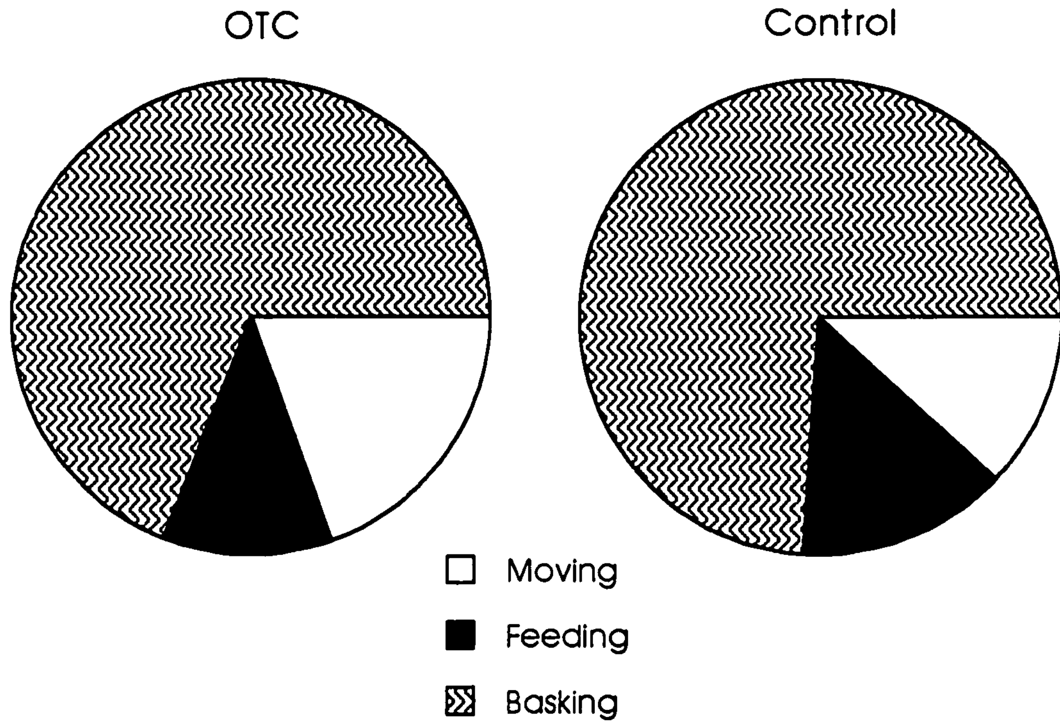


Figure 38. Proportions of time spent moving, feeding, and basking by *Gynaephora groenlandica* larvae during afternoons of favourable weather over the course of their active season in 1996.

Emergence of adult parasitoids held in cages was earlier in 1994 than in 1995 (Table 11) due to the earlier snowmelt in 1994 (*cf.* Figure 19). Adult parasitoids always tended to emerge earlier in OTCs than in control cages, the difference in mean emergence dates being highly significant for all three species in 1995 but significant only for *C. gelida* in 1994. Overall, temperatures in cages within OTCs averaged 2.5°C higher than those in control cages ($n = 22$ temperature measurements at the same times for each of the four cages) and the difference between OTC and control tended to be greater in the cages containing *C. gelida* (3.0°C on average) than in those containing *H. pectinatus* and *Exorista* (2.0°C on average). The proportion of parasitoid puparia or cocoons from which adults emerged in 1995 (comparable data were not collected in 1994) was significantly smaller in the OTCs than in the control cages ($\chi^2_{c'} = 37.532$, $P < 0.001$ for *H. pectinatus*; $\chi^2_{c'} = 61.148$, $P < 0.001$ for *Exorista*; $\chi^2_{c'} = 4.976$, $0.025 < P < 0.05$ for *C. gelida*), excluding the few individuals that were found to have been attacked by *C. leechi*.

Laboratory Rearing

As noted under "Larval activity and moulting frequency" above, larvae of *G. groenlandica* reared in the laboratory at 15°C, 20°C, or 25°C showed the same pattern of development as larvae reared in the field. Specifically, these larvae became active as soon as conditions allowed, developed through a single moult (with a very few exceptions; Table 5), and later spun hibernacula and became dormant. The pattern of growth of these larvae also was similar to that found in larvae reared in the field, with declines in mass associated with moulting and with preparation for dormancy, and the number of days the larvae remained active was inversely related to temperature (Figure 39). Mean RGR based on peak larval mass was comparable at 20°C and 25°C to values determined in the field, but was significantly ($F_{(1)2,24} = 13.944$, $P < 0.0005$) lower at 15°C (SNK, $P < 0.05$). Mean RGR based on final larval mass differed significantly ($F_{(1)2,24} = 14.102$, $P < 0.0005$) at all three temperatures (SNK, $P < 0.05$) and was comparable only at 20°C to values determined in the field (Table 10).

Table 11. Mean emergence dates of adult parasitoids held in cages within (OTC) or without (Control) open-top chambers, and tests for statistical significance of differences in mean emergence dates between treatments.

Species and year	Mean ± standard deviation (n) emergence date (Year Day)			
	OTC	Control	Statistical significance	
Hyposoter pectinatus				
1994	164 ± 4 (32)	166 ± 5 (27)	$t_{(1)57} = 1.163$	$0.10 < P < 0.25$
1995	172 ± 5 (13)	177 ± 5 (45)	$t_{(1)56} = 3.364$	$P < 0.001$
Exorista n.sp.				
1994	164 ± 4 (64)	166 ± 4 (53)	$t_{(1)115} = 1.644$	$0.05 < P < 0.10$
1995	174 ± 6 (35)	178 ± 6 (88)	$t_{(1)121} = 2.668$	$0.0025 < P < 0.005$
Chetogena gelida				
1994	166 ± 3 (17)	168 ± 5 (48)	$t_{(1)63} = 2.040$	$0.01 < P < 0.05$
1995	176 ± 7 (77)	183 ± 10 (51)	$t_{(1)126} = 4.976$	$P < 0.0005$

In contrast, larvae reared at 10°C or 30°C failed to complete development. Although the larvae reared at 10°C became active and most began feeding, only a single individual moulted at this temperature, none spun hibernacula, two individuals began spinning cocoons but failed to complete them, and all larvae eventually died. Several of the larvae reared at 30°C moulted and three spun cocoons and pupated, all within one week of becoming active, but only two larvae spun hibernacula and all larvae and pupae eventually died. Unfortunately, a malfunction of the environmental chamber caused the temperature to increase to approximately 37°C during the second week of rearing and although the temperature was again stabilized at 30°C within 24 h, this temperature increase may have been responsible for the complete mortality of *G. groenlandica* in this chamber.

Mean development rates for larvae (completion of development being defined as spinning a hibernaculum), pupae, and eggs (completion of development being defined as

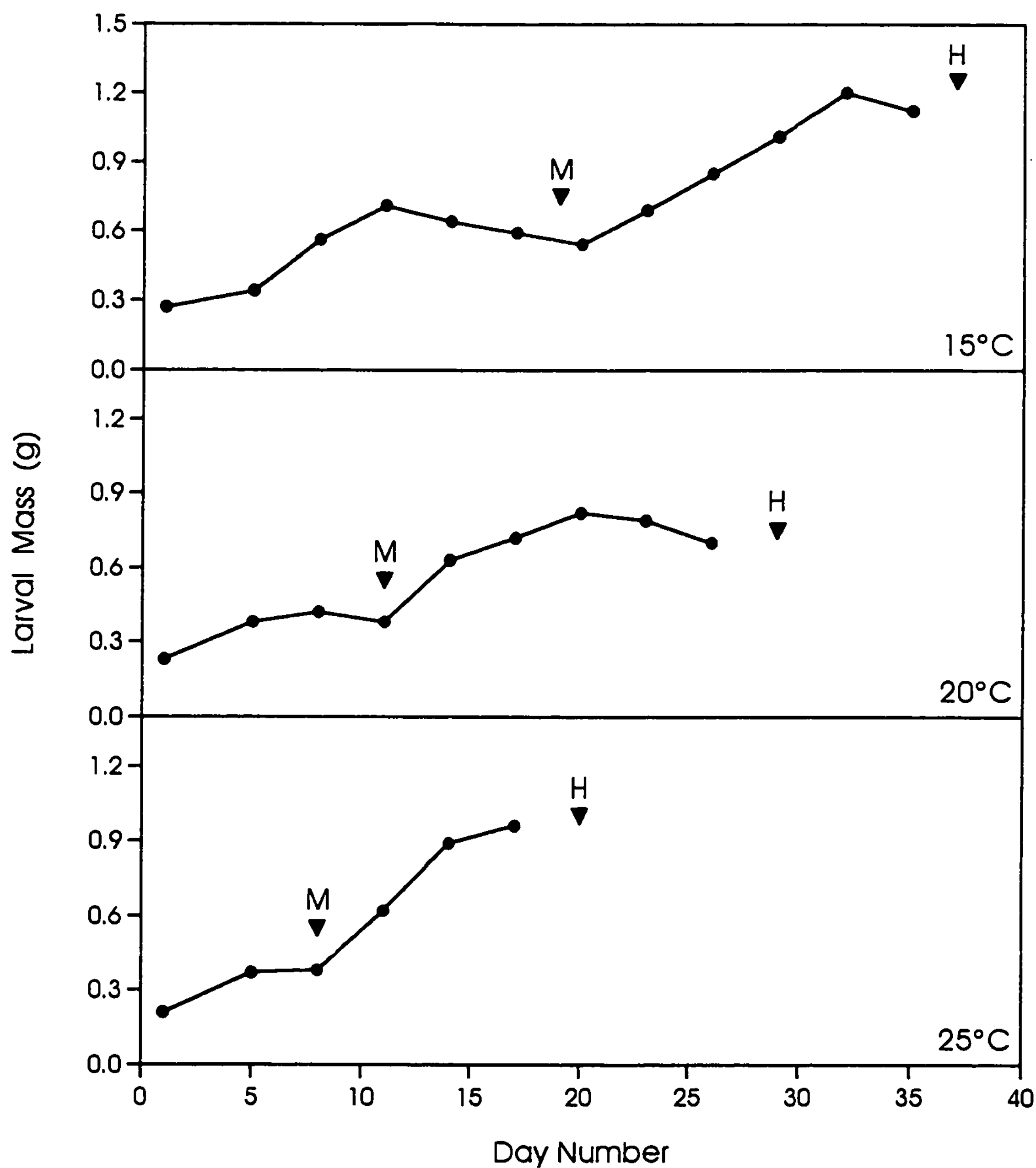


Figure 39. Patterns of mass increase for larvae of *Gynaephora groenlandica* in the laboratory at different constant temperatures, showing increases in mass interrupted by relative declines associated with moulting and with cessation of feeding in preparation for dormancy. These larvae were brought out of subzero temperatures on Day 1; timing of moulting (M) and spinning of hibernacula (H) are indicated for each larva.

the first hatching of eggs from a given egg mass) of *G. groenlandica* showed linear relationships to temperature (Figures 40-42) over the full range of temperatures for which data were obtained (15°C to 25°C). Similarly, a linear relationship to temperature was found for metamorphosis and reproduction of *G. groenlandica*, estimated as development time from emergence of larvae to emergence of adults combined with development time of eggs from oviposition to first hatching (Figure 43).

Hyposoter pectinatus completed development to adult emergence at all five experimental temperatures, and the relationship between development rate and temperature was approximately linear from 10°C to 25°C but showed a distinct decline at 30°C (Figure 44). In contrast, *Exorista* n.sp. failed to complete development at 10°C. Larvae of these parasitoids killed their hosts, many of them pupariated, and some of these completed their metamorphosis, but no adults emerged. On the other hand, there was a linear relationship between development rate and temperature from 15°C to 30°C, with no evidence of a decline at the highest temperature (Figure 45). Like *H. pectinatus*, *C. leechi* completed development to adult emergence at all five experimental temperatures and also showed a linear relationship between development rate and temperature from 10°C to 25°C with a decline at 30°C (Figure 46).

Measured from the day the insects were brought out of subzero temperatures, and thus from the onset of insect activity, development times of *G. groenlandica* larvae and the associated parasitoids showed a striking pattern (Table 12). The first hibernacula were spun by larvae of *G. groenlandica* on or a few days after the day that the first adults of *H. pectinatus* and *Exorista* emerged, and the mean date of hibernaculum-spinning occurred a few days after the mean date of adult parasitoid emergence. In turn, adults of *C. leechi* emerged a few days before adults of *H. pectinatus* and several days before adults of *Exorista*. The relative timing of hibernaculum-spinning by larvae of *G. groenlandica* and emergence of the different species of adult parasitoids was maintained across the range of temperatures for which comparable data were obtained.

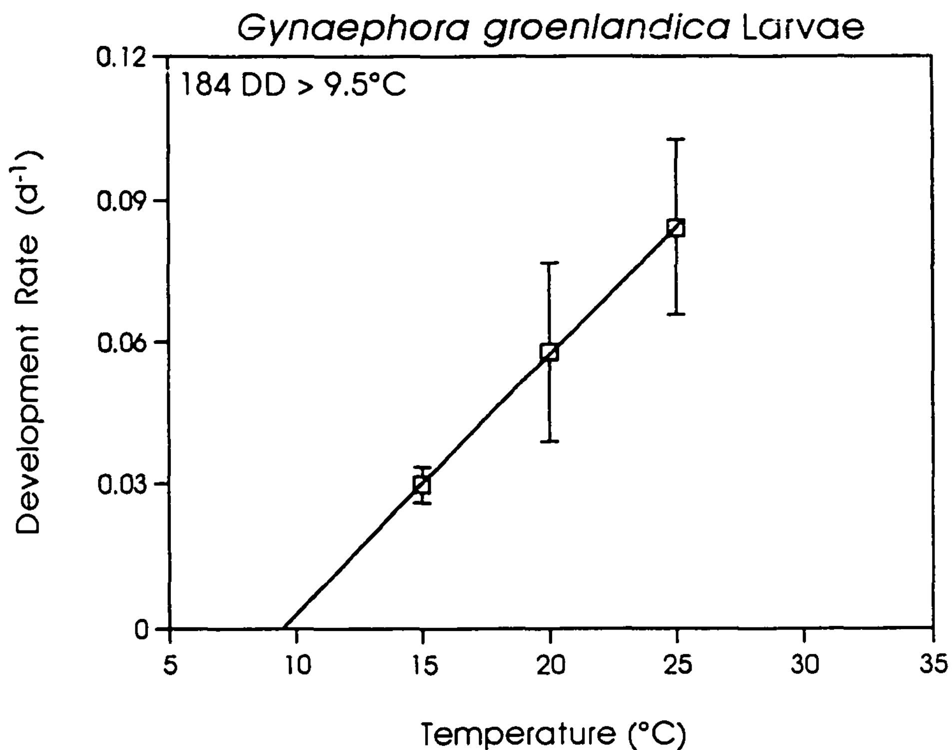


Figure 40. Linear regression of development rate and temperature for larvae of *Gynaephora groenlandica*, complete development being defined as spinning a hibernaculum. Data are mean ± standard deviation at each temperature. The thermal constant is indicated as 184 degree-days above the developmental zero of 9.5°C.

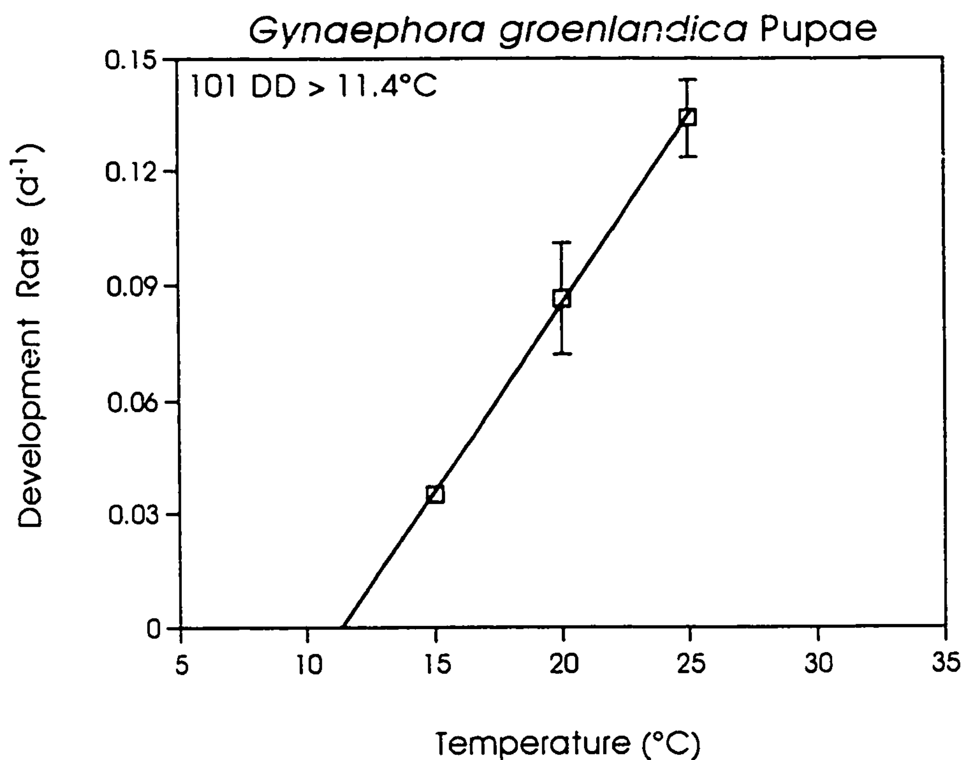


Figure 41. Linear regression of development rate and temperature for pupae of *Gynaephora groenlandica*. Data are mean ± standard deviation at each temperature. The thermal constant is indicated as 101 degree-days above the developmental zero of 11.4°C.

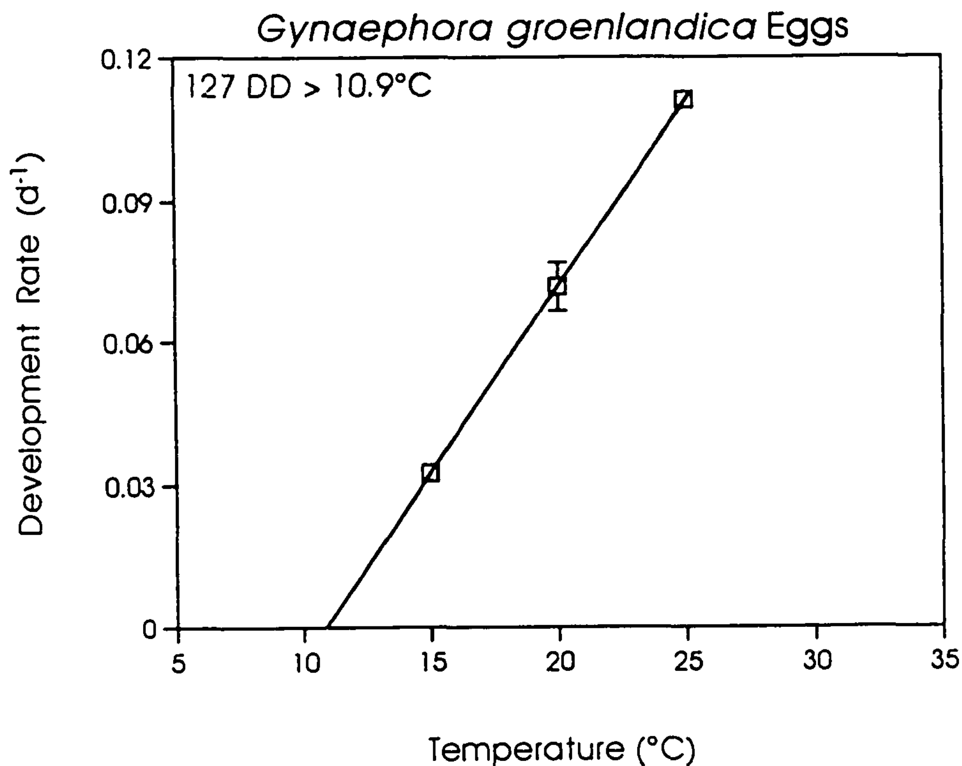


Figure 42. Linear regression of development rate and temperature for eggs of *Gynaephora groenlandica*, completion of development being defined as the first hatching of eggs from a given egg mass. Data are mean ± standard deviation at each temperature. The thermal constant is indicated as 127 degree-days above the developmental zero of 10.9°C.

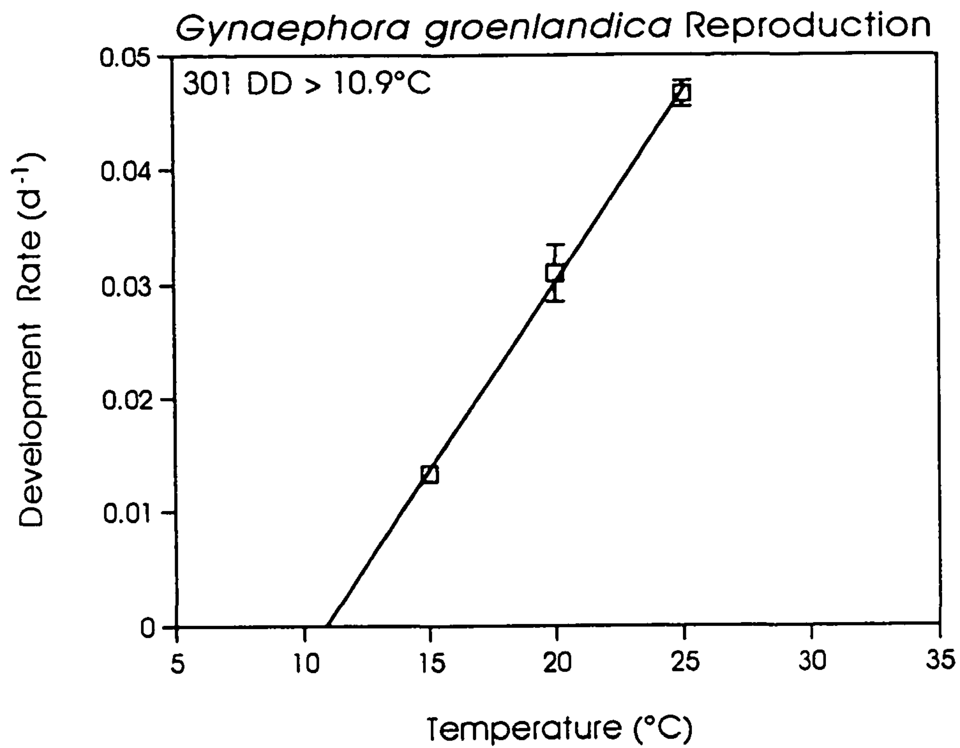


Figure 43. Linear regression of development rate and temperature for reproduction of *Gynaephora groenlandica*. Data are mean ± standard deviation at each temperature, derived by combining development time from larval emergence to adult emergence and from oviposition to first hatch. The thermal constant is indicated as 301 degree-days above the developmental zero of 10.9°C.

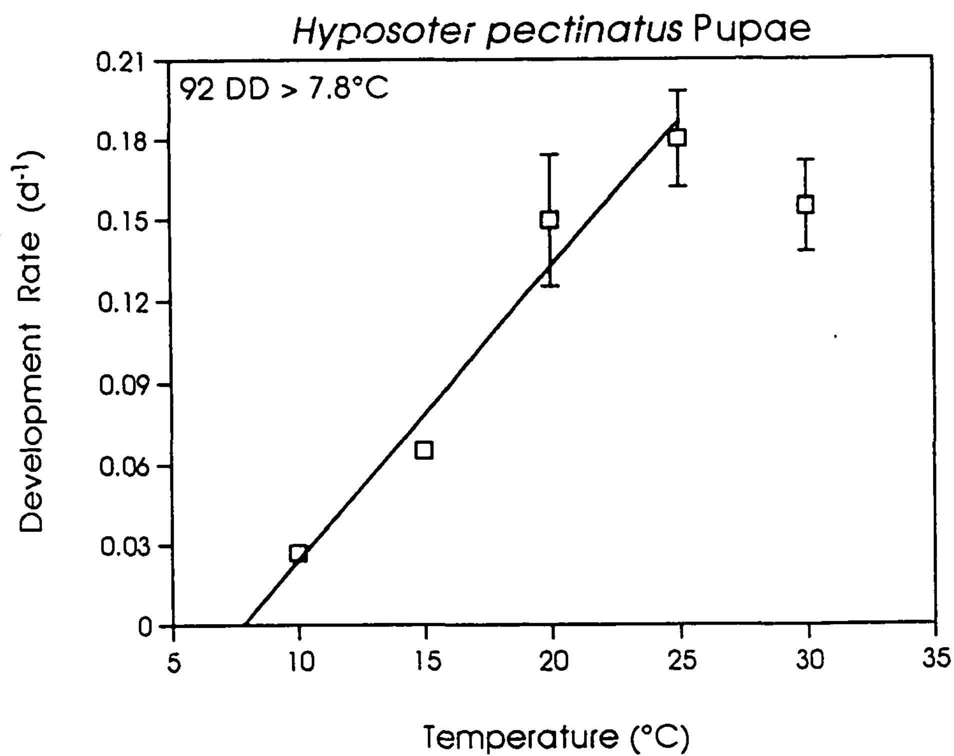


Figure 44. Linear regression of development rate and temperature for metamorphosis of *Hyposoter pectinatus*. Data are mean ± standard deviation at each temperature; development at 30°C is included for comparison but was not used in the regression due to high-temperature inhibition. The thermal constant is indicated as 92 degree-days above the developmental zero of 7.8°C.

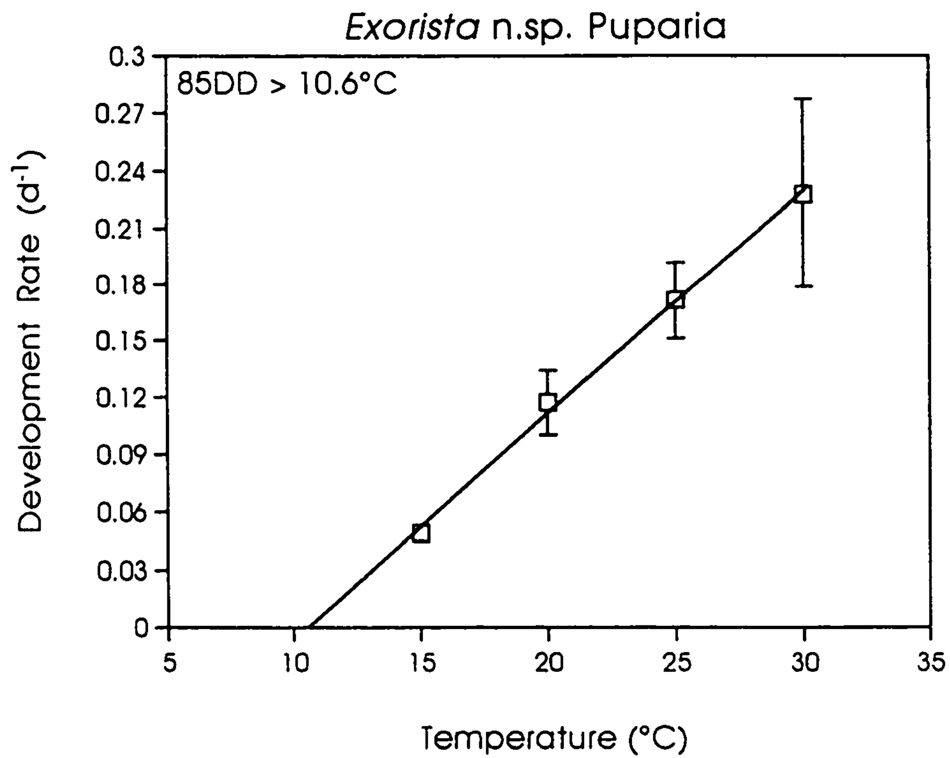


Figure 45. Linear regression of development rate and temperature for metamorphosis of *Exorista* n.sp. Data are mean ± standard deviation at each temperature. The thermal constant is indicated as 85 degree-days above the developmental zero of 10.6°C.

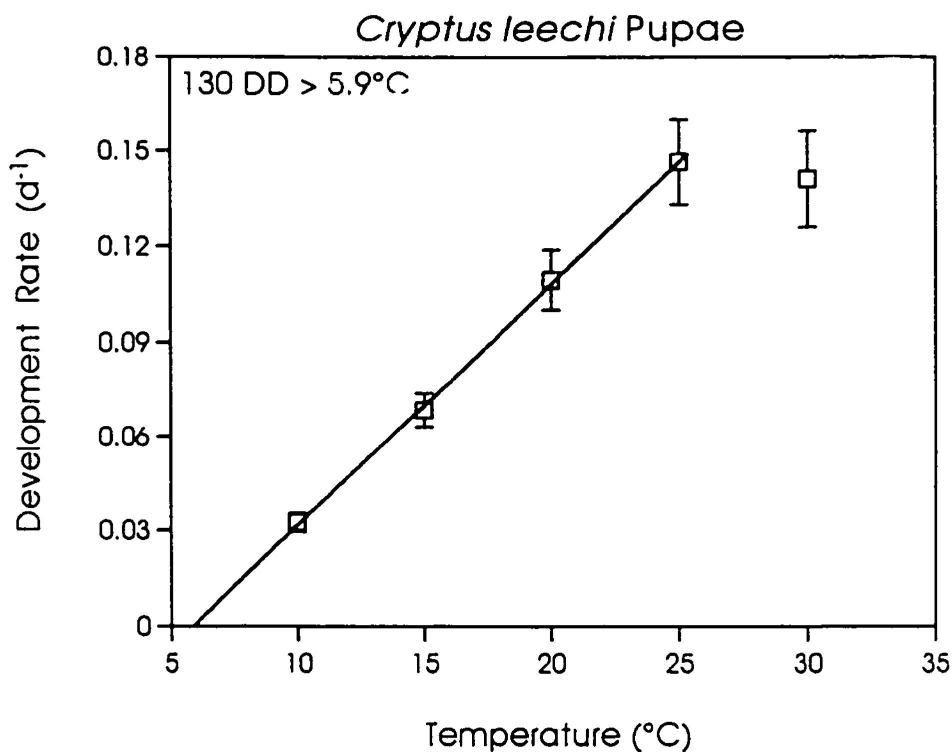


Figure 46. Linear regression of development rate and temperature for metamorphosis of *Cryptus leechi*; development at 30°C is included for comparison but was not used in the regression due to high-temperature inhibition. Data are mean ± standard deviation at each temperature. The thermal constant is indicated as 130 degree-days above the developmental zero of 5.9°C.

Table 12. Laboratory development times of *Gynaephora groenlandica*, the primary parasitoids *Hyposoter pectinatus* and *Exorista* n.sp., and the hyperparasitoid *Cryptus leechi*, measured from the day the insects were brought out of subzero temperatures to the spinning of hibernacula for *G. groenlandica* or to the emergence of adults for the parasitoids. Data for *G. groenlandica* is limited to larvae that developed through a single moult; data for *Exorista* represents the first adults to emerge from each host.

Species	Development time in days [mean / range (*n*)]		
	15°C	20°C	25°C
Gynaephora groenlandica	34 / 32–39 (8)	19 / 10–28 (15)	12 / 9–16 (11)
Hyposoter pectinatus	23 / 22–25 (3)	11 / 10–13 (13)	9 / 9–10 (4)
Exorista n.sp.	33 / 28–40 (45)	15 / 10–17 (41)	11 / 9–13 (43)
Cryptus leechi	15 / 13-18 (33)	9 / 8–11 (27)	7 / 6–8 (31)

DISCUSSION

It is the way of the world
that some people put errors into circulation
while others try then to eradicate these same errors.
This keeps everyone busy...

Arni Magnusson (1663–1730)

Identification of Immature Stages of *Gynaephora* Species

Confusion concerning identification of immature stages of North American *Gynaephora* species dates back to the original description of *G. rossii*. Curtis (1835) described an adult male in some detail and provided a colour illustration that leaves no doubt that the species was *G. rossii*. In contrast, his descriptions of immature stages were rather cursory; however, the "two tufts of black hair on the back [of the caterpillar], followed by two of orange" are unmistakably those of *G. groenlandica*. His description of the cocoons is unfortunately too generalized to assign to either species. The original description of *G. groenlandica*, on the other hand, includes a mention of "the characteristic *Dasychira*-caterpillar hairtufts on the back and the *end segment*" (Homeyer 1874; emphasis added) typical of the larvae of this species. Packard (1877) described all stages of what he thought was *G. rossii*, based on specimens collected in northern Greenland. These descriptions are fairly accurate for *G. groenlandica* and Packard himself noted that the adults differed from the description of *G. rossii* given by Curtis (1835) in that their hind wings had no "broad, blackish margin", which is perhaps the most obvious difference between adults of *G. groenlandica* and *G. rossii* (*cf.* Plate 1 in Ferguson 1978). The brief descriptions published by Scudder *et al.* (1879) as representing *G. rossii* are inadequate for identification of the species; however, they did note that the original "description of the larva does not well accord with the present specimen." It may be that neither Packard (1877) nor Scudder *et al.* (1879) knew of *G. groenlandica*, considering that the description of this species was published in 1874 in Germany and therefore may not have been available to them.

As early as 1875, *G. rossii* had been found above treeline on Mount Washington, New Hampshire, and recognized as the same species as had been described from the Arctic (Grote 1876). Later, Dyar (1896) described larvae from the same locality and noted that they differed from the descriptions published by both Curtis (1835) and Packard (1877). The following year, he received larvae from Greenland that agreed with Curtis' description, obtained an adult *G. groenlandica* from one of them, and concluded that "Curtis must have mixed the species" (Dyar 1897).

Despite Dyar's conclusion and his fairly detailed descriptions of the larvae of *G. rossii* (Dyar 1896) and *G. groenlandica* (Dyar 1897), misidentifications and confusing information may be found in much more recent published literature, as noted in the introduction to this dissertation. In addition, Ryan (1977) and Ryan and Hergert (1977) presented a photograph of a number of specimens from Truelove Lowland, Devon Island, that included both species of *Gynaephora*, but the adults were not shown associated with their cocoons. Both "light and dark colour cocoons" were illustrated and Ryan and Hergert (1977) stated that "both forms [were] found with each species"; however, they made no mention of the structure of the cocoons and submitted only a single specimen (a female of *G. groenlandica* with the cocoon from which it emerged) to the Canadian National Collection of Insects. As described above, cocoons of both species may be light or dark in colour, depending on the extent to which larval hairs of different colours are incorporated into the cocoon and the extent to which the cocoon is weathered, but the structure of the cocoon is species-specific. Descriptions of larvae provided by Ferguson (1978) are accurate, even though they were based on extremely limited material; however, they may give the impression that the differences between the two species are rather subtle when in fact these differences produce a distinctive appearance for each species that is discernible even from a distance.

Pupae of *G. groenlandica* and *G. rossii* have not been described previously, but both species may be identified to genus using the key to genera provided by Patocka (1991). They also fit the generic description of *Gynaephora* pupae except that their antennae are apparently much shorter than those of the European species *Gynaephora*

selenitica (Esper), as described and illustrated by Patocka (1991). The diagrams presented here (Figure 13) are composites that attempt to illustrate "typical" pupae for both sexes of both North American species; however, a considerable amount of individual variation was seen, even among the small number of pupae examined. The only differences between species that were obvious and consistent were overall size and the length of hairs (which may be related to overall size), the presence or absence of hairs on the ventral surface of abdominal segments 9 and 10, and possibly the form (curved or relatively straight) of the maxillae.

It should be noted that the size differences between the two species may not be consistent across their entire range. In fact, the adults illustrated by Ferguson (1978) clearly show that *G. rossii* may be larger than *G. groenlandica* from different localities. The fact that *G. rossii* were found to be consistently smaller than *G. groenlandica* in the current study may reflect the fact that this population of *G. rossii* is in the extreme northern portion of the species' range whereas Alexandra Fiord is more central in the distribution of *G. groenlandica*.

Despite the confusion that is apparent in the literature, most of the immature stages of arctic *Gynaephora* species can be identified to species quite readily and with little more than a cursory examination. The occasional lack of grey plumose hairs in *G. rossii* larvae may cause some confusion and may be responsible for a report of "morphs intermediate between the two ... species" (Kukal 1994b), although the supposed intermediate morphs were not described in that report. The species may be reliably separated by differences in the patterns of black and yellow hairtufts and the much longer overall hairs of *G. groenlandica*. Furthermore, there is strong evidence that they are reproductively isolated at the level of mate recognition and therefore do not produce hybrids (see "Metamorphosis and reproduction"). Hopefully, the descriptions and illustrations provided here will help to prevent future misidentifications.

Life Histories and Biology

Gynaephora Species

Gynaephora species are among the most conspicuous insects on the high arctic tundra and observations on their natural history have been recorded ever since the early arctic expeditions of European explorers. The first comprehensive study of *G. groenlandica* was conducted by Kukal (1984) and later published by Kukal and Kevan (1987). That study provided a significant advance in knowledge of the natural history of *G. groenlandica*; however, it did contain some gaps and inaccuracies due, in part, to the fact that it was conducted during a single summer season. Some of the results presented here differ considerably from those published by Kukal and Kevan (1987), and I am obliged to offer explanations for the differences. In addition, despite the contention of Ryan and Hergert (1977) that they are ecologically equivalent, there are noteworthy differences between the two species of *Gynaephora*.

Head-capsule widths and number of larval instars

The results presented here (Figure 15) indicate that *G. groenlandica* develop through seven larval instars. In contrast, Kukal and Kevan (1987) concluded that *G. groenlandica* developed through six larval instars, but it is not clear how they came to this conclusion beyond the fact that their presumed instars were derived from a distribution of measured HCWs. Various methods have been proposed and/or used to resolve multimodal distributions, such as HCW distributions, into their component parts, such as larval instars (*e.g.* Harding 1949; Forbes 1953; Hasselblad 1966; Bhattacharya 1967; Ross and Merritt 1978; Caltagirone *et al.* 1983; Beaver and Sanderson 1989; McClellan and Logan 1994). Kukal and Kevan (1987) made no reference to any such methods, stating only, "Measurements of larval HCW segregated into six distinct groups, indicating that *G. groenlandica* has six larval instars." No illustration of this distribution of HCWs was presented, however, and the data as published do not appear to support their conclusion. Specifically, larval HCW was measured "to a precision of 0.2 mm" (Kukal and Kevan

1987), yet mean values given for adjacent instars differed by as little as 0.4 mm. Furthermore, HCW ranges of up to 1.0 mm were listed for individual instars, indicating broad overlap in HCW between instars and begging the question of how individuals were assigned to different instars. Again, no mention was made of methods used to distinguish the different instars and it should be noted that, with the exception of the first and last instars, morphological differences between one instar and the next are very subtle.

Setting aside the lack of supporting data, development through six larval instars is not an unreasonable assumption for a lymantriid moth and development through seven larval instars is no less realistic for a member of this family. Most lymantriids for which this information is available typically develop through five or six larval instars, although as few as three and as many as eight have been reported (Payne 1917; Brittain and Payne 1918; McDunnough 1921; Hardy 1945; Campbell 1963; Beckwith 1978, 1982; Reese 1980; Littlewood 1984; Singh and Goel 1986; Nagasawa 1988; Gupta *et al.* 1989; Das 1990; Jobin *et al.* 1992; McClellan and Logan 1994). Many lymantriids are known to be sexually dimorphic, with females developing through one more larval instar than males (Payne 1917; Campbell 1963; Beckwith 1978, 1982; Reese 1980; Sevastopulo 1981; Singh and Goel 1986; Nagasawa 1988; Gupta *et al.* 1989), and female pupae of some lymantriids, including *Gynaephora* species, are known to be larger than male pupae (Payne 1917; Brittain and Payne 1918; Beckwith 1982; Singh and Goel 1986; Gupta *et al.* 1989; Das 1990; Lyon and Cartar 1996; this study). There was no evidence of dimorphism in the distribution of HCWs for either species of *Gynaephora*, however. In particular, there is no indication of a bimodal peak in HCWs for the final instar (Figure 14), the three smallest final-instar individuals of *G. groenlandica* having HCWs of 3.40, 3.35, and 3.15 mm and representing the extreme lower "tail" of the distribution for this instar. Final-instar larvae (n = 571) were identified as such because they had spun cocoons in preparation to pupate and there is no reason to believe that all such individuals were females. It has been reported that female larvae of *Orgyia antiqua* (L.) (Lepidoptera: Lymantriidae) grow larger than male larvae during the final stadium (Littlewood 1984). However, sexual dimorphism in the number of larval instars has also been reported for

that species (Payne 1917; Reese 1980). Thus, it remains to be clearly established whether sexual dimorphism in pupal size of lymantriids may, in some cases, be produced by differential growth during the final larval stadium, but this does appear to be the case in North American *Gynaephora* species.

According to the Brooks-Dyar rule, the ratio of the HCW of a given instar to that of the previous instar, defined as the growth ratio, should be the same for all moults, with any major deviation indicating that one or more instars might have been overlooked (Dyar 1890). The Brooks-Dyar rule has proved useful in some cases, though not in others, for determining the number of instars in a given species (Daly 1985), and the data presented here for *G. groenlandica* provide a good example of a major deviation in growth ratios indicating a missing instar. The HCW data of Kukal and Kevan (1987) indicate mean growth ratios of 2.00 and 1.71 for the first two moults, dropping to 1.14 at the third moult and remaining near this low value for subsequent moults (Table 3). Considering the level of precision of their HCW measurements, it is clear that their presumed first and second instars actually correspond to the first and third instars (Table 3), indicating that they had overlooked the second instar. The HCW data presented here for the early instars were derived from direct rearing of larvae from eggs, leaving no opportunity to miss any of these early instars.

Growth ratios derived from observed mean HCW for each instar are very close to those predicted by the Brooks-Dyar rule, the only large deviation occurring at the third moult (Table 3) and probably arising as an artifact of the relative lack of data for the fourth instar (Figure 14). Although the mean HCW calculated here for the fourth instar is probably somewhat inaccurate, there can be little doubt that the lack of data is just that and not the lack of an instar of this size. Larvae smaller than fifth instar are only occasionally encountered in the field and only a few larvae were reared beyond the fourth instar but these showed that a fourth instar of that size does exist. Furthermore, if the indicated fourth instar did not exist and larvae developed through a sequence of six instars, as indicated by the upper curve in Figure 15, they would have to accomplish a moult with a mean growth ratio of 1.82, much larger than any of the 98 individual growth ratios

measured.

The Brooks-Dyar rule has been criticized as invalid or inapplicable to particular species because of apparent deviations from the predicted pattern of equal growth ratios at all moults, the most common deviation being a steady decline in growth ratios at progressively later moults (Hutchinson *et al.* 1997). For example, both Jobin *et al.* (1992) and McClellan and Logan (1994) concluded that the Brooks-Dyar rule does not apply to larvae of *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae) because of such a decline in growth ratios, which Jobin *et al.* (1992) reported to be statistically significant. A similar, though nonsignificant, decline is evident in individual growth ratios of *G. groenlandica* (Figure 16) and, with the exception discussed above, is also suggested by growth ratios calculated from the observed mean HCW for each instar (Table 3). Unfortunately, as a result of their unusual moulting behaviour, too few data for HCWs and growth ratios were obtained to conduct a similar analysis for *G. rossii*; however, predicting mean HCWs using constant growth ratios produced overestimates of the mean HCWs for the final instars, suggesting a similar decline in growth ratios at later moults in both species of *Gynaephora* (Figure 14). Recently, Hutchinson *et al.* (1997) provided a theoretical framework, based on a power-law growth equation and realistic assumptions about such factors as moulting efficiency and scaling of food intake with size, which not only indicates that growth in arthropods should generally at least approximate the pattern defined by the Brooks-Dyar rule but is consistent with the common observation of declining growth ratios at successive moults.

Larval activity and moulting frequency

First-instar larvae of *Gynaephora* were fully capable of overwintering. All of the larvae of *G. groenlandica* hatched from eggs in the field in 1994 that were recovered in the spring of 1995 were still first instars, and even when eggs were hatched and the larvae reared indoors under relatively warm conditions that might be expected to enhance their development, only about 20% (1994) or 30% (1995) moulted to the second instar before the end of the field season. Similarly, only about 10% of the *G. rossii* larvae reared

indoors in 1995 developed to the second instar before the end of the field season. Obviously, neonates have the potential to develop beyond the first instar before becoming dormant for the winter if conditions allow. However, under field conditions, pupal development requires two weeks, on average, and embryonic development requires about another month, so that neonates do not hatch until late July or early August (Figure 21), by which time temperatures are decreasing and food-plant quality is declining rapidly (*e.g.*, willow leaves turning yellow and senescing; Jones *et al.* 1997 and personal observations). Thus, the potential of neonates to develop beyond the first instar in their first season is unlikely to be realized under field conditions. Overall, these data strongly suggest that the first larval instar is the stage in which individuals of these species normally spend their first winter and, furthermore, there is no obvious reason why first instars of *G. groenlandica* should be incapable of overwintering, as maintained by Kukal (1995), when all subsequent instars do overwinter.

The results of both field and laboratory studies presented here indicate that larvae of *G. groenlandica* normally moult once per year, every year. In contrast, Kukal and Kevan (1987) reported that only about one-third of the individuals in each of their last four instars of *G. groenlandica* moulted within one growing season, suggesting that these instars each require about three years to develop to the next. There are two possible explanations for this discrepancy, both of which probably contribute to the difference in observed moulting frequencies. First, Kukal and Kevan (1987) conducted their study within a single season of fieldwork, collecting larvae from the field and rearing them for the remainder of the field season. Thus, it is possible that some of these larvae had already accomplished their annual moult before they were collected for the study. Second, the larvae reared by Kukal and Kevan (1987) were held in "perforated 20-mL vials" within outdoor cages and "were fed leaves and young buds of *Salix arctica, which were replaced weekly*" (emphasis added). In this study, shoots of arctic willow, when removed from the plant to feed insects kept in vials or Petri dishes, began to wilt within a day or two and were often completely desiccated in less than a week, even when kept out of direct sun. Furthermore, most larvae reared in the laboratory at the University of Victoria usually required daily

feeding, suggesting that it would not be possible to fit a week's supply of food within a 20-mL vial. Thus, it seems likely that the larvae reared by Kukal and Kevan (1987) were not nourished enough to develop as they would have under natural conditions.

In contrast, the field-reared larvae of *G. groenlandica* in this study had ample supplies of a variety of living plants, including *S. arctica*, on which to feed. Thus the pattern of development observed, namely annual moulting of larvae, should more accurately represent the normal development of this species at this site. Admittedly, the sample was smaller than that of Kukal and Kevan (1987); however, the conditions under which the results were obtained in the field were closer to environmental norms and the consistency of the results, both in the field and in the laboratory, further suggests that they are accurate. Specifically, every one of the larvae that was monitored in the field for its entire active season, from the day it emerged from its hibernaculum in the spring to the day it once again spun a hibernaculum in early summer, moulted during that season, and almost every one of the larvae reared in the laboratory showed the same pattern of development. Furthermore, the fact that all of the larvae that were monitored for two consecutive growing seasons moulted during the first and then either moulted again or spun cocoons during the second leaves little doubt that moulting is typically an annual event for *G. groenlandica* at Alexandra Fiord. In addition, all of the *G. groenlandica* larvae hatched from eggs in the field in 1994, and left to develop under natural conditions for the following two years, that were recovered at the end of the field season in 1996 were third instars at that time, indicating that annual moulting is typical of the early, as well as the later, instars.

In contrast, the relatively few data obtained for *G. rossii* indicate that larvae of this species are not limited to a single moult annually but rather remain active and continue to moult as long as conditions remain favourable or until they reach the final larval instar. Oliver *et al.* (1964) reported that there is "probably" an obligate diapause in the last instar of *G. rossii*, although no supporting evidence was presented in that report. The occurrence of an obligate diapause in the last larval instar of *G. rossii* is also suggested by the results of laboratory rearing in this study, with larvae of *G. rossii* reared at 20°C in

1997 developing as far as the final instar but then becoming dormant rather than proceeding to spin cocoons and pupate.

It has been known for some time that larvae of *G. groenlandica* limit their activity to the early part of the growing season (Kukal 1984; Kukal and Kevan 1987) and this will be discussed further under "Life History Strategies" below. In contrast, larvae of *G. rossii* remained active late in the growing season and there are indications that this is consistent throughout the geographic range of the species. Johansen (1921) described larvae of *G. rossii* "crawling around looking for hibernating quarters" in September on the western Arctic coast of North America. Similarly, Schaefer and Castrovillo (1979(1981)) reported larvae of *G. rossii* to be active and feeding in September on both Mt. Katahdin, Maine, and Mt. Daisetsu, Japan. *Gynaephora* larvae were collected for me in the vicinity of the Muskox River on north-central Banks Island in early August of 1993 and this collection consisted of approximately two dozen larvae of *G. rossii* but only a single larva of *G. groenlandica*. In addition, researchers working on the Fosheim Peninsula of west-central Ellesmere Island in 1996 observed larvae of *G. groenlandica* in abundance in late June and early July but larvae of *G. rossii* only in early August (Lewkowicz[5], personal communication 1996).

Larvae of *Gynaephora* spun their hibernacula in sheltered locations on the surface of the tundra and always did so individually except when confined within small areas at very high densities (*i.e.*, in the stock corrals). These results are similar to those published recently by Kukal (1995) and contradict the previous assertion (Kukal *et al.* 1988b; Kukal and Dawson 1989; Kukal 1990, 1991, 1993; Danks *et al.* 1994) that larvae of *G. groenlandica* move down close to the permafrost when they become dormant in early summer. It is noteworthy that within at least some of the cages used for the study published by Kukal (1995), there were deep crevices in the tundra but the larvae chose to remain on the surface and construct their hibernacula in the vegetation and litter. The significance of this is that, although it might be argued that larvae of *G. groenlandica* undergo "voluntary hypothermia" by virtue of the fact that they no longer thermoregulate

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by basking (*cf.* Kukal *et al.* 1988a), temperatures within such hibernacula track ambient temperatures fairly closely (Kukal 1995). Ground-level temperatures, both ambient and within hibernacula, often exceed 20°C and even approach 30°C during sunny weather (Morewood, unpublished data). Metabolism of poikilothermic organisms in general is directly related to temperature and this has been shown experimentally for larvae of *G. groenlandica* (Kukal *et al.* 1988b; Kukal and Dawson 1989). The hypothesis that larvae of *G. groenlandica* move close to the permafrost where "the larval body temperatures range between 0-5°C" (Kukal 1990) and thus reduce maintenance metabolism and conserve energy reserves during their summer dormancy (Kukal 1990; Kukal 1991; Kukal 1993; Danks *et al.* 1994) must be reevaluated in the light of more recent discoveries regarding the location of, and temperature conditions in, larval hibernacula.

On the other hand, the conclusion that hibernacula protect larvae of *G. groenlandica* from parasitism has considerable merit, although the "communal" nature of some of the hibernacula reported by Kukal (1995) is probably an irrelevant artifact of artificially high densities of larvae confined within small areas at a time when they were all spinning hibernacula. Considering that *H. pectinatus* oviposit directly into the host and *Exorista* affix their eggs to the cuticle of the host, neither of these parasitoids would be able to attack larvae of *G. groenlandica* within hibernacula (regardless of whether the hibernacula are isolated or communal). Adult parasitoids might not even recognize hibernacula as containing potential hosts, considering that *H. pectinatus* always probed larvae of *G. groenlandica* with their antennae before ovipositing and *Exorista* apparently used host movement as an oviposition stimulus. The hibernaculum-like shelters spun by larvae of *G. rossii* for moulting may serve the same purpose. These would again prevent adults of *H. pectinatus* and of *C. gelida* from reaching the larvae within during a time when these larvae are relatively more vulnerable due to limited mobility. In the same way, hibernacula and moulting shelters would protect larvae of *Gynaephora* from arthropod predators such as spiders (Leech 1966) and the syrphid larvae observed feeding on larvae of *G. groenlandica* at Alexandra Fiord.

Hibernacula and moulting shelters would also protect larvae of *Gynaephora* from

discovery by birds; however, this is probably irrelevant because birds apparently do not prey on *Gynaephora* larvae. Parmelee (1960) reported no evidence of birds preying on larvae of *Gynaephora* (reported as *Byrdia*) despite the abundance of these larvae on the Fosheim Peninsula of west-central Ellesmere Island, and Kukal and Kevan (1987) reported that birds rejected larvae of *G. groenlandica* as prey. Despite the abundance of *Gynaephora* larvae as potential prey, birds may be deterred from preying on these larvae by the urticating nature of the larval hairs, as described by Morewood and Lange (1995(1997)).

Larvae of *Gynaephora* are clearly opportunistic feeders, accepting a wide variety of plant species as food, but do show definite preferences in their choice of foodplants (Table 6). Curtis (1835) originally reported that larvae of *G. groenlandica* (reported as *G. rossii*) fed mostly on *Saxifraga tricuspidata* Rottböll and *S. oppositifolia*, but the preference of this species for *Salix* has since been noted repeatedly (Wolff 1964; Kukal and Kevan 1987; Kukal and Dawson 1989; this study). The relatively few feeding observations for *G. rossii* in this study probably underestimate the variety of plants that these larvae actually eat, even at Alexandra Fiord. This widely distributed species has been reported to feed on many different plants, ranging from sedges to broad-leaf trees (Schaefer and Castrovillo 1979(1981) and references cited therein) and it has been suggested that some isolated alpine populations show preferences for ericaceous plants, which predominate in alpine habitats (Schaefer and Castrovillo 1979(1981)).

Metamorphosis and reproduction

The distinct double-layered structure of the cocoon of *G. groenlandica* probably represents an adaptation to the high arctic environment, allowing the crucial life stages of pupation and reproduction to be completed within the very short growing season. These cocoons are thought to act as "microgreenhouses" and temperatures within them have been shown to be higher than both ambient temperatures and surrounding substrate temperatures (Kevan *et al.* 1982; Kukal 1984). Furthermore, it has been recently reported that cocoons of *G. groenlandica* significantly enhance the rate of pupal development but that those of

G. rossii, which consist of a single layer, do not (Lyon and Cartar 1996). The similar pupal development times in both species found at Alexandra Fiord might be accounted for by the difference in size of pupae of the two species at this site. Without a development-enhancing cocoon like that of *G. groenlandica*, a decrease in size of *G. rossii* in the northern portion of its range may be necessary for this species to complete pupal development quickly enough to reproduce and still leave time for the resulting eggs to hatch before winter closes in. Initiation of cocoon-spinning very soon after fully grown larvae become active in the spring is probably also necessary to complete metamorphosis and reproduction within the short growing season.

Predation on pupae of *Gynaephora* species by jaegers tearing open the cocoons and consuming the contents has been reported, but not quantified, previously at other sites (Bruggemann 1958; Parmelee and MacDonald 1960). Predation by smaller birds pecking through the cocoons and into the pupae was implied by the report of Kukal and Kevan (1987), although they did not identify the species responsible. This type of predation was never observed directly in this study; however, the most likely candidates are snow buntings, by far the most abundant breeding birds at Alexandra Fiord (Freedman 1994 and personal observations), and possibly also red knots (*Calidris canutus* L.), Baird's sandpipers (*Erolia bairdii* Coues), and/or Lapland longspurs (*Calcarius lapponicus* L.), all of which were seen to nest and forage in the deciduous dwarf shrub – graminoid plant community in which *Gynaephora* cocoons were most often found.

Total bird predation on cocoons of *G. groenlandica* (including some prepupae as well as pupae) was approximately 38% in 1995 and 36% in 1996, excluding cocoons containing *G. groenlandica* known to have been killed by *Exorista*. In contrast, a significantly smaller proportion of the cocoons of *G. rossii* were attacked by birds (15% in 1995 and 29% in 1996), probably due to the much more cryptic nature of these cocoons compared to the very conspicuous cocoons of *G. groenlandica*. The increase in bird predation on cocoons of *G. rossii* in 1996, compared to 1995, although not statistically significant due to the relatively small numbers involved, might be attributed to the smaller number of the more conspicuous cocoons of *G. groenlandica* available that year. In any

case, the rate of predation by birds on cocoons of *Gynaephora* species at Alexandra Fiord was quite consistent for the two years in which it was recorded during this study and was much higher than the estimate by Kukal and Kevan (1987) of 7.4% of viable pupae (excluding pupae killed by *Exorista*) based on "the proportion of damaged (i.e., pecked) to undamaged cocoons collected in nature." Perhaps the most obvious explanation for this discrepancy is year-to-year variation that would require a much longer-term study to document; however, it is not clear whether Kukal and Kevan (1987) included cocoons emptied by jaegers in their estimate of bird predation.

Although no attempt was made to quantify bird predation on adults of *Gynaephora* in this study, snow buntings were frequently seen chasing males in flight and attacking females on their cocoons. This observation suggests that predation on adults is at least as important as predation on pupae and probably more so because in the adult stage females were more vulnerable than males due to their inability to fly and were often attacked before laying eggs. In contrast, Kukal and Kevan (1987) made no mention of predation on adults of *G. groenlandica* and did not attempt to quantify mortality rates of adults due to the difficulty of finding and monitoring adults in the field, but suggested that adult mortality was not important due to the short lifespan (24 h by their estimate) of the adults.

The difference in cross-attraction of males by females of the two species (Table 7) suggests different mechanisms of maintaining reproductive isolation between the species. Males of both *Lymantria monacha* (L.) and *L. dispar* are attracted to the commercially-synthesized pheromone disparlure (Schneider *et al.* 1974), a compound produced by females of both species. However, the sex pheromone of *L. monacha* contains additional compounds that confer species-specificity by enhancing attraction of *L. monacha* males while diminishing the response of *L. dispar* males (Gries *et al.* 1996). The sex pheromone of *G. rossii* may consist of a similar multiple-component blend that attracts males of *G. rossii* almost exclusively. Calling females of *G. groenlandica*, however, attracted males of both species in equal numbers and must therefore use close-range cues for mate recognition. Males of both *L. dispar* (Charlton and Cardé 1990c) and *Orgyia leucostigmata* (J.E. Smith) (Lepidoptera: Lymantriidae) (Grant 1981) that have been

"primed" by exposure to pheromones require contact with female body scales to "release" mating behaviour. This cue appears to be primarily tactile, perhaps with a chemical component, and does not appear to be species-specific (Charlton and Cardé 1990c), although a species-specific cue of this nature would explain the results obtained with *Gynaephora*.

Considering that males made no attempt to mate with heterospecific females, other means of prezygotic reproductive isolation, such as genitalic incompatibility or differences in courtship, are probably unimportant in *Gynaephora*. Furthermore, courtship in lymantriids is almost non-existent; females apparently exercise little mate choice and males attempt to copulate even with models bearing female body scales (Grant 1981; Charlton and Cardé 1990a, 1990c). Visual cues could conceivably be important for *Gynaephora* adults, which mate in the continuous daylight of the arctic summer. The day-flying males of *L. dispar* show virtually no response to visual cues from females, however, and can locate females or models and show normal copulatory behaviour even when blinded (Charlton and Cardé 1990b, 1990c). This suggests that visual cues are not critical for diurnal lymantriids, perhaps because they have retained the mate-location behaviours of nocturnal ancestors (Charlton and Cardé 1990b).

Eggs of *G. groenlandica*, but not of *G. rossii*, laid on cocoons were subject to heavy predation by birds, probably due to the very conspicuous nature of *G. groenlandica* cocoons and the relatively cryptic nature of *G. rossii* cocoons, which may have made the cocoons of *G. rossii* much more difficult to find for both birds and researchers in the field. Snow buntings were observed removing eggs of *G. groenlandica* from egg masses on cocoons placed in the field for observation, and red knots, Baird's sandpipers, and/or Lapland longspurs may also have contributed to the high rate of predation on eggs of *G. groenlandica* observed in this study. Predation by the latter species was never observed directly but may be inferred by the nesting and foraging of these birds in the deciduous dwarf shrub – graminoid plant community where *G. groenlandica* was most abundant. Moreover, snow buntings and Lapland longspurs are primarily seed eaters (Hurd and Pitelka 1955) but have been reported to prey heavily on insects in the Arctic (Hurd and

Pitelka 1955; Tilden 1976). Surprisingly, the only mortality factor identified for eggs of *G. groenlandica* by Kukal and Kevan (1987) was "inviability". With respect to eggs, their study included only "six females observed in nature [which] remained on their cocoons and deposited all of their eggs there" and they concluded that the "eggs hatched within several days of their deposition" without presenting any relevant data (Kukal and Kevan 1987). They apparently found no other eggs masses in the field and this may be due to the facts that eggs are often laid after the female has left her cocoon, such eggs are extremely cryptic, and egg masses laid on cocoons are extremely vulnerable to predation by birds. Egg masses on cocoons are likely to be removed before they are found and, considering the rate of predation recorded in 1994, it seems likely that very few eggs laid on cocoons would escape predation long enough to hatch.

Parasitoids of *Gynaephora* Species

The parasitoid complex of *Gynaephora* at Alexandra Fiord consists of only four species, three primary parasitoids and one hyperparasitoid (Figure 22), representing only two different families. This is considerably less diverse than comparable systems in temperate zones and is perhaps to be expected, considering the general decline in insect diversity with increasing latitude (Danks 1990). Studies of temperate-zone lymantriid moths, even within restricted geographical areas, have revealed far more diverse parasitoid complexes. For example, using a "host exposure technique", Eichhorn (1996) recovered at least ten species of primary parasitoid and 19 species of hyperparasitoid, representing nine different families, from larvae of *L. dispar* in eastern Austria. Similarly, Pristavko and Tereshkin (1981) reported 11 species of primary parasitoid and five species of hyperparasitoid, representing at least five different families, from larvae and pupae of *L. monacha* in the Minsk region of Belarus, and Zaharieva-Pentcheva and Georgiev (1997) listed 15 species of primary parasitoid and six species of hyperparasitoid, representing nine different families, as comprising the parasitoid complex of *Stilpnotia salicis* (L.) in Bulgaria. Even taking into account all reported parasitoids of *Gynaephora* throughout their range in the Arctic (Table 1), their known parasitoid complex is still distinctly

impoverished compared to temperate-zone faunas. For example, Langston (1957) reported that 23 species of Hymenoptera alone were known at that time to parasitize *Malacosoma disstria* Hübner (Lepidoptera: Lasiocampidae) in North America.

The parasitoid complex of *Gynaephora* species at Alexandra Fiord is based almost exclusively on *Gynaephora* larvae; egg parasitoids and pupal parasitoids are conspicuously absent, especially considering the abundant resources *Gynaephora* eggs and pupae would provide. Parasitoids of the eggs and pupae of lymantriid moths are not uncommon elsewhere; for example, of the primary parasitoids of *S. salicis* in Bulgaria listed by Zaharieva-Pentcheva and Georgiev (1997), two species parasitized eggs, eight species parasitized larvae, and six species parasitized pupae of the host. In addition, Young (1995) listed 14 species of egg parasitoids, representing seven different families, known to parasitize eggs of *Orgyia pseudotsugata* (McDunnough) in North America and reared five of these species, representing four different families, from eggs of *O. pseudotsugata* collected within the Kamloops Forest Region of British Columbia.

A number of species in the superfamily Chalcidoidea (Hymenoptera), most of which are parasitoids, particularly of insect eggs (Borror *et al.* 1989), are common at Alexandra Fiord (Morewood, unpublished data). None of these have been identified to species or reared from any host; however, at least one species of *Tetrastichus* Haliday (Hymenoptera: Eulophidae) has been reported from Alexandra Fiord (Kukal 1994a). This genus includes parasitoids of the eggs of *O. pseudotsugata* (Young 1995), but also includes parasitoids of a great variety of other insect species and stages (Burks 1979). A comparison of the Hymenoptera Parasitica reported from Alexandra Fiord by Kukal (1994a) with the host affinities described by Carlson (1979), Marsh (1979), Burks (1979), and Gordh (1979) did not reveal any potential parasitoids of *Gynaephora* pupae; however, both the insect fauna of Alexandra Fiord and the host affinities of most Hymenoptera Parasitica are too poorly known to draw firm conclusions from such a comparison.

In the absence of a potential explanation for the lack of egg parasitoids and pupal parasitoids of *Gynaephora* based on systematic affinities, a functional explanation might be proposed. Considering the high rates of predation on *Gynaephora* eggs and pupae, but not

larvae, by birds at Alexandra Fiord, it could be argued that predation pressure would limit the success of parasitoids specializing on eggs or pupae as hosts. Competition with predators for the host resource and direct mortality through predation of hosts containing developing parasitoids would clearly disfavour such parasitoids, compared to those that specialize on larvae of *Gynaephora* (*cf.* Rathcke and Price 1976).

The absence at Alexandra Fiord of certain species of parasitoids reported from *Gynaephora* elsewhere in the Arctic (Table 1) is perplexing, all the more so because some of these species may actually be present at Alexandra Fiord but have not been reared from *Gynaephora* species there. *Periscepsia stylata* was reportedly reared from *G. groenlandica* in eastern Greenland (Nielsen 1907, 1910) but has not been reported from Alexandra Fiord and was never reared from *G. groenlandica* during this study. However, considerable numbers of *Periscepsia* were collected in pan traps at Alexandra Fiord in 1992 (Morewood, unpublished data) and were almost certainly *P. stylata*, this species being the only representative of the genus in the North American Arctic (Danks 1981) and being known from Hazen Camp and Eureka in northern and west-central Ellesmere Island, respectively (specimens in the Canadian National Collection of Insects, Ottawa). Ryan and Hergert (1977) reported rearing an undescribed species of *Rogas* from larvae of *Gynaephora* at Truelove Lowland, Devon Island. This may or may not be the same "*Rogas* sp." reported from Hazen Camp, Ellesmere Island, by Oliver (1963) but in any case, no representative of this genus has yet been reported from Alexandra Fiord. Ryan and Hergert (1977) also reported rearing *C. gelida* from cocoons of both species of *Gynaephora* at Truelove Lowland but their reported host association is likely inaccurate, considering the host-specificity of *C. gelida* at Alexandra Fiord and the fact that they did not distinguish between the cocoons of the two host species. Finally, *P. byrdiae* is known only from the Low Arctic (Danks 1981) and may be prevented from invading the High Arctic by factors other than host availability, such as lower temperatures or the shorter growing season.

Hyposoter pectinatus (Hymenoptera: Ichneumonidae)

Hyposoter pectinatus is well known as a parasitoid of *G. groenlandica*, but not previously of *G. rossii*, and has been reported only from Europe, eastern Greenland, and Ellesmere Island (Carlson 1979; Kukal 1994a). The report by Johansen (1921) of an unidentified ichneumonid parasitizing *G. rossii* on the western Arctic coast of North America, which spun a cocoon within the host cuticle attaching the host remains to the ground, suggests that this species might also occur there. Unfortunately, that report cannot now be confirmed because apparently no specimens were collected (Brues 1919); however, the congeneric species *H. luctus* (Davis) is known from that area, as well as Ellesmere Island and the alpine region of Mt. Washington, New Hampshire (Viereck 1926; Oliver 1963; Kevan 1973; Carlson 1979; Kukal 1994a), a distribution which parallels that of *G. rossii*. No host association has been reported for *H. luctus* and it is likely that this name represents a junior synonym of *H. pectinatus* (Barron[6], personal communication 1995 & 1996), although the necessary taxonomic review unfortunately was not completed.

Members of the genus *Hyposoter* are parasitoids of larval Lepidoptera, predominantly macrolepidoptera that feed in exposed locations (Carlson 1979), and *H. pectinatus* is typical of the genus in this respect and shows further similarities to a number of congeneric species. The HCW distribution of host remains (Figure 23) indicates that only the larger (no smaller than fifth) instars of *Gynaephora* are suitable for *H. pectinatus* to complete development. The host instar in which females of *H. pectinatus* usually oviposit could not be determined definitively in this study; however, all larval instars of *G. groenlandica* were accepted for oviposition and only the seventh instar caused obvious difficulties for ovipositing females. Other species of *Hyposoter* are known to oviposit into early larval instars of their hosts and emerge as adults from later instars (Bogavac 1956; Langston 1957; Puttler 1961; Browning and Oatman 1984; Beckage and Templeton 1985; Torgersen 1985; Fuester *et al.* 1988; Fuester and Taylor 1991; Lei *et al.* 1997), and females have been shown to accept most available host larvae, but in some

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cases to prefer early instars, for oviposition (Swain *et al.* 1938; Smilowitz and Iwantsch 1975; Campbell and Duffey 1979; Tillman and Powell 1989; Fuester and Taylor 1991). In such species, development of the larval parasitoid is more rapid following oviposition into larger hosts (Puttler 1961; Smilowitz and Iwantsch 1973; Jowyk and Smilowitz 1978) and the prolonged development in smaller hosts has been shown to occur in the early larval instars of the parasitoid (Jowyk and Smilowitz 1978), presumably allowing the host to grow large enough to support the complete development of the parasitoid (Beckage and Templeton 1985).

The acceptance of early instars of *G. groenlandica* for oviposition by females of *H. pectinatus* suggests that delayed development may also be common in *H. pectinatus*, but only a single instance of delayed development was actually documented in this study. Although hosts of *Hyposoter* species continue to grow and develop after being parasitized, parasitism is known to retard host growth, with host HCW becoming progressively smaller with each moult compared to nonparasitized individuals (Vinson and Barras 1970; Iwantsch and Smilowitz 1975; Tagawa *et al.* 1982; Nealis 1987). Thus, if *H. pectinatus* does often oviposit into early host instars and undergo delayed development to emerge from the later instars, then the bulk of *G. groenlandica* killed by *H. pectinatus* probably represent sixth instars rather than both fifth and sixth instars (compare Figures 23 & 15). This is consistent with the number of *G. groenlandica* killed by *H. pectinatus* each year being proportional to the number of *G. groenlandica* adults found the following year, to the extent that the number of adults in a given year would be proportional to the number of sixth-instar larvae in the previous year. The relatively small numbers of seventh-instar larvae of *G. groenlandica* killed by *H. pectinatus* are probably due to the difficulty females of *H. pectinatus* have in ovipositing into larvae of this size; similar difficulties were noted by Langston (1957) for females of *Hyposoter fugitivus* (Say) attacking the last two larval instars of *Malacosoma* species (Lepidoptera: Lasiocampidae). The larger proportion of the *G. groenlandica* killed by *H. pectinatus* that were seventh instars in 1994, compared to 1995 and 1996 (Figure 24), probably reflects a relatively great abundance of potential hosts in this stadium in 1993, as indicated by the very large number of *G. groenlandica*

adults that emerged in 1994 (Figure 20).

Overwintering of *H. pectinatus* always occurred in the larval stage within living hosts and other species of *Hyposoter* have been reported to overwinter in the same way (Bogavac 1956; Lei *et al.* 1997), although reports of overwintering in the pupal (Torgersen 1985; Coffelt and Schultz 1993) or adult (Dustan 1920) stage also exist for members of this genus. Pupation behaviour of *H. pectinatus* has been described (Johansen 1910; Kukal and Kevan 1987) and illustrated (Kukal 1984) previously but the false cocoon was not mentioned in those reports. The false cocoon of *Hyposoter parorgyiae* (Viereck) was described in some detail by Finlayson (1966) and this type of structure has been reported for two other species of *Hyposoter* (Finlayson 1966; Carlson 1979). As far as is known, *Hyposoter* species always spin cocoons in which to pupate and in most cases, but not all (Torgersen 1985; Coffelt and Schultz 1993), these cocoons are spun beneath (Fuester *et al.* 1983) or within (Dustan 1920; Bogavac 1956; Langston 1957; Finlayson 1966; Carlson 1979; Lei *et al.* 1997) the remains of the host. Both the structure of the false cocoon and concealment of the pupal cocoon within the host remains probably help to protect the pupal stage of *Hyposoter* species from hyperparasitoids (Finlayson 1966; Coffelt and Schultz 1993) and from predators, especially those that would not prey on the host, as in the case of birds at Alexandra Fiord.

Pupation of *H. pectinatus* appears to be synchronized with host moulting, considering that parasitized hosts spun silk platforms, like those spun in preparation to moult, before being killed by the parasitoids. Beckage and Templeton (1985) reported that two other species of *Hyposoter* synchronized their metamorphosis with host moulting and suggested that the onset of host moulting allowed the parasitoid larvae to consume the last of the host tissue as the epidermis separated from the cuticle. On the other hand, although larvae of *G. groenlandica* usually moult in exposed locations, they do not normally climb to the highest available point to do so, suggesting manipulation of host behaviour by *H. pectinatus*. Manipulation of host behaviour has been documented for other parasitoids and shown to result in selection of microhabitats favourable to the parasitoids (Brodeur and McNeil 1989; Pivnick 1993). In the case of *H. pectinatus*, selection of the highest point

available would result in greater exposure to wind and thus might help the parasitoids avoid exposure to detrimentally high temperatures during their metamorphosis (*cf.* "Laboratory Rearing" under "Temperature/Development Relationships").

Exorista n.sp. and *Chetogena gelida* (Diptera: Tachinidae)

Exorista n.sp. and *Chetogena gelida* are both placed in the tribe Exoristini (Stone *et al.* 1965; Crosskey 1976; Cantrell 1985; Belshaw 1993) and thus show many morphological and biological similarities. The two species have almost identical life cycles at Alexandra Fiord and are almost indistinguishable superficially, but may be easily separated by differences in the shape of the male terminalia and in both sexes by the very hairy eyes of *Chetogena* compared to *Exorista* (Wood 1987). Most Exoristini are parasitoids of larval Lepidoptera and some species are remarkably polyphagous (Stone *et al.* 1965; Adam and Watson 1971; Crosskey 1973, 1976; Schaefer and Shima 1981; Cantrell 1985; Hubenov 1985; Belshaw 1993; Jamil *et al.* 1993). The precise host-specificity of *Exorista* and *C. gelida* at Alexandra Fiord is surprising (Wood[7], personal communication 1992), especially considering the biological similarities between these species and the fact that their hosts are closely related. The mechanism responsible for the host-specificity of these two species is unknown, but may operate at the level of host recognition. Tachinid flies that oviposit directly onto their hosts (as do all members of the Exoristini; Wood 1987; Belshaw 1993) often rely on visual cues in host selection (Adam and Watson 1971; Belshaw 1993; Shimada *et al.* 1994; this study) and *Exorista sorbillans* (Wiedemann) has been shown to discriminate among different stocks of its host, *Bombyx mori* (L.) (Lepidoptera: Bombycidae), that have different larval body colours and marking patterns (Shimada *et al.* 1994). Thus, *Exorista* n.sp. and *C. gelida* might be able to recognize their respective hosts visually, but oviposition behaviour could also play a role. The distribution of *C. gelida* eggs, often affixed to the dorsal larval hairs of *G. rossii*, suggests that females of *C. gelida* might actually land on their hosts to oviposit, as reported

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for the few other species of *Chetogena* (Terkanian 1993) and *Exorista* (Rahman 1970; Kumar *et al.* 1993) for which such information has been published. In contrast, female tachinid flies might be prevented from successfully landing and ovipositing on larvae of *G. groenlandica* by the long and uneven hairs of these larvae, giving rise to the oviposition behaviour of *Exorista* n.sp. wherein females oviposit from the ground as the host larvae pass by.

Both *Exorista* and *C. gelida* parasitized predominantly final-instar larvae of their respective hosts, with *Exorista* occasionally emerging also from pupae (Figure 23), and this is consistent with congeneric species for which precise host associations have been reported. *Exorista* species generally parasitize the later instars, often the final instar, and prepupae of their hosts (Guppy 1967; Hansen *et al.* 1982; Oshiki and Nakazawa 1987; Hondo 1992) and some species emerge from the pupae (Rahman 1970; Pristavko and Tereshkin 1981; Rishi and Shah 1985; Ragab 1992; McFayden 1997; Zaharieva-Pentcheva and Georgiev 1997). The well-studied species *E. sorbillans* has been reported to attack all instars of potential hosts (Gangwar and Thangavelu 1989; Thangavelu 1993) but to show a preference for later instars (Kumar *et al.* 1993), as might be expected because larger hosts would provide more resources for the development of parasitoid larvae. *Chetogena* species also parasitize late-instar larvae of their hosts (Fritz *et al.* 1986; Terkanian 1993) and at least one species does not kill its host until after host pupation (Terkanian 1993) although Malloch (1919) specifically noted that hosts of *C. gelida*, which had spun cocoons, did not succeed in pupating before being killed by the parasitoids.

Less than 5% of the *G. groenlandica* killed by *Exorista* in each year of this study were pupae, in contrast with almost 60% indicated by Kukal and Kevan (1987). Pupae of *G. groenlandica* killed by *Exorista* tended to contain fewer puparia than final-instar larvae (Figure 28), suggesting that only final-instar larvae parasitized by relatively few *Exorista* are likely to succeed in pupating before being killed by the parasitoids. This would imply that there were relatively few parasitoids developing per host in 1983; however, Kukal and Kevan (1987) reported a mean of 4.4 adults of *Exorista* emerging per host, considerably higher than the mean of three puparia per host in 1994 through 1996, not all of which in

turn produced adults. Considering that at least 77% of the *G. groenlandica* killed by *Exorista* in 1994-96 had at least begun spinning cocoons, an alternative explanation might be that Kukal and Kevan (1987) did not carefully inspect host remains and counted those within completed cocoons as pupae even though they may still have been prepupae.

With one noteworthy exception, the number of *G. groenlandica* and *G. rossii* killed by *Exorista* and *C. gelida*, respectively, was consistently proportional to the number of adults of *G. groenlandica* and *G. rossii* emerging each year, suggesting that rates of parasitism (as a proportion of available hosts) by these tachinid flies are fairly constant from year to year. The exception to this trend occurred in 1994, when a much smaller than expected proportion of *G. groenlandica* was killed by *Exorista*, probably due to the great abundance of potential hosts that were final-instar larvae in 1993, as indicated by the very large number of *G. groenlandica* adults that emerged in 1994 (Figure 20). The relative abundance of final-instar hosts in 1993 is also reflected in the larger mean HCW of *G. groenlandica* killed by *Exorista* in 1994, compared to 1995 and 1996 (Figure 27), and the resulting greater numbers of puparia produced per host that year.

Overwintering of *Exorista* n.sp. and *C. gelida* always occurred in the larval stage within living hosts and this is not uncommon among the Tachinidae although the majority of species overwinter as puparia (Belshaw 1993). The overwintering stage of other species of *Exorista* and *Chetogena* has not been reported, but Hondo (1992) reared *Exorista japonica* (Townsend) from overwintered larvae of *Thanatarctia imparilis* (Butler) (Lepidoptera: Arctiidae) collected from the field in the spring, suggesting that this species overwinters as a larva within its host. Like most Tachinidae (Belshaw 1993), larvae of *C. gelida* almost always emerged from their hosts prior to pupariation and although other species of *Exorista* have been reported to emerge from their hosts prior to pupariation (Rahman 1970; Oshiki and Nakazawa 1987; Jamil *et al.* 1993; Nakamura 1994; Mellini and Campadelli 1996), *Exorista* n.sp. puparia were usually formed within the host remains. As noted for pupation of *H. pectinatus*, pupariation within larval remains of *G. groenlandica* would protect *Exorista* from predation by birds during their metamorphosis; however, this benefit would be lost once the host pupated, thus favouring

Exorista that killed their hosts prior to host pupation. Pupariation within host remains might also provide protection from parasitism, to the extent that puparia within the remains of the primary host would be less accessible to ovipositing hyperparasitoids. That does not appear to the the case in this system, however, because a larger proportion of the puparia of *Exorista* than of *C. gelida* were found to have been attacked by *C. leechi.*

Although the time required by individual insects to complete their metamorphosis was shorter for the tachinid flies than for *H. pectinatus*, this was less evident in the phenology of each population as a whole, with the result that emergence dates for adults of *Exorista* and *H. pectinatus* were very similar (Table 8). In contrast, emergence dates for adults of *C. gelida* were earlier in 1995 and later in 1996 than those for adults of *Exorista* and *H. pectinatus*. Considering that parasitoid metamorphosis is not initiated until the host becomes active in the spring, these differences may be ascribed to the fact that *C. gelida* develops on a different host species than the other two primary parasitoids. It may be that the spring onset of larval activity differed between the two host species; however, any such differences were not documented.

<u>*Cryptus leechi* (Hymenoptera: Ichneumonidae)</u>

Cryptus leechi is the first species documented as a hyperparasitoid in the High Arctic and although this species was known to occur at Alexandra Fiord (Kukal 1994a) it was not mentioned in the study published by Kukal and Kevan (1987) and no host association has been reported previously (Mason 1968; Carlson 1979). Many puparia of *Exorista* n.sp. and *C. gelida*, as well as a very few cocoons of *H. pectinatus* that had parasitized *G. groenlandica*, were parasitized by *C. leechi* in 1994 through 1996. Other species within the subfamily Cryptinae, the largest subfamily of Ichneumonidae, are known to attack puparia of Diptera and most Cryptinae are ectoparasitoids (Carlson 1979), as is the case with *C. leechi*. However, most of the species in the subtribe Cryptina appear to be parasitoids of the pupae or prepupae of Lepidoptera or Hymenoptera Symphyta (sawflies) and all members of the genus *Cryptus* Fabricius (= *Itamoplex* of Townes;

Luhman[8], personal communication 1995) for which host associations have been reported are parasitoids of Lepidoptera (Carlson 1979). The only species of *Cryptus* for which biological information has been published is *C. latigenalis* Pratt (misidentified as *C. inornatus* Pratt; Carlson 1979), which attacks prepupae of *Loxostege sticticalis* (L.) (Lepidoptera: Pyralidae) within cocoons (Ullyett 1949).

The "saw-toothed" ovipositor of *C. leechi* suggests that this species would attack hosts within cocoons (Luhman, personal communication 1993) and, considering the systematic affinities outlined above, it may be that *C. leechi* has shifted hosts from the prepupae and/or pupae of *Gynaephora* to the puparia of the tachinid parasitoids of *Gynaephora*. *Cryptus leechi* occasionally attacked *H. pectinatus* within *G. groenlandica*, as well as the two tachinid species, suggesting that host-recognition cues for *C. leechi* are largely associated with the primary host. The tendency of *C. leechi* to attack a larger proportion of primary hosts that had spun cocoons than of those that had not spun cocoons further suggests that the cocoon of the primary host provides an important cue. A host shift from *Gynaephora* to the tachinid parasitoids of *Gynaephora* would simultaneously eliminate competition with the tachinids for hosts and provide an abundant host resource for *C. leechi*, apparently without competitors for that resource.

Insect parasitoids are often divided into two major groups, termed koinobionts, which allow their hosts to grow and develop after being parasitized, and idiobionts, which complete their development on the stage in which the host was attacked (Haeselbarth 1979; Askew and Shaw 1986). Unlike the primary parasitoids of *Gynaephora* species at Alexandra Fiord, all of which are koinobionts, *C. leechi* is an idiobiont. Idiobiotic parasitoids that attack their hosts in the larval stage paralyse the host with a sting before ovipositing. Egg and pupal parasitoids are generally classified as idiobionts (Godfray 1994); however, it is not clear whether they employ the same strategy because these host stages are already immobile (Mills 1992, 1994). *Cryptus latigenalis* was reported to paralyse its hosts prior to oviposition (Ullyett 1949) and it may be that *C. leechi* does this also, considering the length of time required for oviposition by this parasitoid (several

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minutes) compared to that taken by *H. pectinatus* (a few seconds). That females of *C. leechi* paralyse the host prior to oviposition is further suggested by the presence of *C. leechi* eggs, but not larvae, in puparia of tachinid flies that failed to complete their metamorphosis or died as pharate adults. An alternative explanation that females of *C. leechi* take a long time to oviposit in order to investigate hosts for prior parasitization or suitability of the host stage is refuted by the observations of frequent superparasitism by this species and equal representation of hosts that were immatures or pharate adults.

The geographic distribution of *C. leechi*, known only from the High Arctic of both Canada and Greenland (Mason 1968; Carlson 1979; Kukal 1994a), corresponds well with that of *G. groenlandica* but not with that of *G. rossii*, and this parasitoid attacked a larger proportion of *Exorista* associated with *G. groenlandica* than of *C. gelida* associated with *G. rossii* at Alexandra Fiord. These facts suggest that the original host association of *C. leechi* is with *G. groenlandica* and, in turn, with *Exorista* n.sp. For *C. leechi* to expand its host range to include *C. gelida* in the Canadian portion of its range would not be difficult because the primary host, *G. rossii*, probably provides similar cues for host recognition and because *C. leechi* is an idiobiotic ectoparasitoid and thus needs no specialized adaptations to avoid or overcome the physiological defences of its hosts, as do koinobiotic endoparasitoids (Vinson and Iwantsch 1980a, 1980b).

Temperature/Development Relationships

Field Studies

Although the temperature data presented here are limited (Figure 38), they are consistent with those from more comprehensive studies of the OTCs' performance at this site (Marion *et al.* 1997; Stenström *et al.* 1997), which report similar enhancement of daytime temperatures during favourable weather, but little or no temperature enhancement at night or during poor weather (overcast or stormy conditions), leading to an overall temperature enhancement of 1-2°C averaged over the growing season. Such temperature differences are no greater in magnitude than the range of natural variation at this site

(*cf.* Labine 1994), thus it is perhaps not surprising that there was no difference in development (moulting frequency) or active period between larvae of *G. groenlandica* held in OTCs or control corrals.

Ground-level shaded air temperatures averaged 4.1°C higher within the OTC than in the control corral during the time when behavioural observations were made, allowing the larvae of *G. groenlandica* in the OTC to spend less time basking and less time feeding than those in the control corral. Larvae of *G. groenlandica* spend most of their time basking (Kukal *et al.* 1988b; this study) in order to raise their body temperatures and promote digestion of their food (Kukal *et al.* 1988b; Kukal and Dawson 1989), a behavioural constraint that would be less critical at higher ambient temperatures. Similarly, the larvae in the OTC spent significantly more time moving than those in the control corral and this is consistent with the observation by Kukal *et al.* (1988b) that larvae of *G. groenlandica* are most active during the warmest part of the day.

Mean RGR for larvae of *G. groenlandica* held within OTCs was significantly greater than for those in control corrals when calculated based on peak mass, suggesting that these larvae are more efficient in feeding and converting food to body mass at higher temperatures, as indicated by the limited data (5°C, 15°C, and 30°C only) published by Kukal and Dawson (1989). However, mean RGR did not differ significantly between larvae in OTCs and those in control corrals when calculated based on final mass, suggesting that the benefit of increased feeding efficiency at higher temperatures is lost to greater activity and higher metabolic rates (Kukal *et al.* 1988b; Kukal and Dawson 1989) when the larvae cease feeding. Overall, RGRs determined in this study are comparable to those reported for numerous other species of leaf-feeding Lepidoptera (Slansky and Scriber 1985), but an order of magnitude greater than those reported by Kukal and Dawson (1989) for *G. groenlandica* (Table 10). The larvae studied by Kukal and Dawson (1989), however, were maintained under very unnatural conditions and this probably contributed to their very low RGRs.

Adult parasitoids always tended to emerge earlier in OTCs than in control cages (Table 11), indicating that the temperature enhancement within the OTCs was sufficient to

increase the rate of metamorphosis of the parasitoids. Because of the early snowmelt in 1994, the parasitoids had likely completed a large portion of their metamorphosis before being placed in the cages, thus accounting for the nonsignificant differences in mean emergence dates for *H. pectinatus* and *Exorista*. The significant difference in mean emergence dates for *C. gelida* in 1994 might be explained by the slightly greater temperature enhancement in the OTC used for that species. In 1995, the parasitoid emergence cages were established as soon as the OTC site became snow-free and the parasitoids had likely completed relatively little of their metamorphosis before being placed in the cages, leading to the highly significant differences in mean emergence dates between OTCs and control cages for all three parasitoid species. Mortality during metamorphosis was higher in the OTCs than in the control cages for all three parasitoid species and this might have resulted from temperatures approaching a lethal upper threshold, combined with limited air circulation caused by the high density of host remains within the cages and exacerbated by the OTCs. The conclusion that this increased mortality was an effect of the OTCs can only be tentative, however, because of the lack of replication in this experiment (one OTC and one control cage for each of the two host species).

Laboratory Rearing

Both the pattern of development and the pattern of growth of *G. groenlandica* larvae reared in the laboratory were essentially the same as those of larvae reared in the field, indicating that laboratory rearing conditions were adequate for normal growth and development of these larvae. In addition, mean RGRs for laboratory-reared larvae were comparable to those for field-reared larvae, at least at 20°C and 25°C, indicating that the foodplant offered (*S. scouleriana*) provided nutrition comparable to foodplants selected by larvae in the field. The lack of a difference between peak RGR and final RGR in larvae reared at 25°C is likely an artifact of the three-day interval at which larval mass was measured, considering the very rapid development of larvae reared at this temperature.

Insect temperature/development relationships are usually approximately linear over most of the range of temperatures under which development occurs; however, it is well

known that the temperature/development relationship departs from linear at temperature extremes, curving upward at lower temperatures and downward at higher temperatures (Wigglesworth 1972). Thus, development rate approaches the lower temperature threshold for development asymptotically so that development may occur at temperatures below the developmental zero estimated through linear regression, and development rate actually declines with increasing temperature as the upper lethal temperature threshold is approached.

Various methods have been proposed for fitting insect temperature/development data to nonlinear functions so as to more accurately represent the temperature/development relationship over its full range (*e.g.* Stinner *et al.* 1974; Logan *et al.* 1976; Sharpe and DeMichele 1977; Schoolfield *et al.* 1981; Taylor 1981; Harcourt and Yee 1982; Lactin *et al.* 1995). Although most of these methods are strictly empirical, with little or no theoretical foundation, the method proposed by Sharpe and DeMichele (1977) was built upon fundamental thermodynamic principles of enzyme reaction kinetics, on the assumption that development rates are ultimately dependent upon enzymatic reactions within the organism. This method was reformulated by Schoolfield *et al.* (1981) to make it better suited for nonlinear regression and was formulated into a computer program by Wagner *et al.* (1984), after they reviewed the literature and concluded that it was the best such method known. Unfortunately, this method requires development rates determined at a minimum of seven different temperatures to properly fit the nonlinear relationship and therefore it was not used here. Furthermore, linear approximations often perform at least as well as the more complex nonlinear functions for estimating insect development rates in the field, and the increased accuracy of complex nonlinear functions may not be realized because of the imprecision and variability of estimates and individual insect performance, respectively, in the field (Worner 1991, 1992).

The developmental zero of 9.5°C estimated for larvae of *G. groenlandica* (Figure 40) is corroborated by observations of the larvae reared at 10°C, in that these larvae did show activity and a small degree of development but were unable to complete their development, this temperature being very close to the developmental zero. Estimates of the

developmental zero for pupae and eggs of *G. groenlandica* were 11.4°C (Figure 41) and 10.9°C (Figure 42), respectively, but these were not corroborated by attempted rearing at 10°C because of the failure of larvae to complete development at 10°C.

Estimates of the developmental zero for the three parasitoid species are again corroborated by rearing observations, but the temperature/development relationships for these species also show evidence of nonlinearity. The developmental zero of 10.6°C estimated for metamorphosis of *Exorista* is corroborated by rearing at 10°C, wherein many larvae of *Exorista* formed puparia and some of these underwent metamorphosis but none emerged as adults. The metamorphosis accomplished by some of these individuals may reflect nonlinearity of the lower portion of the temperature/development relationship, which would place the true lower temperature threshold for development below 10°C (Figure 45). On the other hand, there was no evidence of nonlinearity at higher temperatures, indicating that the upper lethal temperature for *Exorista* puparia is well above 30°C. In contrast, both of the ichneumonids, *H. pectinatus* and *C. leechi*, showed clear evidence of nonlinearity in their temperature/development relationships at higher temperatures, manifested as declines in development rates between 25°C and 30°C and indicating that upper lethal temperatures were approached at 30°C. The developmental zero of 7.8°C estimated for metamorphosis of *H. pectinatus* is corroborated by the completion of development by this species at 10°C, and nonlinearity of the temperature/development relationship is suggested by the relative rates of development and 10°C, 15°C, and 20°C (Figure 44). The developmental zero of 5.9°C estimated for metamorphosis of *C. leechi* is also corroborated by the completion of development by this species at 10°C (Figure 46). Nonlinearity in the lower portion of the temperature/development relationship, placing the true lower temperature threshold for development below 5°C, is evidenced by the completion of development by *C. leechi* held at a constant temperature of 5°C (Morewood, unpublished data).

Relative differences in estimated developmental zeros and thermal constants are reflected in the differences in development times of *G. groenlandica* and the associated parasitoids at different constant temperatures in the laboratory (Table 12), with allowances for the different types of development these insects must undergo in the spring. The

estimated developmental zero for metamorphosis of *Exorista* is somewhat higher than that for larvae of *G. groenlandica*, but the estimated thermal constant for metamorphosis of *Exorista* is much smaller than that for larvae of *G. groenlandica*, with the result that overall development times were similar. In contrast, the estimated developmental zero for metamorphosis of *H. pectinatus* is lower than those for either metamorphosis of *Exorista* or larvae of *G. groenlandica*, and the estimated thermal constant for metamorphosis of *H. pectinatus* is also much smaller than that for larvae of *G. groenlandica*, with the result that overall development times were shorter for *H. pectinatus* than for *G. groenlandica* or *Exorista*. In turn, the estimated developmental zero for metamorphosis of *C. leechi* is lower than those for the two primary parasitoids, although the estimated thermal constant is larger, and overall development times to adult emergence were shorter for *C. leechi* than for the primary parasitoids. Contributing to the shorter development times to adult emergence for *C. leechi*, compared to the primary parasitoids, is the fact that *C. leechi* larvae spin cocoons in the fall and are ready to pupate as soon as conditions become favourable in the spring. In contrast, metamorphosis of the primary parasitoids cannot be initiated as soon as conditions become favourable because these parasitoids must first complete their larval development, killing their hosts, and spin cocoons or pupariate.

Comparison of development times in the field and in the laboratory at different temperatures for different stages of *G. groenlandica* and metamorphosis of the primary parasitoids (Table 13) reveals differences in the temperatures these insects experience in the field. Of the active periods for larvae, and development times for pupae, of *G. groenlandica* determined in the laboratory, those determined at 20°C were closest to those observed in the field. Considering that 20°C is well above the mean ambient air temperatures to which these insects are exposed in the field (*e.g.* Figure 38), these data probably reflect the elevation of body temperatures demonstrated in larvae and pupae of *G. groenlandica* exposed to sunshine (Kevan *et al.* 1982; Kukal *et al.* 1988b). In contrast, the development time for eggs of *G. groenlandica* determined at 15°C in the laboratory was closest to that observed in the field, indicating that egg masses are less affected by insolation. Of the development times determined in the laboratory for metamorphosis of

Table 13. Comparison of development times for selected stages of *Gynaephora groenlandica* and metamorphosis of insect parasitoids in the field and in the laboratory at 15°C or 20°C.

Species	Mean ± standard deviation (*n*) development time (d)		
and stage or year	Field	15°C	20°C
Gynaephora groenlandica			
Larvae (active period)	19 ± 3 (17)	32 ± 8 (9)	18 ± 5 (16)
Pupae (development)	15 ± 4 (55)	28 ± 1 (2)	12 ± 2 (18)
Eggs (development)	27 ± 5 (13)	31 ± 1 (3)	14 ± 1 (3)
Hyposoter pectinatus			
1995	13 ± 4 (15)	—	—
1996	15 ± 2 (19)	—	6 ± 1 (5)
1997	—	15 ± 1 (3)	7 ± 1 (8)
Exorista n.sp.			
1995	10 ± 1 (16)	—	—
1996	13 ± 2 (25)	—	9 ± 1 (15)
1997	—	21 ± 1 (44)	9 ± 1 (12)
Chetogena gelida			
1995	10 ± 2 (12)	—	—
1996	14 ± 4 (4)	—	9 ± 0 (2)
1997	—	—	9 ± 1 (6)

the tachinid parasitoids *Exorista* and *C. gelida*, those determined at 20°C were again closest to those observed in the field. This is perhaps to be expected, considering that these tachinids pupariate within the remains or cocoons of their hosts. In contrast, of the development times for metamorphosis of *H. pectinatus* determined in the laboratory, that determined at 15°C was closest to those observed in the field. Although *H. pectinatus* also complete their metamorphosis within the remains of their hosts, they do so usually at the

highest point available, thus removing themselves from the boundary layer of warmest air at ground level and exposing themselves more to the cooling influence of wind. The relative differences in time required by individuals of the different parasitoid species to complete their metamorphosis in 1995 and 1996 (Tables 8 & 13) might be ascribed to the relatively poor weather in 1996. Overall, the summer of 1996 was approximately 10% more cloudy than the summer of 1995, and the month of June was almost 20% more cloudy in 1996 than in 1995, based on differences in measured solar radiation *versus* theoretical clear sky radiation (Labine[9], personal communication 1998 & 1999). This would result in less solar heating of the ground and therefore less of a temperature difference between the microhabitats in which the different parasitoid species undergo metamorphosis.

Life History Strategies

The data and observations presented here indicate that the life cycle of *G. groenlandica* is much shorter and is simpler than was previously postulated by Kukal and Kevan (1987), with annual moulting and overwintering in each larval stadium leading to a life cycle of seven years' duration (Figure 47). It should be noted that although this revised life cycle is presented as typical of the population, it may be subject to individual variation in the number of instars and/or moulting frequency. For example, some other lymantriids show individual variation in the number of larval instars (Payne 1917; Beckwith 1978; Sevastopulo 1985; Nagasawa 1988; Das 1990). As demonstrated by Schmidt *et al.* (1977), such variation cannot be detected by analysis of HCW distributions but only through direct rearing, especially if only a small proportion of the population develops through a different number of instars, and this is not likely to be accomplished with *G. groenlandica* in the foreseeable future because of its multiyear life cycle.

Moulting frequency also may be subject to individual variation, with the potential for some individuals to fail to moult in a year with adverse conditions and some individuals

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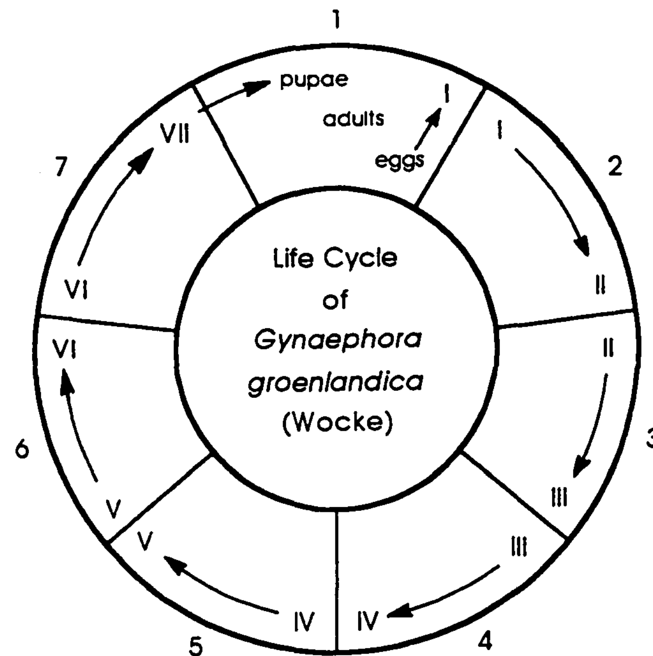

Figure 47. Diagrammatic representation of the life cycle of *Gynaephora groenlandica* at Alexandra Fiord, Ellesmere Island, after the style of Kukal and Kevan (1987) but based on seven larval instars, annual moulting, and overwintering in each larval stadium. Blocks in the ring represent summer growing seasons separated by lines representing winters. Arabic numerals outside the ring indicate years of development and Roman numerals within the ring denote larval instars.

to moult more than once in a year with especially favourable conditions. There was no evidence of such variation among larvae reared under field conditions, however, and the fact that none of these larvae failed to accomplish their annual moult in 1996, despite the late snowmelt and poor weather that year, suggests that such failure is rare. On the other hand, the potential for some larvae to develop through more than one moult in a given year was evident in laboratory-reared larvae, especially among neonates reared indoors at the field site. This inherent potential for larvae to extend their active period and develop through additional moults is strongly limited, however, by external factors. As noted under "Larval activity and moulting frequency" above, activity of neonates is curtailed by the approach of winter soon after they eclose. In subsequent years of their life, larvae "voluntarily" curtail their activity long before environmental conditions become adverse, apparently limiting themselves to a single moult each year, and there have been two main hypotheses proposed to account for this life history strategy.

One of the main hypotheses proposed to explain why larvae of *G. groenlandica* cease feeding, spin hibernacula, and become dormant so early in the growing season is that they restrict their feeding activity to the early portion of the season when the available food has the greatest nutritional value and become dormant when the benefits of continued feeding on foodplants of declining quality are outweighed by the metabolic costs of remaining active (Kukal and Dawson 1989). This hypothesis is supported by observations that larvae of *G. groenlandica* feed primarily on buds, expanding leaves, and developing catkins of *S. arctica* (Kukal and Dawson 1989; this study), a food source that rapidly declines in nutritional value as the leaves and catkins mature (Kukal and Dawson 1989; Dawson and Bliss 1993; Klein and Bay 1994). Continued feeding on foodplants of declining quality while metabolizing carbohydrates to maintain activity would result in lower carbohydrate reserves at the end of the growing season. This, in turn, might reduce overwinter survival because carbohydrate reserves are converted to glycerol which enhances cold hardiness (Kukal *et al.* 1988a; Kukal *et al.* 1989) and resistance to desiccation (Ring and Danks 1994).

There is, however, no direct evidence that larvae of *G. groenlandica* cease feeding,

spin hibernacula, and become dormant in response to declining foodplant quality, and there is now evidence to the contrary. Although the decline in nutritional quality of *S. arctica* has been well documented, it has never been directly correlated with the cessation of feeding by larvae of *G. groenlandica*, not even in the study that gave rise to this hypothesis (Kukal and Dawson 1989). The laboratory-reared larvae of *G. groenlandica* in this study ceased feeding, spun hibernacula, and became dormant even though they were provided with food of essentially unchanging quality, indicating that it is not foodplant quality but some other factor that is responsible for this pattern of development. Furthermore, with respect to nutrition and overwinter survival at Alexandra Fiord, larvae of *G. rossii* should be subject to the same constraints as *G. groenlandica*. Larvae of *G. rossii*, however, remain active late in the growing season and appear to be less particular about seeking out food sources of maximal nutritional value, yet clearly survive. The fact that *G. rossii* larvae consumed developing fruits, but not foliage or mature fruits, of *C. tetragona* suggests that a similar selection of optimal food sources is possible later in the summer.

The other main hypothesis proposed to explain why larvae of *G. groenlandica* cease feeding, spin hibernacula, and become dormant so early in the growing season is that this pattern of development is an adaptation of these larvae to avoid being active when adults of their primary parasitoids, *H. pectinatus* and *Exorista*, begin seeking new hosts in early summer (Kukal and Kevan 1987). This hypothesis is supported by the observational correlation between the disappearance of *G. groenlandica* larvae and the emergence of adult parasitoids in the field (Figure 48) and by the fact that larvae reared in the laboratory maintain the same pattern of development as larvae in the field, even in the absence of any obvious environmental cues such as changes in temperature, light, or foodplant quality.

Further support for the parasitoid-avoidance hypothesis is provided by the consistency of the timing of hibernaculum-spinning by larvae of *G. groenlandica* compared to the emergence of adult primary parasitoids at different temperatures (Table 12). In contrast with foodplant quality, which would involve cues that the larvae could respond to directly, the only obvious cue provided by adult parasitoids is direct contact, and larvae coming into contact with adult parasitoids are not likely to remain part of the gene pool

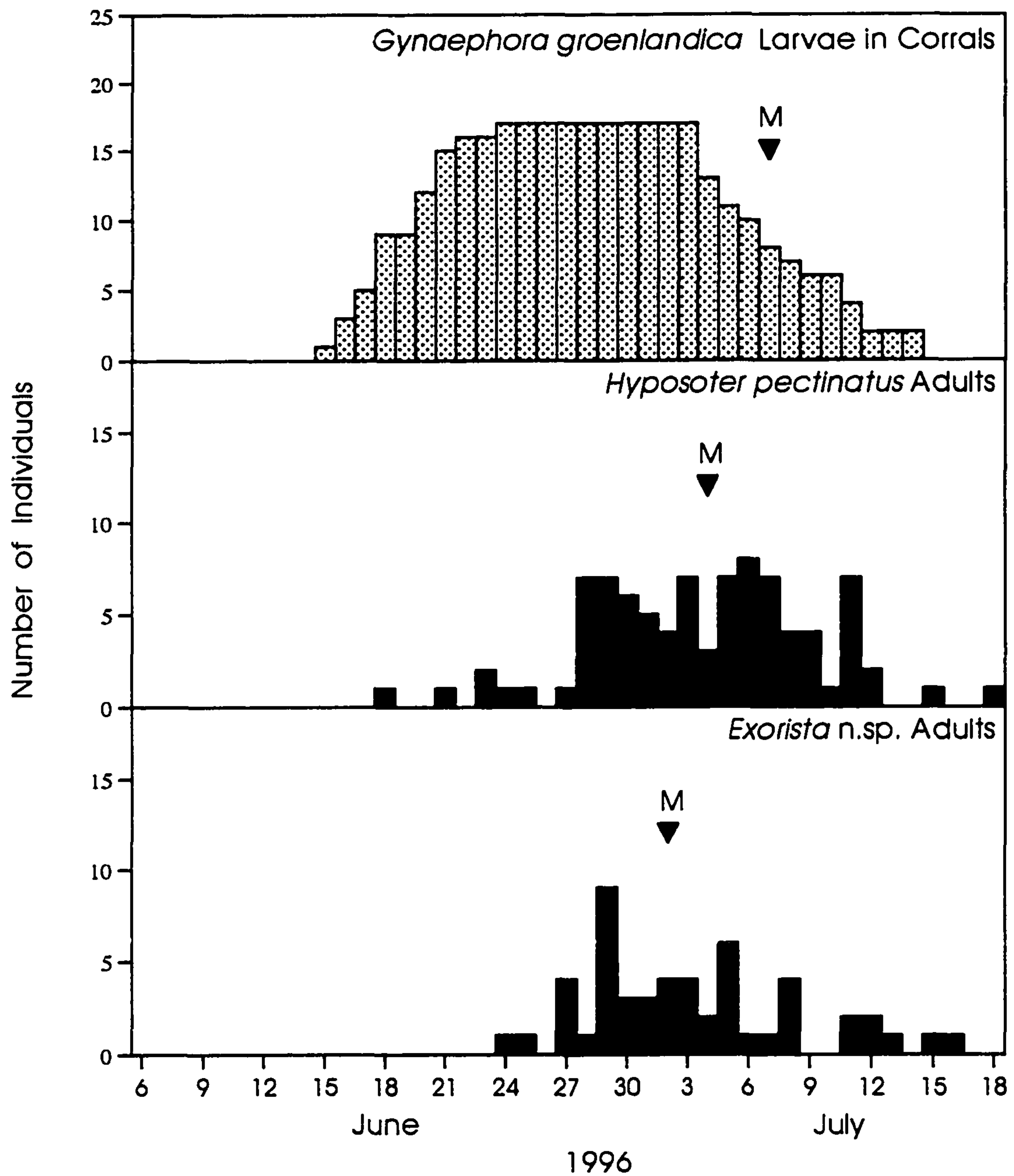

Figure 48. Larval activity of *Gynaephora groenlandica*, as observed in experimental corrals, compared to adult emergence of the primary parasitoids of *G. groenlandica*, as observed on the open tundra. Median dates of hibernaculum-spinning by larval *G. groenlandica* and of adult parasitoid emergence are indicated (M). Data from Figures 18, 25, and 29.

long enough to reproduce. Considering the levels of parasitism reported by Kukal and Kevan (1987; Kevan and Kukal 1993) and observed in this study, parasitoid-induced mortality would represent a very strong selection pressure against larvae that extend their active period long enough to moult more than once. Thus, the potential to accomplish more than one moult in a given year is probably suppressed by the removal of such individuals from the population by parasitoids, primarily by *H. pectinatus* because this species generally attacks earlier instars than does *Exorista*. The end result of this selection would be larvae of *G. groenlandica* that have evolved to remain active each year only for a certain amount of "physiological time", measured in terms of development as modified by temperature (Taylor 1981), representing development through a single moult and corresponding to the amount of physiological time required by the parasitoids to complete development and emerge as adults.

An alternative hypothesis to explain why larvae of *G. groenlandica* cease feeding, spin hibernacula, and become dormant so early in the growing season is that they simply "play it safe" by limiting themselves to a single moult, rather than risk getting caught in the middle of a moult when winter sets in (Danks[10], personal communication, 1998). Two lines of evidence can be used to refute this hypothesis as applicable to *G. groenlandica*. First, as mentioned above, larvae of *G. rossii* would be subject to the same environmental constraints at Alexandra Fiord but remain active late in the growing season and apparently develop through two or three moults each year. Second, and more importantly, metamorphosis and reproduction of *G. groenlandica* require at least seven weeks to complete, a period of time more than twice as long as larvae of this species remain active. Thus, if subject only to environmental constraints, larvae of *G. groenlandica* should be able to remain active long enough to develop through two or three moults each year. The key difference is that larvae of *G. groenlandica* are subject to parasitism, pupae and eggs are not.

The life history strategy of *G. rossii* is more opportunistic and less specialized than that of *G. groenlandica*. Metamorphosis and reproduction of *G. rossii* at Alexandra Fiord

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show approximately the same phenology and time requirements as metamorphosis and reproduction of *G. groenlandica*; however, larvae of *G. rossii* apparently develop through six (rather than seven) larval instars, accomplish two or three moults each summer, and thus probably complete their life cycle in as little as three years. The primary constraint for *G. rossii* is that metamorphosis must be initiated early in the growing season in order for reproduction to be completed before winter closes in. The apparent obligate diapause in final-instar larvae of *G. rossii* ensures that these larvae do not initiate metamorphosis late in the growing season but are ready to do so early in the spring.

Unlike larvae of *G. groenlandica*, larvae of *G. rossii* do not limit their activity to the early portion of the growing season, even though they are exposed to essentially the same types of parasitoids at Alexandra Fiord. The apparent absence of this parasitoid-avoidance strategy might be explained with reference to the much more widespread distribution of *G. rossii*. Because this species occurs in many other areas, which have different environmental constraints and different types of parasitoids that attack *G. rossii*, the narrowly focussed selective pressure to which *G. groenlandica* has been subject would not apply to *G. rossii* as a species. On the other hand, moulting within silk shelters would help larvae of *G. rossii* avoid attack by parasitoids later in the season and when these larvae are especially vulnerable due to reduced mobility. This strategy for parasitoid avoidance would be effective against *H. pectinatus* but probably irrelevant for *C. gelida* because tachinid flies in the tribe Exoristini lay unincubated eggs that take a number of days to hatch (Belshaw 1993), so that eggs laid on a host preparing to moult would likely be lost along with the host exuviae before the parasitoid larvae eclose and penetrate the host.

The life history strategies of the parasitoids are not unusual, to the extent that related species are known to have similar life histories. Larvae of the primary parasitoids develop during the summer but do not complete their development until the following spring. Overwintering within living hosts may help the primary parasitoids survive exposure to cold and avoid exposure to desiccation during the winter. In addition, delaying completion of their larval development, which involves killing their hosts, until

after the hosts become active in the spring ensures that the primary parasitoids initiate their metamorphosis in favourable microhabitats. Optimal conditions for metamorphosis of the parasitoids are crucial, in terms of maximizing the availability of new hosts to the newly emerged adult parasitoids, especially for *H. pectinatus* and *Exorista*, which rely on larvae of *G. groenlandica* as hosts, which in turn begin spinning hibernacula soon after the adult primary parasitoids begin to emerge. The hyperparasitoid *C. leechi* also overwinters in the larval stage but, unlike the primary parasitoids, kills its hosts and completes larval development before the end of the growing season. As a result, *C. leechi* can initiate metamorphosis earlier in the spring and thus reach the adult stage while its hosts, the primary parasitoids, are still undergoing metamorphosis.

Implications of Global Warming

Data presented by Maxwell (1992) indicate average predicted temperature increases of 3°C to 5°C and an average predicted precipitation increase of 20% during spring and summer in the Canadian arctic islands. To the extent that the temperature enhancement produced by the OTCs is comparable to these predictions for increased temperatures, and that the heavy snowpack and poor spring and summer weather in 1996 compared to 1995 might be considered analogous to the predicted increase in precipitation, the results of this study provide insight into the potential responses of *Gynaephora* species and their insect parasitoids to global warming in the Canadian High Arctic.

Temperature increases predicted under global warming are unlikely to have any effect on the life cycle of *G. groenlandica* at Alexandra Fiord but might allow a shorter generation time for *G. rossii*. The prolonged larval development of *G. groenlandica* is the result of the parasitoid-avoidance strategy of this species, rather than the constraints of the short growing season and low summer temperatures. For this reason, increased temperatures would not affect the pattern of development through a single moult each year and thus the typical generation time of seven years would remain unchanged, as evidenced by the maintenance of this pattern of development under a variety of temperature conditions both in the field and in the laboratory. In contrast, larvae of *G. rossii* are more

opportunistic and should be able to accomplish more development each summer with higher temperatures and/or a longer growing season. However, the constraint imposed by the time required for metamorphosis and reproduction, and the associated obligate diapause in the final larval instar, limits the flexibility in overall development time for this species. The length of the life cycle of *G. rossii* under current conditions is uncertain, but is probably three or four years. Enhanced larval development resulting from increased temperatures and a longer growing season could reduce overall generation time from four years to three and possibly to two if neonates were to develop beyond the first instar in their first year of life; however, the constraints associated with reproduction would prevent shortening of the life cycle to less than two years.

Host-parasitoid interactions of *Gynaephora* species and their insect parasitoids at Alexandra Fiord also are unlikely to be affected by temperature increases predicted under global warming. The rate of metamorphosis of the primary parasitoids was increased by the enhanced temperatures within OTCs while the length of the active period for larvae of *G. groenlandica* was unchanged; however, differences in time required for metamorphosis of individual parasitoids was not reflected in the phenology of the population as a whole. Individual differences in phenology originating with differences in dates of host emergence from overwintering hibernacula produced a range of adult parasitoid emergence dates much wider than the total time required for any individual parasitoid to complete metamorphosis in the field. Thus, differences in rates of metamorphosis caused by differences in temperature are overwhelmed by differences among individuals in the timing of initiation of metamorphosis. In addition, both species of *Gynaephora* show parasitoid-avoidance strategies that would not be adversely affected by changes in temperature conditions. In particular, the strategy employed by larvae of *G. groenlandica* is based on physiological time and is therefore inherently temperature-dependent, with the result that the relative timing of hibernaculum-spinning and adult parasitoid emergence is maintained over a broad range of temperatures. That the numbers of *Gynaephora* killed by parasitoids each year was in almost all cases consistently proportional to the numbers of *Gynaephora* surviving suggests that populations of *Gynaephora* species and their insect parasitoids are indeed in a

fine balance at Alexandra Fiord and that this balance is maintained in spite of large year-to-year changes in weather conditions and population sizes.

The most influential effect of global warming for *Gynaephora* species and their insect parasitoids could be the predicted increase in precipitation and the associated increase in cloud cover. The very heavy snowpack at Alexandra Fiord in 1996 caused a marked delay in the onset of the active season for these insects and this, combined with the subsequent poor spring and summer weather, resulted in most eggs of *Gynaephora* remaining unhatched in the middle of August. These eggs were viable, as evidenced by the hatching of those that were returned to the laboratory and held at room temperature, but it is unlikely that those remaining in the field could have hatched in the rapidly declining temperatures of August. Based on this observation, it is conceivable that heavy snow accumulations and extensively cloudy weather during spring and summer could lead to the inability of *Gynaephora* species to reproduce at the high latitude of Alexandra Fiord. It is unclear whether the increase in ambient temperatures and the potentially lengthened growing season would be sufficient to compensate for the lack of direct solar heating. However, the relatively high developmental zeros (lower temperature thresholds for development) estimated for these insects, compared to ambient shaded air temperatures in the field, and the inability of at least *G. groenlandica* and *Exorista* to complete development at temperatures close to their developmental zeros, underscores the importance of insolation and the potential adverse effects of cloud cover. Considering the extended life cycles and overlapping generations of these *Gynaephora* species, consistently adverse weather over many consecutive years would be required to cause a local extinction. On the other hand, host-parasitoid interactions might be affected even by a single year of reproductive failure in either *Gynaephora* species because the primary parasitoids rely on specific instars of their hosts and require access to those host resources every year to reproduce and maintain their populations.

CONCLUSIONS

Most of the immature stages of *G. groenlandica* and *G. rossii* are easily identified to species using morphological features. Eggs of the two species are essentially identical morphologically but may be distinguished by association with the cocoons on which they are usually found; eggs not laid on cocoons are unlikely to be found in the field. In first-instar larvae, the cuticle is black in *G. groenlandica* and pale in *G. rossii*. Older larvae show distinct differences in the colour patterns of the larval hairtufts, the form of the hairs, being spinulose in *G. groenlandica* and predominantly plumose in *G. rossii*, and the length of the hairs, being longer and less uniform in *G. groenlandica* than in *G. rossii*. Cocoons often may be distinguished by size and colour, those of *G. rossii* being smaller and darker than those of *G. groenlandica*; however, these features are variable whereas the structure of the cocoons, single-layered in *G. rossii* and double-layered in *G. groenlandica*, is definitive. Like eggs, pupae may be distinguished by association with the cocoons in which they are found and they also show species-specific differences in the shape of the maxillae and in the presence or absence of hairs on abdominal segment 10, although larger samples are required to confirm the consistency of these differences. The two species are reproductively isolated at the level of mate recognition and therefore do not produce hybrids, thus eliminating any confusion that might be caused by intermediate forms.

Both *G. groenlandica* and *G. rossii* overwinter only as larvae and complete their metamorphosis and reproduction within a single summer, requiring most of the growing season to do so. Larvae of *G. groenlandica* typically develop through seven instars and limit their activity to the time required to develop through a single moult in the spring of each year, after which they spin hibernacula and become dormant again until the following spring. Larvae of *G. rossii* apparently develop through six larval instars, remain active late in the growing season, and will continue to grow and develop as long as conditions remain favourable or until they reach the final instar wherein they enter an obligate diapause. Thus the life cycle of *G. groenlandica* requires seven years to complete whereas that of *G. rossii* may be completed in three or four years at Alexandra Fiord.

Only four species of insect parasitoids use *Gynaephora* species as hosts at

Alexandra Fiord, one solitary ichneumonid primary parasitoid, two gregarious tachinid primary parasitoids, and one solitary ichneumonid hyperparasitoid. The ichneumonid primary parasitoid, *H. pectinatus*, develops mainly in the penultimate larval instar of both *Gynaephora* species whereas the tachinid primary parasitoids, *Exorista* n.sp. and *C. gelida*, attack mainly the final larval instar of only *G. groenlandica* or *G. rossii*, respectively. The hyperparasitoid, *C. leechi*, attacks both species of tachinid parasitoids, and occasionally *H. pectinatus*, while these primary parasitoids are undergoing metamorphosis. Eggs and pupae of *Gynaephora* species are not attacked by parasitoids at Alexandra Fiord but are subject to extensive predation by birds.

All three of the primary parasitoids are koinobiotic endoparasitoids, developing within living hosts that maintain their normal pattern of activity and development after being parasitized, whereas the hyperparasitoid is an idiobiotic ectoparasitoid, developing on rather than within hosts that do not develop further after being parasitized. With the possible exception of *H. pectinatus*, all of the parasitoids are univoltine, completing one generation each year. Although *H. pectinatus* may complete its life cycle in one year when eggs are laid into hosts that are of a suitable size for development of the parasitoid larvae, this species may also undergo delayed development in which eggs are laid into smaller host larvae and the parasitoid larvae develop only after the host has grown to a suitable size, as is known in other species of *Hyposoter*. All of the parasitoids overwinter as larvae and complete their development to adult emergence in the spring. The primary parasitoids overwinter within living hosts and must complete their larval development prior to initiating their metamorphosis after their hosts become active in the spring. The hyperparasitoid overwinters as fully grown larvae within cocoons spun in preparation to pupate in the spring and is therefore phenologically more advanced than the primary parasitoids at the onset of the active season.

The short active season for larvae of *G. groenlandica* is an adaptation for avoiding parasitism, hibernaculum-spinning by these larvae coinciding with emergence of adult primary parasitoids. In the absence of any direct cues associated with adult parasitoid activity, larvae of *G. groenlandica* avoid adult parasitoids by remaining active only for the

amount of physiological time required by the parasitoids to complete development and emerge as adults. Larvae of *G. rossii* do not employ this strategy but, unlike larvae of *G. groenlandica*, spin silk shelters in which to moult, these moulting shelters providing protection from parasitoids when the larvae are particularly vulnerable. Both of these strategies appear to be effective in maintaining consistent rates of parasitism despite large differences in absolute population sizes from year to year.

Temperature increases predicted under global warming scenarios will not affect the overall generation time of *G. groenlandica* but might reduce that of *G. rossii* because the length of the life cycle of *G. groenlandica* is dictated by its parasitoid-avoidance strategy whereas that of *G. rossii* is subject to climatic constraints. Predicted temperature increases also are unlikely to disrupt the seasonal synchronization of *Gynaephora* species and their insect parasitoids because the current seasonal synchronization is largely the result of temperature-dependent rates of development and these are similar enough to maintain the relative phenologies of the different species over a broad range of temperatures. On the other hand, increased precipitation and associated cloud cover predicted under global warming scenarios might prevent ground-level temperatures from rising much above lower temperature thresholds for development, due to the lack of heating by direct sunshine. This effect would be most critical for the metamorphosis and reproduction of *Gynaephora* species because even a small increase in the time required to complete these processes could lead to reproductive failure. Such a reproductive failure, especially if repeated for more than a very few consecutive years, would have serious repercussions for the insect parasitoids and birds that rely on *Gynaephora* species as hosts or food resources in the High Arctic.

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APPENDIX

FORTRAN Computer Program

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Department of Statistics
University of California at Riverside
(personal communication)

```
c     INSTAR DETERMINATION
c     FROM MEASURED HEAD-CAPSULE WIDTHS.
c     THIS PROGRAM READS IN THE DATA
c     FROM THE HISTOGRAM N(I) AND X(I)
c     AND THEN USES DR. BEAVER'S PROCEDURE
c     TO ESTIMATE MEANS AND VARIANCES.
c
      integer nbin,niter,miter,ndist,r,i,j,nn
      parameter (nbin=80,niter=250,ndist=7,nn=1781)
      real n(80),x(80),w(80,7)
      real mug(niter,ndist),varg(niter,ndist),pg(niter,ndist)
c
c     READ IN THE DATA FROM THE TERMINAL
c
      write(6,*) 'enter the n-scores'
      read(5,*) (n(i),i=1,nbin)
      write(6,*) 'enter the bin values'
      read(5,*) (x(i),i=1,nbin)
c
c     NOW WHAT ARE THE INITIAL GUESSES
c
      mug(1,1)=0.703960396
      varg(1,1)=(0.029660743)**2
      pg(1,1)=0.113419427
c
      mug(1,2)=0.957344633
      varg(1,2)=(0.052247878)**2
      pg(1,2)=0.099382369
c
      mug(1,3)=1.295967742
      varg(1,3)=(0.074243276)**2
      pg(1,3)=0.069623807
c
```

```
      mug(1,4)=1.818831169
      varg(1,4)=(0.134516425)**2
      pg(1,4)=0.043234138
c
      mug(1,5)=2.364342629
      varg(1,5)=(0.173243951)**2
      pg(1,5)=0.140932061
c
      mug(1,6)=3.072955145
      varg(1,6)=(0.177804737)**2
      pg(1,6)=0.212801797
c
      mug(1,7)=3.945796848
      varg(1,7)=(0.202938555)**2
      pg(1,7)=0.320606401
c
c     NOW START THE ITERATION PROCESS BUT FIRST CALCULATE
c     WHAT THE WEIGHTS WOULD BE AT THE FIRST STEP
c
      do 30 r=1,ndist
         do 20 i=1,nbin
            sumw=0
            do 10 j=1,ndist
               sumw=sumw+pg(1,j)*gauss(x(i),mug(1,j),varg(1,j))
10          continue
            w(i,r)=pg(1,r)*gauss(x(i),mug(1,r),varg(1,r))/sumw
20       continue
30    continue
c
c     NOW ITERATE AND KEEP TRACK OF THE RESULTS
c     FOR EACH ITERATION
c
      miter=2
      do while (miter.lt.niter+1)
c
```

```
c     CALCULATE THE MEANS
c
        do 50 r=1,ndist
          sumn=0
          sumd=0
          do 40 i=1,nbin
            sumn=sumn+n(i)*w(i,r)*x(i)
            sumd=sumd+n(i)*w(i,r)
40        continue
          mug(miter,r)=sumn/sumd
50      continue
c
c     CALCULATE THE VARIANCES
c
        do 70 r=1,ndist
          sumn=0
          sumd=0
          do 60 i=1,nbin
            sumn=sumn+n(i)*w(i,r)*((x(i)-mug(miter,r))**2)
            sumd=sumd+n(i)*w(i,r)
60        continue
          varg(miter,r)=sumn/sumd
70      continue
c
c     CALCULATE THE PROBABILITIES
c
        do 90 r=1,ndist
          sumn=0
          do 80 i=1,nbin
            sumn=sumn+n(i)*w(i,r)
80        continue
          pg(miter,r)=sumn/nn
90      continue
c
```

```
c    NOW CALCULATE THE WEIGHTS FOR THE NEXT ITERATION
c
        do 120 R=1,ndist
            do 110 i=1,nbin
                sumw=0
                do 100 j=1,ndist
                    sumw=sumw+pg(miter,j)*gauss(x(i),mug(miter,j),varg(miter,j))
100         continue
                w(i,r)=pg(miter,r)*gauss(x(i),mug(miter,r),varg(miter,r))/sumw
110     continue
120 continue
c
c    UP THE ITERATION COUNTER
c
        miter=miter+1
    end do
c
c    PRINT THE OUTPUT ON THE TERMINAL SCREEN
c
    write(6,*) 'These are the estimates of HCW parameters'
    write(6,*) 'means'
    write(6,130) ((mug(i,j),j=1,ndist),i=1,niter)
    write(6,*) 'variances'
    write(6,130) ((varg(i,j),j=1,ndist),i=1,niter)
    write(6,*) 'proportions'
    write(6,130) ((pg(i,j),j=1,ndist),i=1,niter)
130 format(7f12.9)
c
c    END THE PROGRAM
c
    end
c
c
    function gauss(x,mu,var)
    real x,mu,var
    data pi/3.14159265358979/
    gauss=exp(-(x-mu)**2/2.0/var)/sqrt(2.0*pi*var)
    return
    end
```