

Seasonal Patterns of Abundance of Tundra Arthropods near Barrow

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ABSTRACT. Arthropods active on the surface of the tundra near Barrow, Alaska, were trapped throughout four summer seasons (1966-1969), using "sticky-board" traps. More than 95 per cent of the arthropods (excluding Acarina and Collembola) captured were of the order Diptera. Adults of most species of Diptera emerged in the middle two weeks of July; the abundance of arthropods on the tundra surface was maximal at that time. Year-to-year variations in abundance of various arthropod taxa are related to prevailing weather conditions and to the cycle of tundra disturbance and recovery associated with the abundance of brown lemmings.

RÉSUMÉ. *Modalités de l'abondance des arthropodes de la toundra selon les saisons, près de Barrow.* Près de Barrow, Alaska, on a, au cours des quatre étés (1966-1969), capturé au moyen de pièges à glu les arthropodes actifs à la surface de la toundra. Plus de 95 pour cent des arthropodes capturés (à l'exclusion des Acariens et des Collemboles) appartenaient à l'ordre des Diptères. Les adultes de la plupart des espèces de Diptères apparaissaient au cours des deux semaines du milieu de juillet : c'est à ce moment que les arthropodes étaient les plus nombreux à la surface de la toundra. Les variations annuelles d'abondance des divers *taxa* d'arthropodes sont liées aux conditions du temps et au cycle de déprédation et de reprise de la toundra selon l'abondance des lemmings.

РЕЗЮМЕ. *Сезонные изменения в численности членистоногих (Arthropoda) на поверхности тундры в районе Барроу (Аляска).* Членистоногие, обитающие на поверхности тундры в районе Барроу, исследовались в течение четырех летних сезонов (1966-1969 гг.). Свыше 95% всех собранных членистоногих (за исключением отрядов Асагина и Collembola) являлись представителями отряда Diptera. Взрослые особи большинства видов отряда Diptera появлялись в течение второй декады июля и в тот же период численность всех членистоногих достигала максимальных значений. Отмеченные изменения в численности различных таксонов типа Arthropoda обуславливаются климатическими условиями, а также колебаниями в численности бурых леммингов, обитающих в тундре.

INTRODUCTION

The abundance of insect activity near the tundra surface is a conspicuous feature of the short arctic summer. During favourable weather conditions at the height of the season the tundra may appear as a continuous swarm of insects, particularly representatives of the order Diptera. They are heavily preyed upon by birds. In fact, there is reason to believe that the breeding of tundra shorebirds, the most important group of insectivores in many tundra areas, is timed so that the young birds hatch during the period of maximum abundance of adult insects (Hurd and

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Pitelka 1954; Holmes 1966a; MacLean 1969). At other times of the summer the birds feed on larvae of these same insect species (Holmes 1966b; Holmes and Pitelka 1968).

The relationship of arthropods to avian predators is but one aspect of their important role in the flow of energy and cycling of nutrients in tundra ecosystems (Pitelka 1969). Since in many groups the adults do not feed, the trophic and energetic function is concentrated in the immature forms (larvae and nymphs). The numbers of the more conspicuous and readily sampled adults serve as an index of the abundance of immature forms.

This paper reports the results of systematic sampling of arthropods on the tundra surface throughout 4 summer seasons near Barrow, Alaska. The tundra arthropods of arctic Alaska have received comparatively little attention. Weber (1950a) surveyed the insects of the arctic slope. Although the investigations of Hurd (1958), Strandmann (1967), and Bohnsack (1968; Challet and Bohnsack 1968) studied the soil arthropods of the Barrow area broadly, they paid particular attention to soil mites (Acarina) and springtails (Collembola). Hurd (1958) developed a check-list of the terrestrial arthropods known to occur in the immediate vicinity of the Naval Arctic Research Laboratory. Holmes (1966b) sampled larval and adult insects to assess food availability for sandpiper populations. In that study few taxonomic distinctions were made.

All of the studies mentioned above have either anticipated or confirmed Downes' (1964) contention that the tundra insect fauna is low in diversity. Many orders that are important in temperate regions are lacking or are represented by only a few families and species. The order Diptera, and especially the family Chironomidae, contribute the largest number of species to the tundra insect fauna.

The questions of arthropod life cycles, trophic and energetic roles, and their importance in the decomposition process all require much investigation in tundra regions. Until more data are available, extrapolation from studies in temperate regions may be dangerous. Because of this our interpretations of the data presented here are often incomplete and speculative. Still, we believe that significant patterns relating to the functioning of the tundra ecosystem emerge. It is our hope that this paper will serve as an introduction to the detailed work, especially on Diptera, which must follow.

STUDY AREA

Barrow is situated near the northern tip of the coastal plain of northern Alaska, at 71°20'N., 156°46'W. Surface relief in this area is slight, resulting primarily from old, raised beaches which form longitudinal ridges and from frost features such as low-centred and raised polygons and ice-cored mounds (Hussey and Michelson 1966). Because of the limited relief and presence of permafrost near the surface, water runoff is retarded and much of the tundra remains wet or saturated for most or all of the summer season. The vegetation is dominated by grasses and sedges. These form nearly all of the cover in the low-lying, wetter areas which comprise the majority of the tundra near Barrow. Prostrate willows and flowering herbs appear in greater abundance on more elevated sites; however,

grasses and sedges remain dominant on all but the most exposed sites. Most of the tundra is covered by an understory of moss and lichens.

An important aspect of the tundra ecosystem near Barrow is the periodic disruption of vegetation and soil surface which results from heavy grazing by brown lemmings (*Lemmus trimucronatus*) during the winter preceding their cyclic population high. Such disruptions occur at three to five-year intervals and have a severe impact on the tundra. During the long winter lemmings feed on the narrow bands of meristematic tissue of grasses and sedges near ground level, but leave the dead blades. The blades fall to the ground at spring melt; when grazing is heavy nearly every blade is cut over large areas of tundra. This changes the insulating layer over the tundra, thus influencing soil temperature and depth of thaw. It also produces a sudden, large pulse of dead organic material entering the saprovores food chains. Since many, even most, of the insect larvae are saprovores, and since the growth of larvae in tundra sod is directly related to soil temperature, it is likely that both of these effects of lemmings grazing will influence insect populations. A lemming high occurred at Barrow in 1965. The insect sampling reported here occurred in the summers of 1966 to 1969. Thus, one complete cycle of tundra recovery is included in this report.

The climate of the Barrow area is strongly influenced by the immediate proximity of the Beaufort and Chukchi seas. Summers are short and cool. Melt-off usually begins in early June, with most of the snow melting between 13 and 19 June. The average daily maximum, minimum, and mean temperatures, as recorded by the U.S. Weather Bureau station in Barrow Village, are given in Fig. 1. The daily mean temperature does not reach 0°C. until 11 June, and the daily minimum temperature remains below freezing throughout June. The warmest days (daily mean temperature 4.5°C.) occur in mid- to late July. Even then, daily low temperatures below freezing are not uncommon. Cold rain and fog frequently occur in the last half of July and in August.

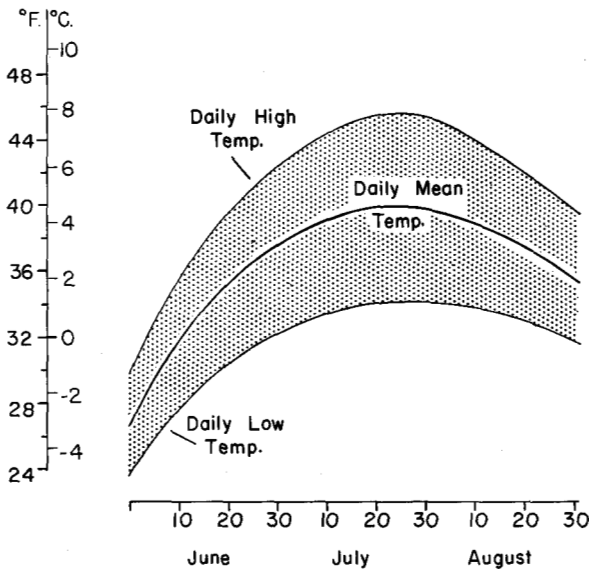


FIG. 1. Average daily maximum, mean, and minimum temperatures during the summer season at Barrow, Alaska.

The temperature conditions encountered in the 4 years of this study, expressed as cumulative deviation from normal temperature, are shown in Fig. 2. This 4-year period included extremes of temperature conditions: 1966 and 1967 were somewhat cooler than normal; the period between mid-July and mid-August of 1968 was unusually warm; the comparable period of 1969, in contrast, was quite cold. In a normal year 270 centigrade degree days above freezing are accumulated between 11 June (the 0°C. threshold) and the end of August; 232 of these accumulate in the months of July and August. The temperature increments for July and August of 1968 and 1969 were 351 and 77 centigrade degree days, respectively. (The temperature deviations of Fig. 2 include values below freezing, and thus are not directly translatable to these values.) These significant deviations

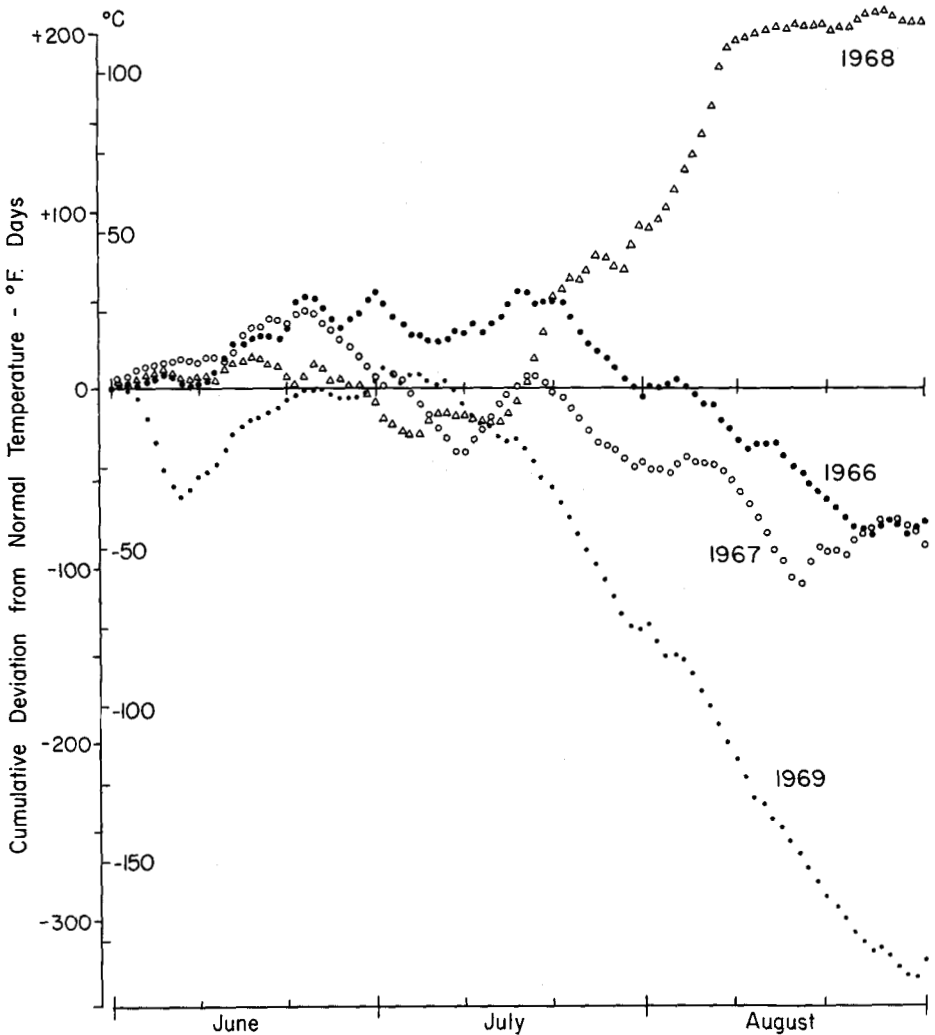


FIG. 2. Seasonal temperature conditions in the summer months at Barrow, Alaska, 1966-69, expressed as cumulative deviation from normal temperature in degree-days.

TABLE 1. Summer season precipitation (inches) recorded at Barrow, Alaska, 1966-1969.

	1966	1967	1968	1969	Long-term average
<i>June</i>	0.37	0.28	0.45	0.29	0.36
<i>July</i>	2.01	1.43	0.19	0.34	0.77
<i>August</i>	0.57	0.32	0.09	0.88	0.90
<i>Totals</i>	2.95	2.03	0.73	1.51	2.03

from the normal thermal regime must have a considerable impact on the growth and emergence of arthropods.

Because of the flat topography, surface drainage is limited; immediately after snow melt all of the tundra except the most elevated polygons and ridges is saturated with or covered by melt water. This gradually drains and evaporates during the season. The degree of drying of the tundra is dependent on the incidence of rain in July and August. In years with little rain the intermittent ponds, and even the margins of permanent ponds, may lose their water. This alters the habitat for developing arthropods, and also exposes these areas to heavy avian predation. Both of these factors may influence the survival and development of arthropods in these areas, and thus influence emergence in the following season. The effect of habitat desiccation on tundra arthropods is not known and should be studied, especially in view of the large variation in summer precipitation indicated in Table 1.

METHODS

All data reported here were collected at 2 study sites approximately 2 and 3 km. southeast of the Naval Arctic Research Laboratory. At each site 6 masonite strips 1 m. x 0.1 m., covered by a sticky resin ("Tree Tanglefoot", The Tanglefoot Co., Grand Rapids, Michigan) on the upper surface, were placed on the ground (Fig. 3). The boards were distributed to sample 3 habitat types; at each study site 2 boards were placed on saturated meadow tundra, 2 on mesic tundra, and 2 on dry, elevated tundra (polygon tops and ridges). The same sampling locations were used throughout the study. Each board was protected by an

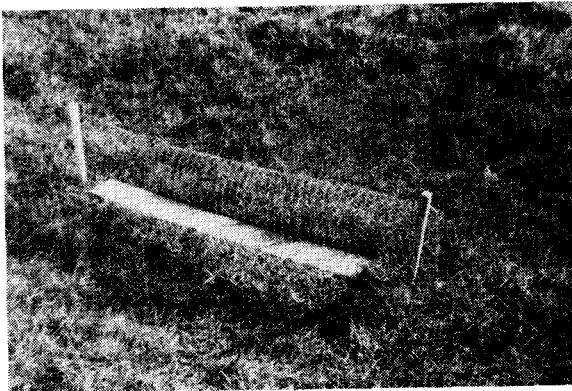


FIG. 3. A sampling board (1 m. x 10 cm.) in typical grass-sedge tundra near Barrow, Alaska (photographed July, 1969).

enclosure of 1-inch "chicken-wire" mesh to prevent disturbance by birds or lemmings; the wire has no noticeable effect on the movement of arthropods. Arthropods that encountered the boards were trapped in the resin and remained to be counted when the boards were removed from the tundra and taken into the laboratory. A dissecting microscope and laboratory counter were used to identify and count the arthropods on the boards.

The boards were placed on the tundra as soon as the snow had left the study sites. Boards were changed at 3-day intervals in June and July, and at longer intervals in August. In the figures which follow, exposure periods of more than 3 days are indicated by a horizontal line through the data point. The length of the line indicates the total length of the exposure period. The data for such periods have been adjusted to give mean catch per 3-days of exposure, and thus are directly comparable to the values for the standard 3-day exposure period.

The two study sites included boards in similar habitats and produced almost identical results. They differed only slightly in phenology. In the analysis that follows results obtained at the 2 sites are combined. Our observations at other sites near Barrow indicated no large departures in species represented or in timing and extent of emergence of adult arthropods. Thus, we feel that these results are representative of events in the arthropod populations in the Barrow area as a whole.

The effectiveness of this sampling method is influenced by a number of factors. The number of animals of a given taxon captured in any period is a function of 1) their absolute abundance, 2) the probability that any individual animal will encounter one of the sampling boards, and 3) the probability that an encounter with a board will trap the animal. The second factor, above, is influenced by the dispersion pattern of the animals and by their mobility; this in turn is influenced by ambient temperature and, possibly, by population density as well. The probability of capture is influenced by presence or absence of wings, length and strength of legs, etc. Because of these variables the numbers of individuals captured do not have the same significance from one taxon to another.

The sticky-boards thus give a relative estimate of arthropod activity rather than a measure of absolute abundance (Southwood 1966). A comparison of results obtained using absolute sampling techniques along with simultaneous relative sampling methods, including sticky traps, is given by Hadley (1969) for a species of crane-fly (Diptera, Tipulidae) found on British bogs. He found that sticky traps and direct enumeration of emerging adults gave similar information on the dates of first, last, and mean captures. The sticky-board estimate is extremely useful in documenting seasonal patterns and year-to-year variation in the activity of the various taxa of surface-moving arthropods. It is also useful in indicating habitat preferences. It is in these ways that sticky-board results are used in this paper.

RESULTS

DIPTERA

The crane-flies (Tipulidae) are one of the most prominent groups of tundra insects. Three species occur abundantly in the Barrow area (Hurd 1958): *Tipula*

carinifrons Alexander, *Prionocera gracilistyla* (Holmgren), and *Pedicia hannai antennata* Alexander. The former 2 species are large crane-flies (body length c. 15 mm.) of the subfamily Tipulinae; *P. hannai* is a smaller species (body length usually 10 mm. or less) of the subfamily Limoniinae (Wirth and Stone 1956). Females of *T. carinifrons* and *P. hannai* lack wings. The males of these species are winged but use the wings only in fluttering along the tundra surface rather than in sustained flight. Both sexes of *P. gracilistyla* have wings, and on the occasional warm and wind-free days they are capable of sustained flight. On most days, however, they remain near the tundra surface and behave much like the other 2 species. Males of all 3 species are more conspicuous than females. Males move actively over the tundra whereas females move slowly about the surface and stop frequently to insert their ovipositor into the tundra. Males are much more frequently trapped on the sticky-boards.

The numbers of crane-flies trapped during each of the 4 seasons are shown in Fig. 4. In all 4 seasons *P. gracilistyla* was the least abundant species. In 1967 *T. carinifrons* was most abundant; in 1968, 1969, and apparently 1966, *P. hannai* was the most abundant species. The total catch of crane-flies was approximately the same in 1967 and 1968. The numbers of *P. gracilistyla* and *T. carinifrons*

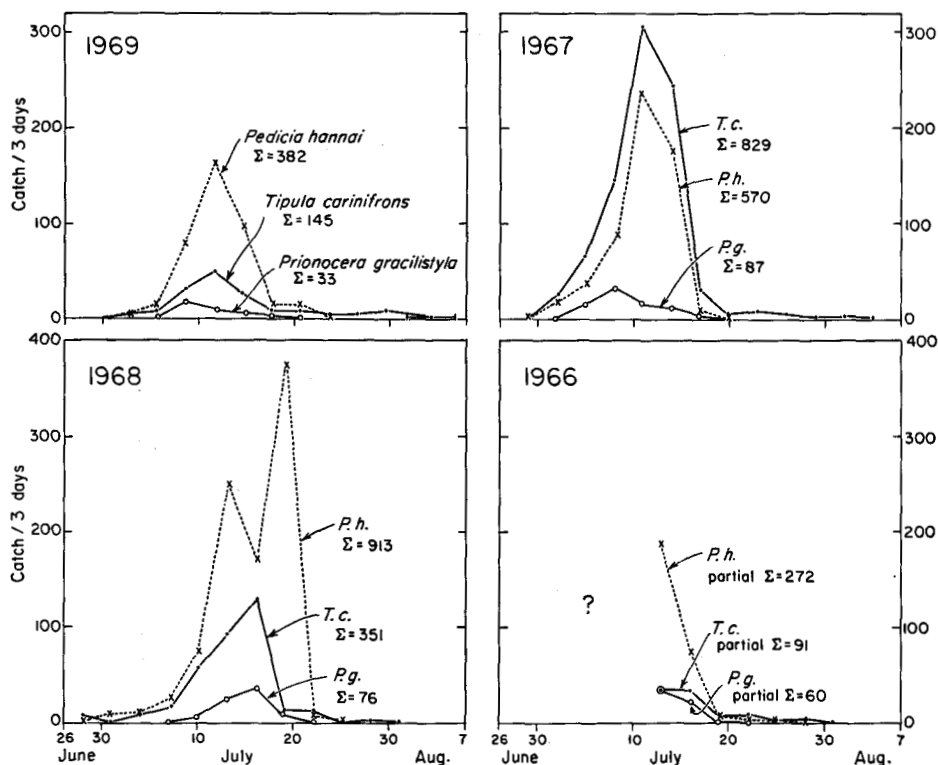


FIG. 4. Seasonal patterns of abundance of adults of the crane-flies *Pedicia hannai*, *Tipula carinifrons*, and *Prionocera gracilistyla* near Barrow, Alaska, 1965-69. On this and the following figures results are expressed as total number caught on 16 sticky-board traps per three days of exposure.

decreased from 1967 to 1968, whereas the numbers of *P. hannai* increased in the same period. Thus there is no evidence that the warm weather of 1968 increased crane-fly abundance.

In 1969, when the July weather was unusually cold, the catch of each species was less than half that of 1968 (*T.c.*, 41 per cent; *P.g.*, 43 per cent; *P.h.*, 42 per cent). The populations of *P. hannai* larvae in tundra sod were also sampled in 1968 and 1969. This sampling indicated that there were more large larvae in June of 1969 than in June of 1968, and in early August of 1969 many large larvae remained in the soil (MacLean, unpublished results). The presence of this population of large larvae argues against the importance of habitat desiccation in the warm, dry summer of 1968 as a factor influencing later adult abundance (also see below). But in 1969, low temperatures in the normal pupation period resulted in a reduced emergence, not because of fewer larvae, but because of a failure of larvae to pupate.

TABLE 2. Timing of emergence of Tipulidae and Trichoceridae, 1967-1969.

	1967	1968	1969
<i>T. carinifrons</i> males			
Median capture date	11 July	13 July	12 July
Middle 67% (days)	7.3	7.4	11.6
Middle 95% (days)	15.3	19.3	30.2
Total number captured	671	293	136
<i>T. carinifrons</i> females			
Median capture date	12 July	14 July	
Middle 67% (days)	5.3	8.9	
Middle 95% (days)	13.2	23.5	
Total number captured	158	58	9
<i>P. gracilistyla</i> males			
Median capture date	9 July	15 July	10 July
Middle 67% (days)	8.3	5.0	6.2
Middle 95% (days)	16.1	10.5	11.1
Total number captured	80	67	26
<i>P. hannai</i> males			
Median capture date	11 July	16 July	12 July
Middle 67% (days)	6.3	4.4	6.2
Middle 95% (days)	12.7	13.9	15.2
Total number captured	515	861	353
<i>P. hannai</i> females			
Median capture date	11 July	15 July	11 July
Middle 67% (days)	5.1	4.5	3.8
Middle 95% (days)	8.6	11.4	12.6
Total number captured	66	52	29
<i>Melusina saltator</i> (Trichoceridae)			
Median capture date	30 July	20 July	29 July
Middle 67% (days)	11.6	14.1	10.1
Middle 95% (days)	31.0	24.0	33.9
Total number captured	138	58	73

Characteristics of the seasonal timing of activity of adult Tipulidae are summarized in Table 2. In all three years for which data are complete, the median captures for the 3 species fell within a 3-day period. Thus there is a very strong interspecific synchrony of adult activity. All 3 species showed similar changes in the date of median emergence: earliest in 1967, latest in 1968, intermediate

in 1969. The magnitude of change was greatest in *P. gracilistyla*, which occupies the lowest (wettest) habitat, and least in *T. carinifrons*, which occupies the most elevated (driest) habitat. This can be related to pattern of snow melt: In 1968 cold weather between 16 and 21 June resulted in a protracted melt-off; elevated sites were exposed normally, while low-lying sites retained their snow cover later than usual. This difference in date of exposure and onset of growth could influence the timing of pupation, which begins only 2 to 3 weeks later. The degree of retardation matches the habitat characteristics of the 3 species. Although the magnitude of change (6 days in *P. gracilistyla*, 5 days in *P. hannai*) was small, especially by temperate-latitude standards, its effect is magnified by the short duration of the period activity.

Intraspecific synchrony of activity was more pronounced in *P. gracilistyla* and *P. hannai* than in *T. carinifrons*. *T. carinifrons* is more eurytopic in larval habitat than the other species (MacLean, unpublished results), and thus is subject to a wider range of melt-off dates and conditions for growth and pupation.

In 1968 the period of activity of *T. carinifrons* and *P. hannai* began gradually, but ended abruptly. Both species went from their seasonal mode to low numbers in successive 3-day periods, even while the weather remained warm. In fact, the period of abrupt decline in numbers in *T. carinifrons* was the period of peak catch of *P. hannai*. It appeared that, under the warm conditions, all crane-flies that began pupation quickly completed it and emerged as adults, leaving none to emerge later in the season.

The cold July of 1969 resulted in a prolonged period of activity of *T. carinifrons* and *P. hannai*. This is evident in the period encompassing 95 per cent of the catch of these species.

These data seem to indicate a more synchronous emergence in female than in male *P. hannai*; however, Hadley (1969) interpreted the small difference between sticky-trap catches and direct enumeration of emerging adults as indicating greater locomotory activity in flies emerging into a low density population, i.e., early and late in the emergence period. This would increase the probability of capture and thus flatten the apparent emergence curve. In *P. hannai* the male is the more mobile sex and would be effected more by this phenomenon. The sexual difference shown in Table 2 may reflect locomotion rather than abundance.

The winter crane-flies (Trichoceridae) are closely related to the Tipulidae. At Barrow, this family is represented by a single species, *Melusina saltator* Harris (Hurd 1958). In 1966 the number of captures of this species was not recorded. In the following years, 138 (1967), 58 (1968), and 73 (1969) were trapped. In each year the median capture occurred in late July, after the median captures of the 3 tipulid species (Table 2). The later period of emergence gives the larvae of this species more time to be influenced by prevailing temperature conditions. In the warm season, 1968, the emergence of *M. saltator* was significantly advanced and compressed in duration compared with 1967 and 1969; however, there was no evident effect of temperature on the total numbers captured.

Five other families of the suborder Nematocera are represented at Barrow (Hurd 1958): Chironomidae (40 to 50 species), Culicidae (1 species), Mycetophilidae (7 species), Sciaridae (8 or more species), and Cecidomyiidae (1 species).

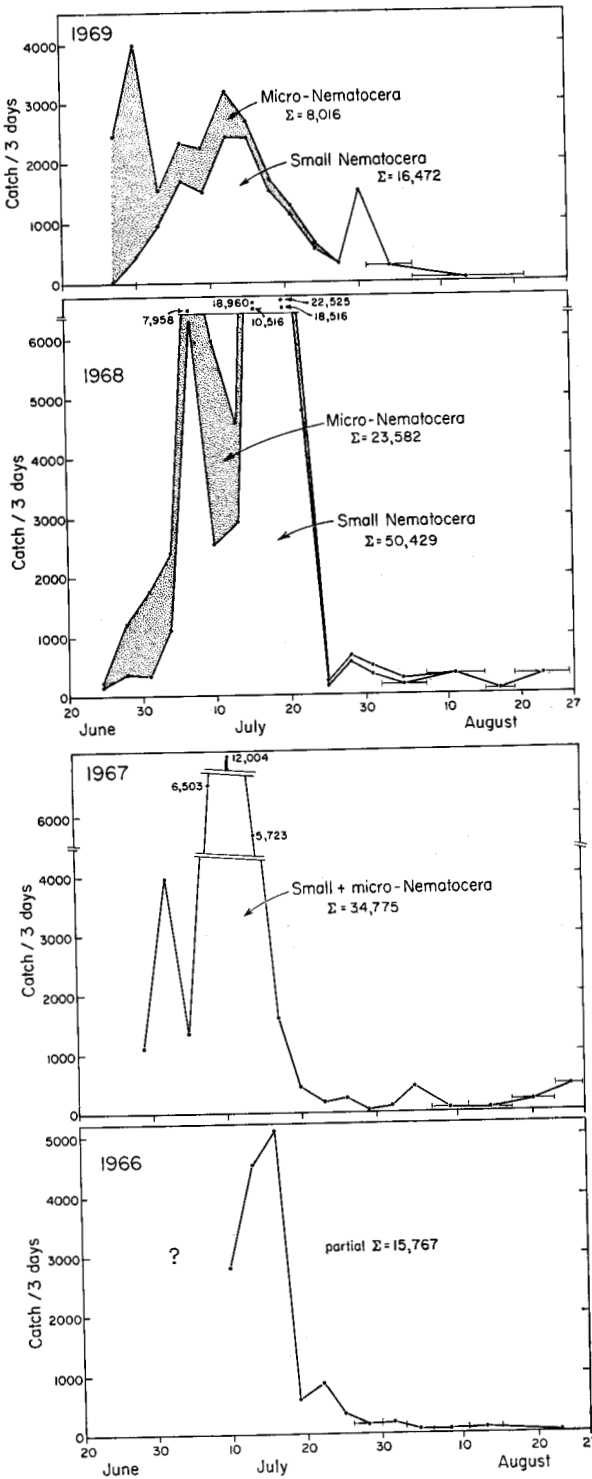


FIG. 5. Abundance of adult Nematocera (Diptera) other than Tipulidae near Barrow, Alaska, 1965-69.

These were counted together as "small Nematocera" in 1966 and 1967. The Cecidomyiidae are actually much smaller than the others. They are, apparently, too small to serve as prey for the insectivorous birds whereas the other families are used extensively (Holmes 1966b; Holmes and Pitelka 1968). In 1968 and 1969 this difference was recognized and the Cecidomyiidae were counted separately from the other "small Nematocera". The distinction was made on the basis of size, and it is possible that some very small species of the other families were counted with the Cecidomyiidae. Thus this group is distinguished collectively as "micro-Nematocera", defined as flies with a total length of 2 mm. or less.

The number of flies of these groups trapped on the sticky-boards is shown on Fig. 5. In all years there was a peak in abundance in mid-July followed by a sharp decline, with very few flies trapped in August. This mid-July peak is synchronous with the peak in abundance of the tipulid species. In 1967, 1968, and 1969 the July peak of the 2 groups fell in the same 3-day sample periods. Unlike the Tipulidae, the other Nematocera showed another peak in abundance earlier in the season in the 3 years for which the data are complete. In 1969 this peak consisted entirely of micro-Nematocera and fell at the end of June. In 1968 the peak occurred later in the season and consisted of both small and micro-Nematocera. In both years the emergence of micro-Nematocera occurred significantly earlier in the season than the emergence of species grouped together as small Nematocera. In 1967 an early season peak occurred in the first sampling period in July, comparable to the similar peak in 1969. The distinction between small and micro-Nematocera was not made in 1967. In 1967 and 1968 the early peak was smaller than the later peak, whereas in 1969 the early peak was the larger.

The total number of flies of these groups trapped on the sticky-boards increased strongly from 1966 through 1968. The increase of more than 100 per cent from 1967 to 1968 may be, in part, a result of the warm weather of 1968. For instance, in most years mosquitoes (Culicidae) are uncommon near Barrow; however, in 1968 they were common and were frequently trapped on the boards. In the cold 1969 season the catch of these insects decreased markedly, even more than that of the Tipulidae. The catch of small Nematocera was 33 per cent, and of micro-Nematocera, 34 per cent, of the catch of these same groups in 1968. It is possible that this reduction was, in part, the result of drying and shrinkage of ponds in August of 1968, which reduced the amount of favourable habitat for aquatic Nematocera, especially Chironomidae. None of the trapping boards, however, was adjacent to a pond and we believe that the majority of the Nematocera captured were terrestrial species. As is shown below, the captures of small Nematocera were distributed about equally in 3 major terrestrial habitat divisions, and the reduction from 1968 to 1969 involved all of these habitats.

Hurd (1958) identified 15 additional families of Diptera near Barrow; in this analysis they are grouped together as Brachycera, *sensu lato*. Of these the Muscidae, and especially the genus *Spilogona* (11 species now known from Barrow), are most abundant. In fact, the Brachycera, *sensu stricto*, are represented by but 3 species in 2 families (Empididae, Dolichopodidae), and these did not contribute significantly to the numbers captured. Most of the captures were members of the genus *Spilogona*.

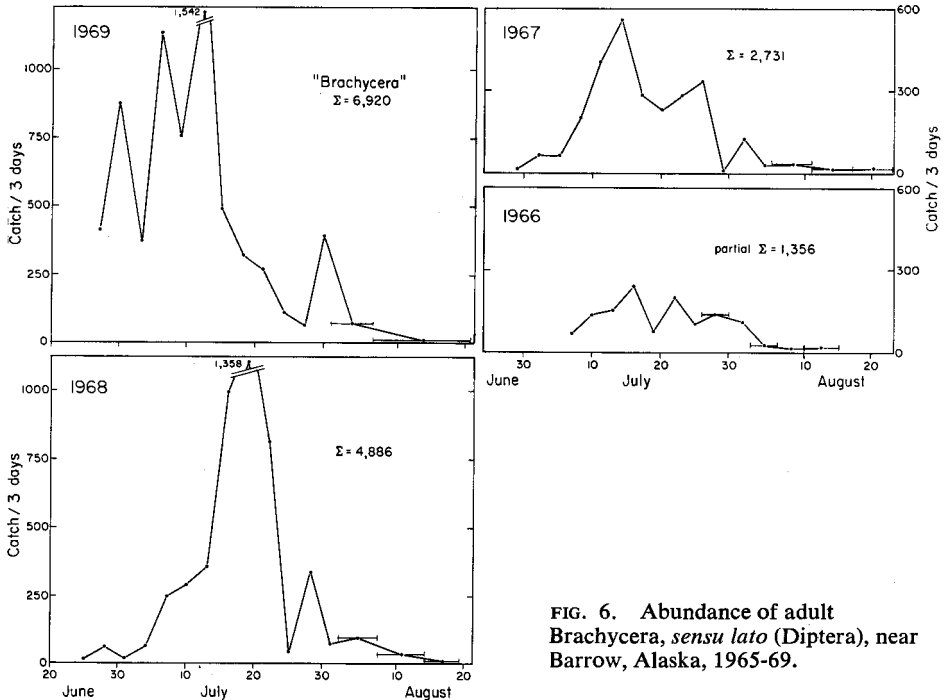


FIG. 6. Abundance of adult *Brachycera, sensu lato* (Diptera), near Barrow, Alaska, 1965-69.

Fig. 6 shows the patterns of relative abundance recorded for these flies. The seasonal peak of abundance of this group is less pronounced than in the Nematocera discussed above. Still, in each of the 4 seasons, maximum numbers were trapped in mid-July and few were trapped in August.

Unlike the Nematocera, the numbers of *Brachycera* increased steadily throughout the study (1966-67, + 100 per cent; 1967-68, + 79 per cent; 1968-69, + 42 per cent). The abundance of *Brachycera* is thus not clearly related to weather conditions. It is probable that the increase involves only one or several of the species of *Spilogona*. For instance, the increase in number captured 1968 to 1969 resulted from the appearance of several peaks before the main mid-July peak. Each of these early peaks may reflect a large emergence of one species.

HYMENOPTERA

The family Tenthredinidae is one of the relatively few families of herbivorous insects found near Barrow (Hurd 1958). Adult sawflies were present at the first sampling interval in June and decreased to zero by late July (Fig. 7). In 1967 and 1969 maximum numbers were trapped in late June and early July. In 1968, in contrast, sawflies increased in abundance to a peak in mid-July, then declined rapidly. Like the *Brachycera*, the sawflies increased in numbers throughout the 4 seasons of this study. They were uncommon in 1966, although the data for that season are not complete. They increased 28 per cent from 1967 to 1968, and 67 per cent from 1968 to 1969; no relationship with weather conditions is evident. The association of this increase with the recovery phase of the lemming cycle is again suggested. The sawflies feed primarily upon willow leaves and while lem-

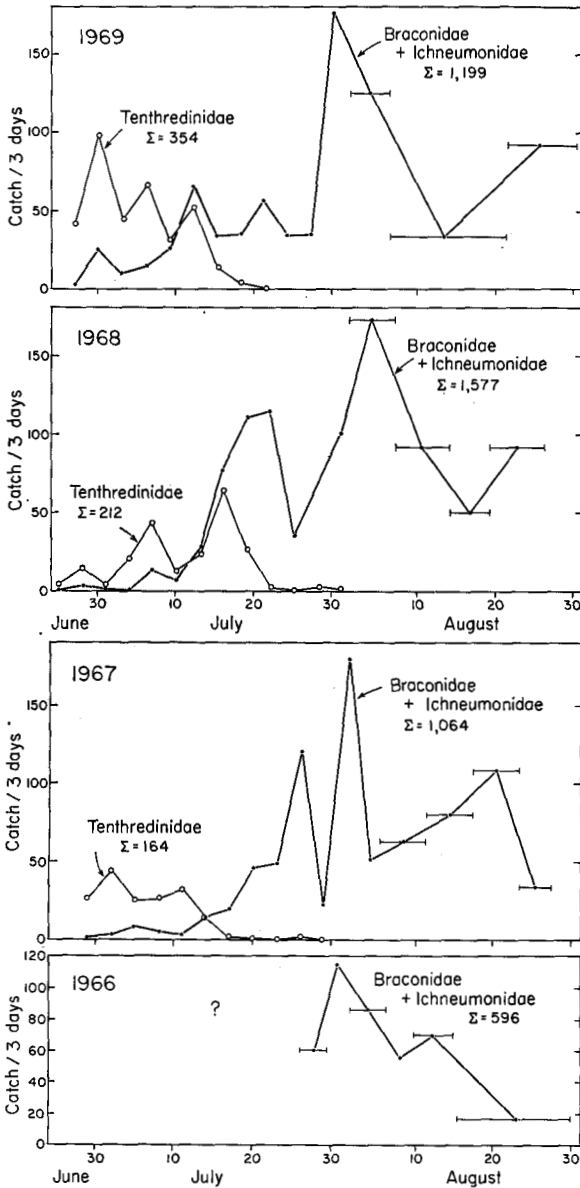


FIG. 7. Abundance of adult Tenthredinidae and Braconidae + Ichneumonidae (Hymenoptera) near Barrow, Alaska, 1965-69.

mings usually concentrate on grasses and sedges, in cyclic highs they browse willow twigs and it can be assumed that they influence foliage production in succeeding years.

The catch of Braconidae and Ichneumonidae is also given in Fig. 7. Hurd (1958) listed 1 species of Braconidae and 17 species of Ichneumonidae collected near Barrow. Thus the latter family is the more important in this grouping. The group differs from all other insect groups recorded on the sticky-boards in reaching maximum abundance in late July and August. In 1968 and 1969 many were trapped in the last sampling period in late August, just before tundra freeze-up.

Braconids and ichneumonids are parasitic on other insects. The adults appear after the larvae of other insects have hatched and grown to sufficient size to be parasitized. The numbers of braconids and ichneumonids increased from 1966 to 1968 then declined in 1969. Only the small and micro-Nematocera exceeded this group in total number captured.

Another group of parasitic Hymenoptera, members of the superfamily Chalcidoidea (probably *Anaphes alaskae*, family Mymaridae; one species of the family Pteromalidae was also recorded by Hurd), appeared in abundance on the boards in 1969. They were trapped most frequently in the latter half of July, but were also trapped throughout August. Thus their seasonal activity period overlapped that of the Braconidae and Ichneumonidae but the peak in numbers occurred earlier in the season.

TRICHOPTERA

Hurd (1958) recorded caddisflies belonging to 3 families (Limnephilidae, Brachycentridae, Phryganeidae) in the Barrow area. The species making up nearly all of our catch was identified by H. H. Ross (in letter 30 August 1968) as *Lenarchus expansus* Martynov (Limnephilidae). Unlike most caddisflies the larvae of this species are not found in streams and ponds but occur in saturated tundra sod (MacLean, unpublished data). The emergence of adults occurs between mid-July and mid-August, and is thus later in the season than the emergence of most other adult insects in the Barrow area.

More adult Trichoptera were captured in 1969 than in any previous year of this study (1966 — 26; 1967 — 14; 1968 — 20; 1969 — 50). This pattern (least in 1967, most in 1969) was not recorded for any other group and its significance is not clear. The emergence was not noticeably inhibited by cool weather. The numbers of trichopterans (and other groups mentioned below) are small, but they do represent the take in a large systematic sampling effort, and accordingly can suggest degrees of relative abundance in spite of the smaller absolute differences year to year.

COLEOPTERA

Very few beetles were trapped on the sticky boards (1966 — 4; 1967 — 10; 1968 — 1; 1969 — 0). Most of these belonged to the families Carabidae and Staphylinidae. Beetles are more readily captured in pitfall traps (Bohnsack, 1968). A series of pitfall traps that produced numerous carabid and staphylinid beetles in 1967 produced none in 1969. Thus although the sticky-board results are scanty they apparently reflect a true decline in the abundance of beetles.

HEMIPTERA

Hurd (1958) noted only 2 species of Hemiptera near Barrow: *Hardya youngi* Beirne (Cicadellidae) and *Chiloxanthus stellatus* (Curtis) (Saldidae). Both of these differ from the insects discussed above in having immature forms (nymphs) that are active on the tundra surface (Usinger 1960), and are thus subject to sticky-board trapping. As a result, no seasonal peaks are evident for these species; the relatively few animals caught were distributed evenly throughout the summer

season. The total catch in the 4 seasons of sampling varied widely. The herbivorous leaf-hoppers, like the Tenthredinidae, increased in number, at least from 1967 to 1969. (1966 — ?; 1967 — 4; 1968 — 7; 1969 — 19). The predacious Saldidae alternated years of greater and lesser abundance (1966 — 1; 1967 — 9; 1968 — 1; 1969 — 9). The small number of captures of Hemiptera probably reflects their scarcity near Barrow, since they are also rarely captured by other sampling techniques.

SPIDERS (ARANEAE)

One species of wolf spider (Lycosidae) and 10 species of Linyphiidae are known from the Barrow area (Hurd 1958). Hurd, Pitelka, and Britton (unpublished manuscript) reported that 90 per cent of their total spider collection belonged to 2 species of Linyphiidae with the wolf spider “. . . found sparingly on high tundra.” The lycosid is a large, robust species and was not trapped on the boards. All captures shown in Fig. 8 are of linyphiid spiders. There were, however, changes in composition of species, with the most common species in 1968 noticeably different from that trapped most frequently in other years.

Immature spiders are active on the tundra surface and were trapped frequently. In 1966, 1967 and 1969 spiders were most abundant early in the season. Most of

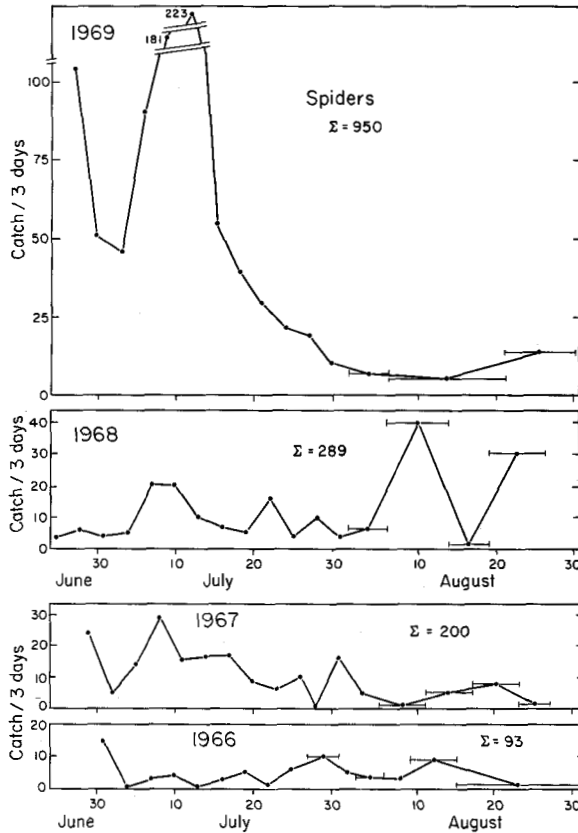


FIG. 8. Abundance of spiders (Araneida) near Barrow, Alaska, 1965-69.

these, particularly in 1969, were very small. In 1968, in contrast, maximum numbers were captured in August. Many of these were immature. Either the different species have different breeding seasons or the warm weather of 1968 led to rapid hatching and development of young. The first alternative seems more likely.

TABLE 3. Proportion (per cent) of catch occurring in three major terrestrial habitat divisions: Diptera¹.

		Trichoceridae	T. carinifrons, males	T. carinifrons, females	P. gracilistyla, males	P. gracilistyla, females	P. hannai, males	P. hannai, females	Micro-Nematocera	Small Nematocera	Brachycera
1967	Wet	22.5	14.6	22.8	45.0		36.1	36.5		58.7	37.2
	Mesic	45.7	40.2	34.2	47.5		53.1	52.4		19.9	24.6
	Dry	31.8	45.2	44.0	7.5		10.8	11.1		21.4	38.2
	N	138	671	158	80	7	507	63		34,775	2,731
1968	Wet	19.0	6.8	10.3	50.7		69.9	69.2	75.8	30.2	31.0
	Mesic	48.3	43.0	60.3	37.3		21.0	19.2	15.1	38.2	31.8
	Dry	32.8	50.2	29.4	12.0		9.1	11.5	9.1	31.6	37.2
	N	58	293	58	67	9	861	52	23,582	50,429	4,886
1969	Wet	20.6	11.8		69.2		68.3	72.4	88.9	21.6	39.5
	Mesic	43.8	43.4		15.4		25.8	20.7	6.7	45.8	36.2
	Dry	35.6	44.8		15.4		5.9	6.9	4.4	32.6	24.3
	N	73	136	9	26	7	357	29	9,072	15,416	6,920
Total	Wet	21.2	12.2	19.6	50.9	65.2	59.7	55.6	79.5	28.2	36.2
	Mesic	45.7	41.4	41.3	38.7	21.7	31.4	34.0	12.8	40.0	32.6
	Dry	33.1	46.4	39.1	10.4	13.0	8.9	10.4	7.7	31.8	31.2
	N	269	1,100	225	173	23	1,725	144	32,654	65,845	14,537

¹Yearly habitat distribution data are not given for groups with 20 or less occurrences.

TABLE 4. Proportion (per cent) of catch occurring in three major terrestrial habitat divisions: Arthropods other than Diptera¹.

		Tenthredinidae	Ichneumonidae and Braconidae	Chalcidoidea	Trichoptera	Cicadellidae	Saltidae	Araneida
1967	Wet	19.6	25.5					52.5
	Mesic	47.2	27.8					27.0
	Dry	33.2	47.7					20.5
	N	163	1,064		14	4	9	200
1968	Wet	29.7	37.6					83.7
	Mesic	34.9	29.4					7.6
	Dry	35.4	33.0					8.7
	N	212	1,577		20	7	1	289
1969	Wet	28.8	35.3	42.3	82.0			81.9
	Mesic	43.2	30.4	32.6	16.0			10.9
	Dry	28.0	34.3	25.1	2.0			7.2
	N	354	1,199	1,181	50	19	9	949
Total	Wet	27.0	33.4		73.8	0	21.0	78.2
	Mesic	41.7	29.1		16.7	13.3	15.8	12.4
	Dry	31.3	37.5		9.5	86.7	63.2	9.4
	N	729	3,840		84	30	19	1,438

¹Yearly habitat distribution data are not given for groups with 20 or less occurrences.

The total number of spiders captured increased each year from 1966 to 1969. Since the major increase in 1969 involved large numbers of small spiders, the increase in biomass was much less than the increase in numbers shown in Fig. 8.

HABITAT DISTRIBUTION

At each of the 2 sample sites 2 boards were placed on wet meadow tundra, 2 on mesic tundra, and 2 on relatively dry, elevated tundra. Wholly aquatic habitats were not sampled. By comparing the catch of the various taxa in these habitats we can reveal the distribution of each taxon along the moisture gradient. This is shown for the Diptera in Table 3 and for the other taxa in Table 4. The analysis pertains only to the 3 seasons for which data are complete.

Of the 3 species of Tipulidae, *T. carinifrons* was most frequently captured on mesic and dry habitat, whereas the others were more often captured on wet habitat. The difference between male and female *T. carinifrons* was significant, indicating that females were more likely to be found on wet habitat than males. (All statements of significance refer to the chi square test for homogeneity of distribution, interpreted at the 0.05 level.) The differences in habitat distribution between the sexes of *P. gracilistyla* and *P. hannai* were not significant.

Significant year-to-year differences were found in habitat distribution of the catch. For instance, in 1967 both male and female *P. hannai* were captured less frequently on wet tundra than in other years. In the same year *T. carinifrons* were captured more often on wet tundra than in later years. Thus, the patterns were not consistent for the several species.

The majority of the captures of Trichoceridae occurred on mesic and dry tundra. There was very little year-to-year variation in habitat distribution.

Micro-Nematocera were trapped predominately on wet tundra, whereas small Nematocera occurred on all three habitats. The effects of habitat preference by individual species are no doubt cancelled out in a large heterogeneous assemblage such as small Nematocera. The micro-Nematocera consisted almost entirely of a single species of the family Cecidomyiidae, and the preference of that species for wet habitat is evident. The effect of cancellation of habitat preferences is also seen in the Brachycera, Tenthredinidae, and parasitic Hymenoptera; that is, these data reveal no strong habitat selection in those groups. Year-to-year changes in habitat distribution of those groups probably result from changes in abundance of the species making up the group.

The Trichoptera we trapped preferred wet meadow habitat. This preference was most strongly expressed in the year of maximum abundance. Perhaps when density is lower there is more dispersal in search of mates than in years of higher density.

The 2 species of Hemiptera were most frequently captured on dry habitat. Of the 30 captures of Cicadellidae, 26 were on boards on dry tundra, as were 12 of 19 captures of Saldidae. This apparent preference of Saldidae for dry tundra is somewhat surprising, since bugs of this family are most commonly found along the shores of streams, ponds, and the ocean, or in bogs and marshes (Borror and DeLong 1964; Usinger 1956), but the same was found by Usinger (1960).

The spiders strongly preferred wet habitat. This occurred in all years, even though species composition changed. Challet and Bohnsack (1968) found more spiders along transects through polygon troughs and through a low, wet swale than along transects on a xeric slope and across polygons. Our results agree with their observations.

The habitat distribution data, taken together, indicate that habitat preferences are expressed as frequencies of occurrence on the various habitat types rather than restriction to one or two of the 3 habitat divisions. This occurred for single species as well as for multi-species assemblages. Only the Cicadellidae, of which merely 30 were captured, showed complete avoidance of one of the major habitat divisions. Egg laying and larval distribution, however, may occur with greater habitat specificity. Individuals of various species and groups recorded on other than the preferred habitat may have been captured during a dispersal phase of the life cycle.

DISCUSSION

The order Diptera is clearly a very important element of the tundra fauna. Of the arthropods, only the mites and collembola exceed the Diptera in abundance (Challet and Bohnsack 1968), and only the mites include more species (Bohnsack 1968). Since individuals of these two groups are much smaller than most of the Diptera the total biomass of the mite and collembolan fauna is probably comparable to that of the flies. Other tundra arthropod groups are far less abundant. More than 95 per cent of the arthropods comprising the samples for this study belonged to the order Diptera.

A striking feature of tundra arthropod populations is the sharp peak in surface activity in mid-July followed by a rapid decline. This is largely a product of the dominance of Diptera, since the other taxa reach seasonal peaks at other times (Hymenoptera, Trichoptera, Araneae), or, apparently, not at all (Hemiptera). Two possible advantages of a synchronous emergence, *per se*, are: 1) increasing the probability that, in relatively short-lived species, the sexes meet for production; 2) reducing the impact of predation on a vulnerable phase of the life cycle by "swamping" the predators. The first advantage pertains to intraspecific synchrony only, whereas the second advantage would be enhanced by inter- as well as intra-specific synchrony. The fact that the 3 species of Tipulidae and the majority of other Nematocera as well reach their seasonal peaks synchronously in mid-July argues for the importance of the second advantage. The major predators, the shorebirds, feed on the more accessible surface-active arthropods, supplemented by larvae as necessary. At the height of the July emergence period, the avian predators feed almost exclusively on adult insects but can consume only an insignificant part of the total. When fewer adults are emerging per day the proportion lost to predation may be much greater. This could provide a strong selective pressure favouring individuals emerging near the peak period.

In the past, synchrony of activity has been attributed to the short arctic growing season. However, it is clear from Fig. 1 that the abrupt decline in adult activity occurs as the temperatures are reaching their seasonal peak. There is no

evident climatic change in late July of sufficient magnitude to explain the abrupt decline in emergence of adults of many groups. While it is true that time must be allotted for hatching of eggs and larval growth before winter, it seems unlikely that an identical period would be required by each of the species of this diverse group.

Synchronous emergence, of course, is not limited to flies in arctic regions. Hadley (1969) documented the emergence of *Molophilus ater* Meigen, a small crane-fly of the subfamily Limoniinae, on bogs of the Moor House National Nature Reserve in Great Britain. He found a degree of synchrony comparable to that of *Pedicia hannah* at Barrow. At Moor House, however, the various species of Tipulidae emerge out of phase (Coulson 1969). It may be that the Moor House area (high Pennines) lacks an abundant predator fauna to make predator swamping an important adaptation or that, with the much longer growing season and predominately annual life cycles, the advantages of reduced competition by temporal separation are more important than possible reduction of predation.

Although adult shorebirds take both adult and larval insects, the newly hatched birds are dependent upon adult prey for the first 2 weeks of life (Hurd and Pitelka 1954; Holmes and Pitelka 1968). Thus, the adult birds must time their breeding so that the young reach this age before the decline in availability of adult insects. This may explain the abrupt termination of egg-laying by shorebirds in late June, when availability of surface-active prey is increasing rapidly (MacLean 1969).

Among the external factors likely to influence year-to-year variations in arthropod abundance are essentially random variations in weather conditions and the more regular cycle of tundra disturbance and recovery associated with lemming abundance. In this study only the Tipulidae, "small" Nematocera, and Cecidomyiidae showed clear changes in abundance which could be related to weather conditions. In the Tipulidae this consisted of a decrease in adult numbers in the cold season. In the other Nematocera there was a large increase in the numbers of adults captured in the warm season as well. A similar pattern was seen in the parasitic Hymenoptera (Braconidae and Ichneumonidae); however, the changes in number captured were of lower magnitude than in the Nematocera. More data are needed before such changes may be attributed to weather patterns.

Changes in adult abundance associated with weather may be attributed to differential survival of larvae and pupae, or to altered timing of life cycles. Sampling of larval populations of crane-flies indicates that these insects require several growing seasons to complete larval development (MacLean, unpublished results). Prolonged larval development, apparently, also occurs in the Chironomidae, since large larvae are found at all times of the season, including the period just after adult emergence. This was observed in the Chironomidae of tundra ponds by Oliver (1968) as well. As indicated previously, there was no decrease in the density of *P. hannah* larvae associated with the reduced emergence of 1969. Thus, the mechanism of response to weather appears to be to extend the larval period when conditions are adverse and to speed development when conditions are favourable, thus varying the number of emerging adults. Insects with obligatory one-year life cycles do not enjoy this flexibility; they must complete development

and risk emergence regardless of conditions. Unfortunately, the life cycles of very few tundra insects have been worked out; however, preliminary evidence gathered in 1970 indicates that muscid flies of the genus *Spilogona* and the winter crane-fly *Melusina saltator*, both of which showed no decrease in abundance in 1969, have one-year life cycles.

The relationship of arthropod abundance to the lemming cycle, first critically noted by Weber (1950b), is difficult to evaluate without more information on the effects of lemmings on the tundra and on the diets of the arthropods. Of the arthropods considered in this study, the Tenthredinidae, Cicadellidae, Cecidomyiidae and, possibly, Trichoptera are herbivorous. These use different plant species and parts. The sawflies feed on the leaves of prostrate willows and a few other vascular plants (e.g., *Petasites frigidus*); the leafhoppers feed on grass leaves, probably *Festuca* (H. H. Ross, personal communication); the terrestrial caddisflies, if they are herbivorous, probably feed on grass and sedge roots; the cecidomyiids are gallformers. All of these insects increased in abundance during the study, although they were never common. If their increase is related to the lemming cycle it must be via the very general effect of recovering vegetation to cause a similar response in these functionally diverse herbivores.

The predatory arthropods include spiders, larvae of *P. hannai* (Tipulidae), most of the Coleoptera, and Saldidae. Additionally, several species of parasitic Hymenoptera occur in the Barrow area. Spiders increased in abundance throughout the study. *Pedicia hannai* peaked in 1968, as did the parasitic Hymenoptera. Coleoptera and Saldidae peaked in 1967 and then declined sharply in 1968 (based on few captures). Thus no common pattern is evident. However, if the 1969 decline in *P. hannai* is attributed to weather, it may be that they generally increase in abundance through the recovery phase of the cycle and thus resemble the spiders.

Most of the Diptera that occur near Barrow are saprovores. The two saprovores species of Tipulidae, *T. carinifrons* and *P. gracilistyla*, and the single species of Trichoceridae were most abundant in 1967, two seasons after the lemming high. The small Nematocera were most abundant in 1968. The Brachycera (or, at least, *Spilogona* spp.) increased in abundance each year from 1966 through 1969. Thus these groups of saprovores reached peaks in successive years. If these changes are related to the lemming cycle, they would suggest that each of these groups acts on dead organic matter at a different stage of decomposition, i.e., there is a successional sequence of saprovores acting upon the pulse of organic material which enters the saprovores food chain following the lemming high. The Trichoceridae and saprovores Tipulidae may feed on the material soon after it becomes available. Abundance of food could result in high survival of larvae leading to a peak 2 years after the lemming high, with some effect remaining in the Tipulidae after 3 years, since a complete life cycle probably takes 3 years in *T. carinifrons* and *P. gracilistyla* (MacLean, unpublished results). The other Nematocera might feed only on material that had been processed by Tipulidae or otherwise altered through time. Thus the effect of the lemming activity would be evident in this group later than in the others mentioned above. Finally, the Brachycera may represent yet a later phase in the reducer sequence.

This hypothesis is highly speculative and requires observation through additional cycles of tundra disturbance and recovery as well as examination of the gut contents of larvae.

Regardless of their cause, variations in the abundance of tundra arthropods of the magnitude recorded in this study must have an influence on other components of the tundra ecosystem. We might expect that the reduced availability of arthropods in the 1969 season would have a negative effect on the growth and survival of insectivorous birds; however, the supply of adults is abundant and the prolonged period of their emergence would make the readily accessible adult prey available for a longer period of time. Similarly, low numbers of arthropods coupled with a reduction in metabolic rate resulting from low temperatures must have severely retarded the rate of energy flow and nutrient release associated with this important segment of the tundra fauna. Clearly, the patterns of interaction of arthropods with other ecosystem components are complex. These various effects must receive more attention if we are to understand the functioning of the tundra ecosystem, and in particular the roles played by various insect groups in decomposition phases of nutrient cycles.

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