



**DISTRIBUTION AND BEHAVIOR OF
BARREN-GROUND CARIBOU IN RELATION
TO WEATHER AND PARASITIC INSECTS**

**A
THESIS**

*Many thanks for
your support.
Ray Cameron*

MASTER OF SCIENCE

**By
Jim Dau, B.S.**

**Fairbanks, Alaska
September 1986**

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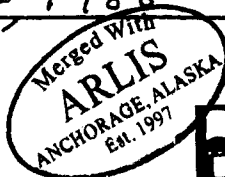
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Presented to the Faculty of the University of Alaska
in Partial Fulfillment of the Requirements
for the Degree of
MASTER OF SCIENCE

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ABSTRACT

Relationships between weather and the activity of mosquitoes (Culicidae) and oestrid flies (Oestridae), and responses by caribou (Rangifer tarandus) to insect harassment, were examined near Milne Point, Alaska. Weather conditions were usually unfavorable for insects within 20 km of the Beaufort Sea, and were least favorable within 1-3 km of the coast. Weather affected the occurrence more than the level of insect activity. Mosquitoes were rarely active within 1 km of the coast; maritime weather conditions had little effect on oestrids. Weather conditions and insect activity were more variable through time than through space; this necessitated models predicting: (1) the presence of insects, and (2) levels of insect activity when insects were present. Insect harassment caused caribou to travel rapidly to coastal areas at the expense of feeding and lying, and form large, mixed groups. Insect activity was most highly correlated with caribou rate of travel and behavior.

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BACKGROUND

In the winter of 1981-82, CONOCO, Inc. (CONOCO) built 29 km of gravel roads and five drilling pads near Milne Point, Alaska, during initial development of the Milne Point Production Unit; two additional drilling pads were constructed by other oil companies (Figure 1). This development raised two concerns regarding caribou (Rangifer tarandus granti) of the Central Arctic Herd (CAH): (1) possible displacement of maternal females from a high-use calving area (Whitten and Cameron 1985), and (2) disruption of daily movements between inland feeding sites and coastal insect-relief terrain (White et al. 1975, 1981; Roby 1978; Smith and Cameron 1985). The Alaska Department of Fish and Game (ADFG) was contracted by CONOCO and Continental Pipeline Company to investigate these concerns.

Aerial surveys of the Milne Point area were conducted annually in June 1982-85 to determine the distribution of caribou near Milne Point during calving. Effects of the Milne Point roads on the distribution of caribou were examined by comparing this information with data collected during 1978-81 (Dau and Cameron, in press). Results of this study indicate that maternal caribou have been displaced from areas within approximately 3 km of Milne Point roads.

The second concern was examined through road surveys conducted between May and early August, 1982-84. Areas frequently used by caribou were identified along the Milne Point road system.

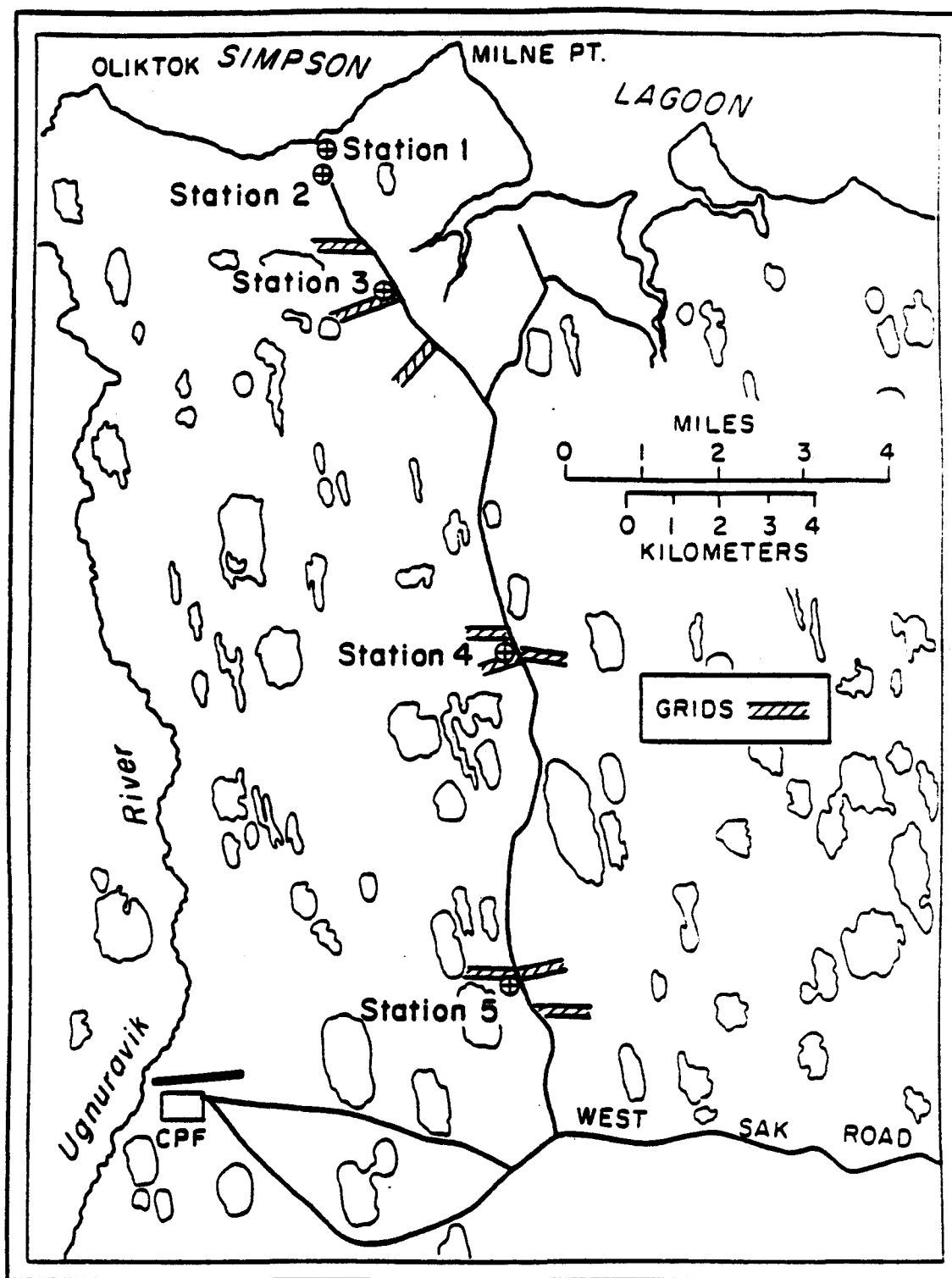


Figure 1. The Milne Point study area and surrounding region.

Recommendations to minimize potentially deleterious effects of surface development on caribou that use these areas were submitted to CONOCO via Habitat Division of ADFG (Dau and Cameron 1985). Annual variability in snow ablation and insect harassment confounded any possible effects of the Milne Point road and pipeline complex on movements of caribou through this area. However, caribou are clearly more sensitive to roads, the pipeline, and associated activity in this area during June than in May, July, or early August (Dau and Cameron 1986).

Weather-mediated harassment by mosquitoes (Aedes nigripes, A. impiger, and A. cataphylla: Culicidae), warble flies (Oedemagena tarandi: Oestridae), and nose bots (Cephenemyia trompe: Oestridae) substantially influences the distribution and behavior of caribou during July and early August (White et al. 1975, 1981; Thomson 1977; Roby 1978). Therefore, weather data and estimates of insect activity were recorded during this period, in addition to observations of caribou, along the Milne Point road system. Insect activity was modeled as a function of weather, and the effects of insect harassment on the distribution and behavior of caribou were examined. This portion of the investigation is presented here, and is the result of a cooperative agreement between ADFG, the Alaska Cooperative Wildlife Research Unit, and the University of Alaska.

CHAPTER 1. EFFECTS OF WEATHER ON INSECT ACTIVITY

Introduction

Barren-ground caribou are a principal host of mosquitoes, gad flies (Tabanidae), black flies (Simuliidae), and biting midges (Ceratopogonidae), and are the sole host of warble and bot flies (collectively, "oestrids"), throughout northern circumpolar regions (Bennett and Sabrosky 1962; Oldroyd 1964; Thomson 1977; Pank et al. 1984). The effects of harassment by imagoes of these insects, particularly mosquitoes and oestrids, on the distribution and behavior of Rangifer have been widely documented (Espmark 1968; White et al. 1975, 1981; Reimers 1977; Roby 1978; Wright 1980; Thing and Thing 1983). Many reports have noted that harassment of caribou by insects is mediated by weather factors (Thomson 1971, 1977). Until the mid-1970's, however, most investigations concerning weather-insect-Rangifer relationships focused on the latter two components of this system; documentation of the relationships between weather factors and insect activity was largely anecdotal, and rarely addressed more than the seasonal periodicity of insect activity or the range of climatic conditions favorable for flight.

Several researchers (Thomson 1973 as reported by Thomson 1977; Curatolo 1975; White et al. 1975; Roby 1978) further examined weather-insect relationships by looking at the effects of individual

or pairwise combinations of weather parameters on levels of mosquito and oestrid activity. However, due to the considerable time and effort required to estimate insect activity on a ratio or interval scale, these investigations subjectively classified activity into ordinal categories (e.g., none, low, moderate, or severe). Helle and Aspi (1983) refined this approach by quantitatively estimating simuliid and tabanid activity, and using linear regression analyses to investigate the effects of habitat on insect harassment. Additionally, entomologists have quantitatively examined the effects of climatological factors on levels of mosquito activity in Alaska and northern Canada (Hocking et al. 1950; Gjullin et al. 1961).

This portion of the study is similar to the latter investigations in that it quantitatively examines the relationships between insect activity and weather factors; however, it is not an entomological investigation. Instead, this phase of the study was designed to formulate predictive models of mosquito and oestrid activity from weather data for estimating levels of insect harassment experienced by caribou. In so doing, it became necessary to evaluate the types of information provided by each technique used to capture insects, and to examine the nature of weather-insect relationships beyond merely reporting correlation. The objectives of this portion of the study were:

1. to quantify the relationships between weather factors and the activity of adult mosquitoes and oestrids; and

2. to develop models quantitatively predicting levels of activity (i.e., caribou harassment) for alate mosquitoes and oestrids from weather parameters.

Methods

The study area is a strip transect extending 21 km south of the Beaufort Sea near Milne Point, Alaska (Figure 2). Terrain elevation ranges from 0-33 m. Vegetation and soil characteristics are typical of the Arctic Coastal Plain (Wahrhaftig 1965) and similar to those described for the Prudhoe Bay area (Neiland and Hok 1975; Webber and Walker 1975). Access was via the Milne Point Road that included all but the northernmost 0.8 km of the study area. Weather and insect data were recorded from 13 July to 5 August 1982, and from 4 July to 4 August 1983; additional observations of insect activity were made opportunistically between 19-26 August of each year.

In 1982, weather parameters and levels of insect activity were measured at four stations (2-5); an additional station (1) was established in 1983 (Figure 2). Minimum straight-line distances to the Beaufort Sea for stations 1-5 were 0.0, 0.8, 3.4, 9.4, and 15.8 km, respectively, based on measurements using a 1:63,360 scale U.S. Geological Survey map.

Weather data were recorded at each station three times daily at 0900-1030, 1600-1730, and 2200-2230 h Yukon Daylight Time. The following measurements were taken: current, maximum, and minimum ambient air temperatures ($^{\circ}\text{C}$); relative humidity (%); wind direction (degrees from true North to the nearest 45 degrees); wind velocity (m per s); cloud cover (%); precipitation (subjective rating, 0-3); and insolation (W per square m). Annual effects of precipitation, as

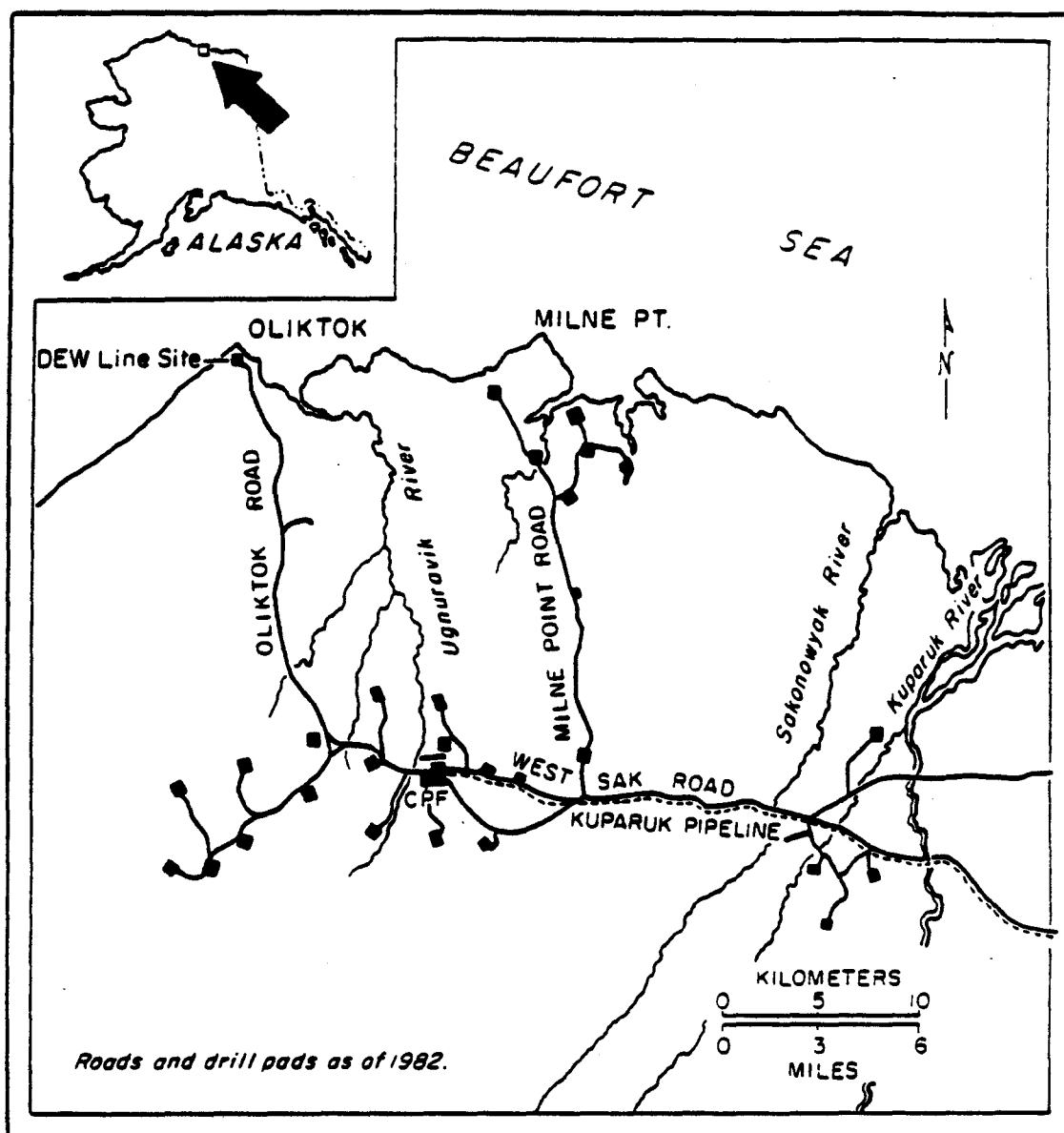


Figure 2. The Milne Point road system with sampling stations and grids.

considered by Gjullin et al. (1961), were not addressed in this investigation. Ambient air temperatures were measured using Taylor model 5458 maximum-minimum thermometers mounted 0.5 m above ground in ventilated wooden boxes. Indicators for maximum and minimum temperatures were reset to the current temperature after each reading. Relative humidity was determined using a Taylor model 1324C sling psychrometer spun 10-20 s and read until 3 consistent values of wet and dry bulb air temperatures were obtained. Wind velocity was determined at approximately 1.3 m above ground using a Taylor model G589 hand-held anemometer; the average velocity over 60 s was recorded. Cloud cover directly overhead was visually estimated to the nearest ten percent. Light intensity was measured using a Solar-Ed Corporation insolation meter.

Distance from the Beaufort Sea was determined from odometer readings along the Milne Point Road. It was included with weather variables for possible selection by models discriminating between periods when insects were present or absent, and in models estimating levels of insect activity, in an attempt to account for north-south variability in insect activity not attributable to weather factors. For example, if a gradient in the quality or quantity of larval-rearing habitat for mosquitoes existed along the road, then this variable could show such an effect.

Midrange temperature ($^{\circ}\text{C}$) and saturation deficit (mbar) were calculated as:

$$\text{midrange } T_a = (\text{maximum } T_a + \text{minimum } T_a)/2$$

and

$$\text{saturation deficit} = E - V,$$

where T_a is the current ambient shade air temperature, E is the maximum vapor pressure possible at a given air temperature (List 1958), and V is the actual vapor pressure determined as:

$$V = (\text{relative humidity} \times E)/100.$$

The activity of mosquitoes and oestrids was estimated three times daily in conjunction with weather observations. For this study, "insect activity" denotes the number of airborne mosquitoes or oestrids captured per unit effort, and the "occurrence" of insects refers to the presence of airborne insects. Two capture techniques were used to estimate insect activity: (1) sweep nets, and (2) sticky traps.

Sweep net counts provided essentially instantaneous estimates of mosquito activity. The canvas net was 0.5 m in diameter with a 1-m long handle. Each sample was based on 100 sweeps made in a figure-eight motion at approximately one sweep per s; sweeps spanned 0.5-2.0 m above ground.

Initially, sweeps were conducted while standing or while walking

over tundra, both upwind and downwind, to determine which method appeared to best indicate perceived levels of mosquito activity. No technique yielded a total count greater than 17 mosquitoes even though many mosquitoes were airborne. Variations in levels of mosquito harassment that were painfully evident during sampling were not apparent in sweep counts despite 20 replications at weather stations 3-5. Ultimately, sweep net counts were conducted in the lee of the observers' vehicle, as they appeared to best reflect levels of mosquito activity. In 1983, two additional, consecutive counts of 50 sweeps each were made 50 m from the road while standing and facing downwind to evaluate the effects of time spent sampling and a gravel road on mosquito samples.

Sticky traps quantified trends in the activity of mosquitoes and oestrids. Each trap consisted of a cylindrical 18.9 l (5 gal) metal fuel container (0.29 m diameter, 0.34 m height) supported 0.2 m above ground. The sides were coated in 1-2 mm of a viscous, nonattractant insect trapping adhesive (Tangle Trap, Tangletrap Company, Grand Rapids, Michigan). Traps were scraped and recoated with fresh adhesive every 7-10 days. In 1982, one sticky trap was placed 10 m from the road at each of stations 2-5. In 1983, a second trap was placed 50 m from the road at each of these stations, and one trap was established at station 1. All mosquitoes and oestrids caught on sticky traps were counted and removed when weather data were recorded. Traps were counted and cleaned as quickly as possible (roughly 30-180 s per visit) to avoid trapping mosquitoes attracted

to the observer; mosquitoes caught while traps were being tended were excluded from the total count. In 1982, mosquitoes and oestrids were identified to family by gross anatomical characteristics; in 1983, warbles and bots were distinguished to assess their respective abundance (Bennett and Sabrosky 1962; Espmark 1968; Dieterich and Haas 1981).

Simple linear regression and stepwise multiple linear regression analyses were used to model levels of insect activity from weather parameters. Likewise, discriminant and logistic regression analyses were used to predict the presence of mosquitoes and oestrids. The Kolmogorov-Smirnov test was used to examine differences in the distribution of data between 1982 and 1983, and between periods when insects were present vs. absent. Differences in median locations of the data were tested using Mann-Whitney and Kruskal-Wallis tests; multiple comparisons were made using the Kruskal-Wallis test after Conover (1980). Contingency table tests examining wind direction follow Batschelet (1981). Canonical correlation analyses were conducted to evaluate the correlation between all indices of insect activity (sweep counts of mosquitoes, trap counts of mosquitoes, and trap counts of oestrids), and all weather parameters.

The relationships between insect activity and weather were independently modeled for sweep counts of mosquitoes, trap counts of mosquitoes, and trap counts of oestrids. I began modeling this relationship using all individual samples recorded at each station ($n = 667$). I suspected that stronger correlations between these

parameters could be identified if the linear regression analyses were limited to periods when insects were active. Therefore, I adopted a two-stage approach to: (1) predict the presence of insects, and (2) estimate their level of activity when insects were present.

Discriminant and logistic regression analyses were used to predict the presence of insects. Jackknifed estimates were used to determine the percentage of observations correctly classified by discriminant analyses. Engleman (1980, 1983) reported that logistic regression analysis is superior to discriminant analysis for predicting a binary response using independent variables with skewed distributions; also, the response function for binary indicator variables frequently follows a logistic curve (Neter and Wasserman 1974). Since log transformations did not completely normalize the distribution of any variable, I compared results of the two techniques. Levels of insect activity were estimated using stepwise multiple linear regression analysis with Mallows Cp criteria to select weather variables (Neter and Wasserman 1974).

Insect activity was modeled as a function of weather at three levels. First, individual measurements of weather and insect activity were used in the modeling process; however, all of these parameters were highly variable. Therefore, I pooled samples and repeated the analyses on daily means of weather and insect activity for each station, and on daily means for all stations combined. This minimized the effects of short-term natural variability (i.e., "noise") in weather factors and insect activity.

Residual error terms from all initial models predicting levels of insect activity, and pairwise plots of insect activity and weather factors, suggested that variability in insect activity was correlated with the magnitude of weather parameters; however, this effect was not clear. Therefore, both the raw and log values of each weather variable were considered for possible inclusion in multiple linear regression models predicting levels of insect activity. Whenever both values for a single weather parameter entered a model, the value with the lowest "F to enter" statistic was omitted, and the model was recomputed. Similarly, a model was developed for each of the raw and log values of sweep counts of mosquitoes, trap counts of mosquitoes, and trap counts of oestrids. The model containing either the raw or log transformed value of insect activity having the highest coefficient of determination (r^2) was defined as best.

Multiple comparisons were made using a FORTRAN program for the Kruskal-Wallis test. Detailed descriptions of data, simple multiple linear regressions, stepwise linear regressions, stepwise discriminant analyses, stepwise logistic regressions, and canonical correlation analyses were performed using BMDP-81 and -83 statistical software (Dixon 1981, 1983). Kolmogorov-Smirnov tests were conducted using SPSS (Nie et al. 1975). All computer-assisted operations were conducted on a Honeywell 66/40 or VAX 11-785 (VMS 4.1) computer. Alpha levels (P-values) < 0.05 were considered statistically significant.

Results

Relationships between weather and insect activity

Alate mosquitoes were first observed before sampling began in both years (29 June 1982 and 2 July 1983); therefore, all of the data were used to investigate relationships between weather factors and mosquito activity. Oestrid imagoes were not consistently caught until 25 July 1982, and 16 July 1983. Thus, weather data used to analyze weather-oestrid relationships were restricted accordingly. Mosquitoes and oestrids were present when sampling ended each year; however, the frequency of periods when mosquitoes were present, and levels of mosquito activity, were very low by 25-27 July of both years. Oestrids maintained low levels of activity later during summer than mosquitoes during 1982 and 1983. This is supported by observations recorded between 19-26 August 1982. During that time, several oestrids were observed on one uncharacteristically warm and sunny afternoon (20 August), yet mosquitoes were absent at all stations.

Mosquitoes were caught by sweeps or traps on 14 of 22 (64%) days during 1982, and on 28 of 33 days (85%) during 1983. Oestrids were trapped on 4 of 22 days (18%) and 13 of 33 days (39%) during the two years. In 1983, nasal bots made up 11% (17 of 150) of the total catch of oestrids.

The distributions of each weather variable (all stations

combined) were significantly different between 1982 and 1983 (Table 1). However, pairwise plots of all variables did not reveal discrete clusters of points in each year. Since my intent was to examine the relationships between weather factors and insect activity, rather than identify between-year differences in either of these factors, I combined data from 1982 and 1983 to increase sample sizes, and to broaden the range of conditions over which insect activity was modeled.

During the model-selection process, stepwise discriminant analysis never selected precipitation or insolation as significant variables for predicting the presence of mosquitoes or oestrids. Likewise, stepwise multiple linear regression analyses did not select these variables for estimating levels of insect activity. Therefore, I omitted these variables from all subsequent analyses to reduce the effects of multicollinearity among weather variables, and to prevent obscuring significant relationships between insect activity and other weather parameters (Neter and Wasserman 1974).

Pairwise plots of each dependent variable (sweep and trap counts of mosquitoes, and trap counts of oestrids) against each independent variable (weather parameters) indicated that the variance of a dependent variable was often weakly proportional to the value of the independent variable, and that no simple linear relationships existed. Semi-log and log-log plots of all pairwise combinations of dependent and independent variables verified the absence of any simple linear relationships, and showed that log transformations

Table 1. The statistical significance of differences in medians of weather parameters between 1982 and 1983 (all stations combined).

Weather parameter	1982		1983		Z ^a	P-value ^b	U ^c	P-value ^b
	Median	n	Median	n				
Current air temp. (°C)	8	272	6	455	1.77	0.004	58891	<0.001
Maximum air temp. (°C)	11	272	9	455	1.74	0.005	58124	<0.001
Minimum air temp. (°C)	4	272	3	455	1.59	0.013	57802.5	<0.001
Midrange air temp. (°C)	8	272	6	455	1.98	0.001	58644	<0.001
Relative humidity (%)	88	220	86	447	3.56	<0.001	52320.5	0.19
Saturation deficit (mbar)	1.31	220	1.22	447	4.43	<0.001	47137	0.36
Wind direction (degrees)	180	272	90	455	205.02 ^d	<0.001	53115	0.09
Wind velocity (m/s)	3.00	272	3.87	455	2.89	<0.001	36824.5	<0.001
Cloud cover (%)	100	272	30	455	2.74	<0.001	58111	<0.001

^a Kolmogorov-Smirnov test statistic (except where noted) for the null hypothesis "no difference in distributions between 1982 and 1983"

^b observations of weather parameters were serially correlated (Durbin-Watson test; $P < 0.05$); therefore, P-values should be viewed with caution

^c Mann-Whitney test statistic for the null hypothesis "no difference in median location of distributions between 1982 and 1983"

^d Chi-squared test statistic

often reduced the correlation between variance of a dependent variable and the magnitude of an independent variable; similar results have been previously reported (Cook 1921; Williams 1951; Johnson 1969).

Spearman rank correlation coefficients (Table 2) were stronger than linear correlation coefficients for nearly all pairwise combinations of variables. Insect activity was most strongly correlated with levels of ambient air temperature. This relationship was strongest between sweep counts of mosquitoes and current temperature; trap counts of mosquitoes and oestrids were correlated most strongly with maximum and midrange temperatures, respectively. Saturation deficit was the second most highly correlated weather parameter with each measure of insect activity.

Peak levels of insect activity were higher in 1983 than in 1982 for sweep counts of mosquitoes, trap counts of mosquitoes, and trap counts of oestrids (Figures 3-5, respectively). Comparison of Figures 3-5 and 6-10 indicate that periods of maximum insect activity coincided with periods of high ambient temperature, low wind velocity, low atmospheric humidity (i.e., relative humidity and saturation deficit), and low cloud cover, particularly in 1983. With the exception of wind direction, distributions of each weather variable were significantly different between periods when insects were present vs. absent for each measure of insect activity (Table 3).

With the exceptions of cloud cover and wind direction, medians

Table 2. Spearman rank correlation coefficients for weather parameters and indices of insect activity for 1982-83 (n=668)^a.

	Dist. from coast	Current temp.	Max. temp.	Min. temp.	Mid. temp.	Rel. hum.	Sat. def.	Wind vel.	Cloud cover	Mosq. act. (sweeps)	Mosq. act. (traps)	Oest. act. (traps)
Dist. from coast (km)	1.0											
Current air temp. (°C)	0.21	1.0										
Maximum air temp. (°C)	0.28	0.72	1.0									
Minimum air temp. (°C)	0.15	0.58	0.65	1.0								
Midrange air temp. (°C)	0.25	0.73	0.95	0.86	1.0							
Relative humidity (%)	-0.22	-0.65	-0.44	-0.29	-0.42	1.0						
Saturation deficit (mbar)	0.21	0.77	0.54	0.38	0.53	-0.97	1.0					
Wind vel. (m/s)	-0.15	-0.06	-0.25	-0.07	-0.20	-0.01	-0.01	1.0				
Cloud cover (%)	0.03	-0.29	-0.29	-0.18	-0.28	0.42	-0.43	-0.04	1.0			
Mosq. act. (no./100 sweeps)	0.23	0.54	0.49	0.30	0.46	-0.47	0.52	-0.34	-0.24	1.0		
Mosq. act. (no. per trap/hr.)	0.34	0.37	0.45	0.29	0.42	-0.32	0.36	-0.18	-0.07	0.30	1.0	
Oestrid act. (no. per trap/hr.)	0.05	0.33	0.35	0.24	0.35	-0.22	0.28	-0.09	-0.19	0.33	0.43	1.0

^a $|r| > 0.20$ is significantly different from 0 at $P < 0.05$; $|r| > 0.26$ is significantly different from 0 at $P < 0.01$

Mosquito Activity (Sweeps)

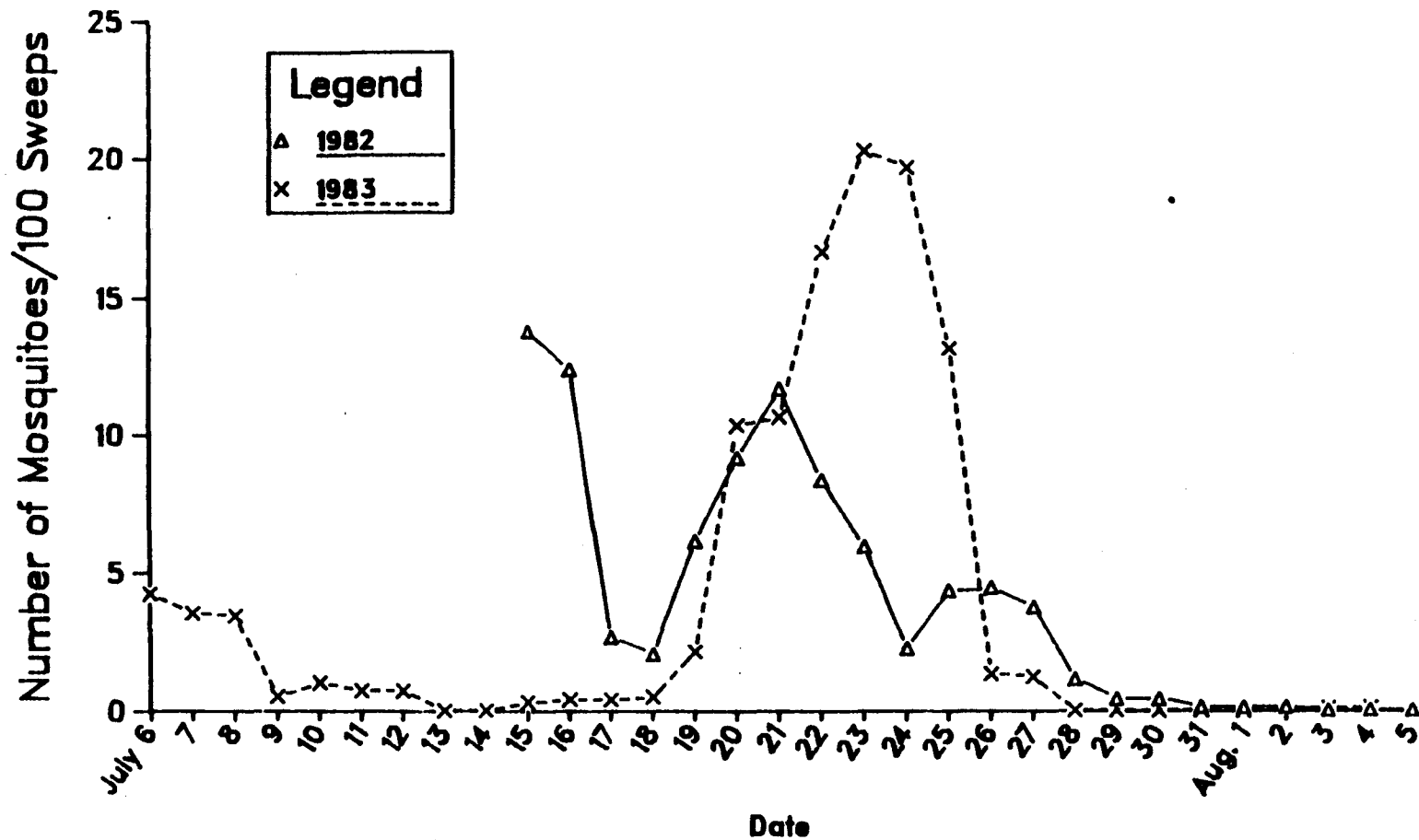


Figure 3. Three-day moving averages of sweep counts of mosquitoes near Milne Point, Alaska (n = 272, 1982; n = 455, 1983).

Mosquito Activity (Traps)

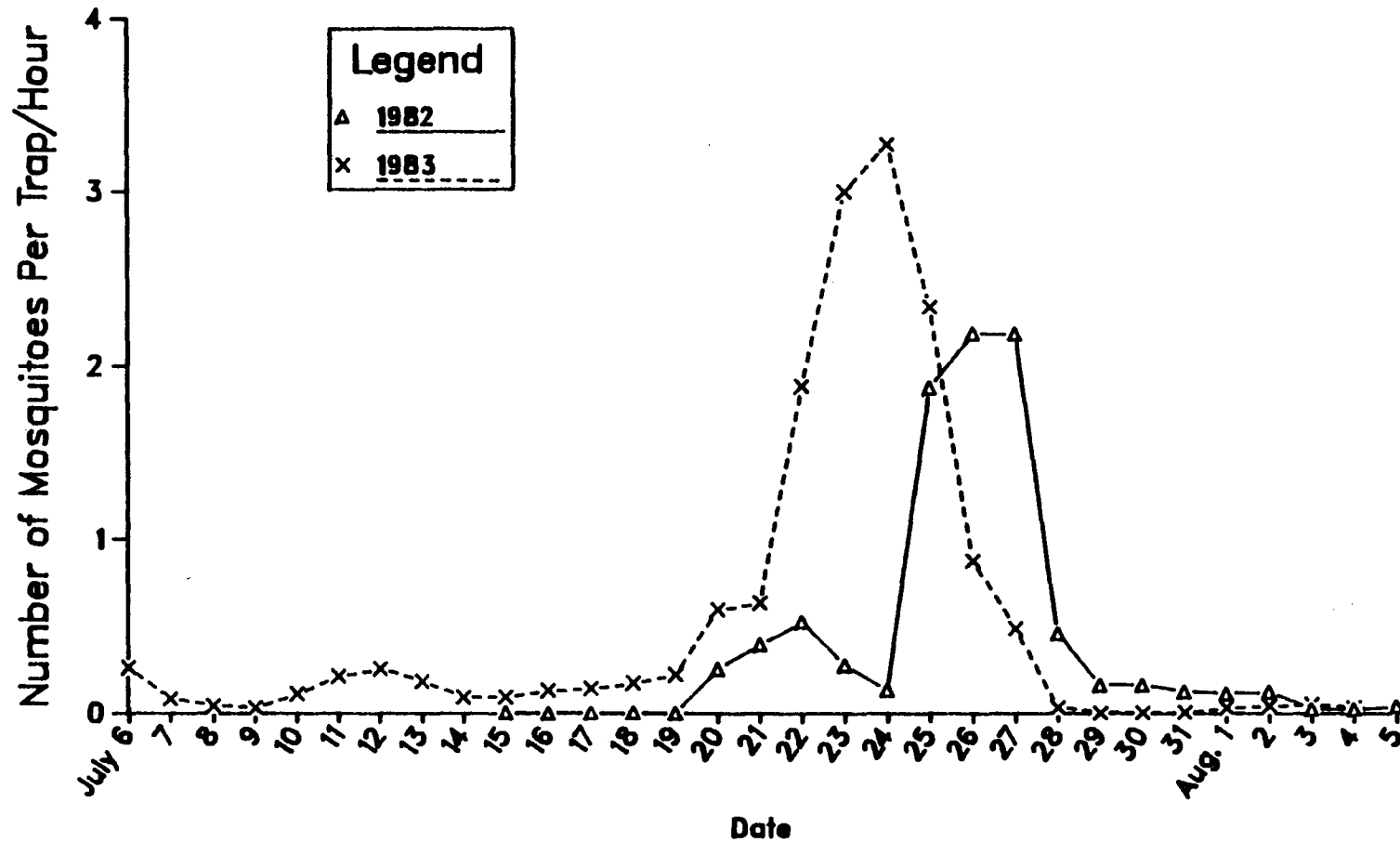


Figure 4. Three-day moving averages of trap counts of mosquitoes near Milne Point, Alaska (n = 272, 1982; n = 455, 1983).

Oestrid Activity (Traps)

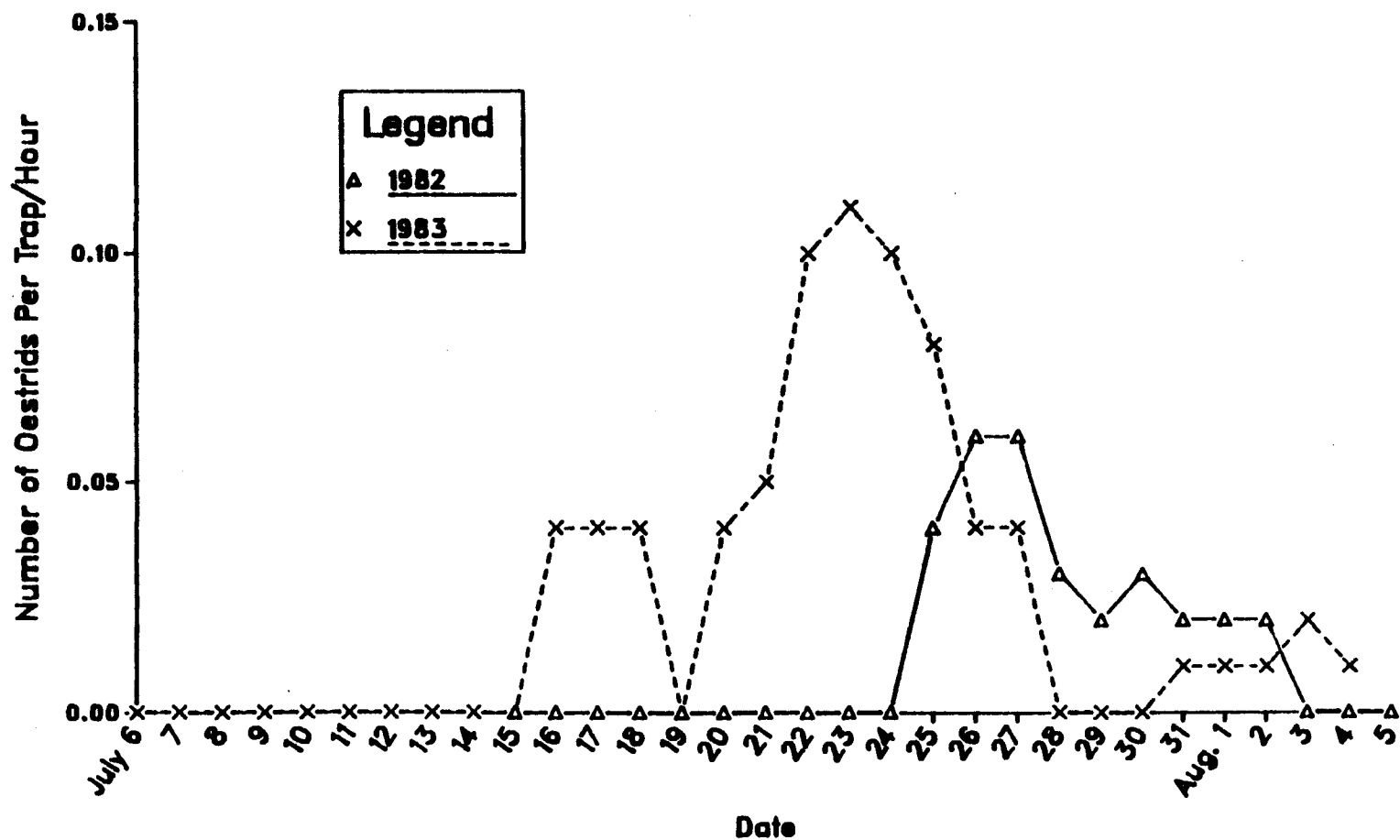


Figure 5. Three-day moving averages of trap counts of oestrids near Milne Point, Alaska (n = 272, 1982; n = 455, 1983).

Current Ambient Air Temperature

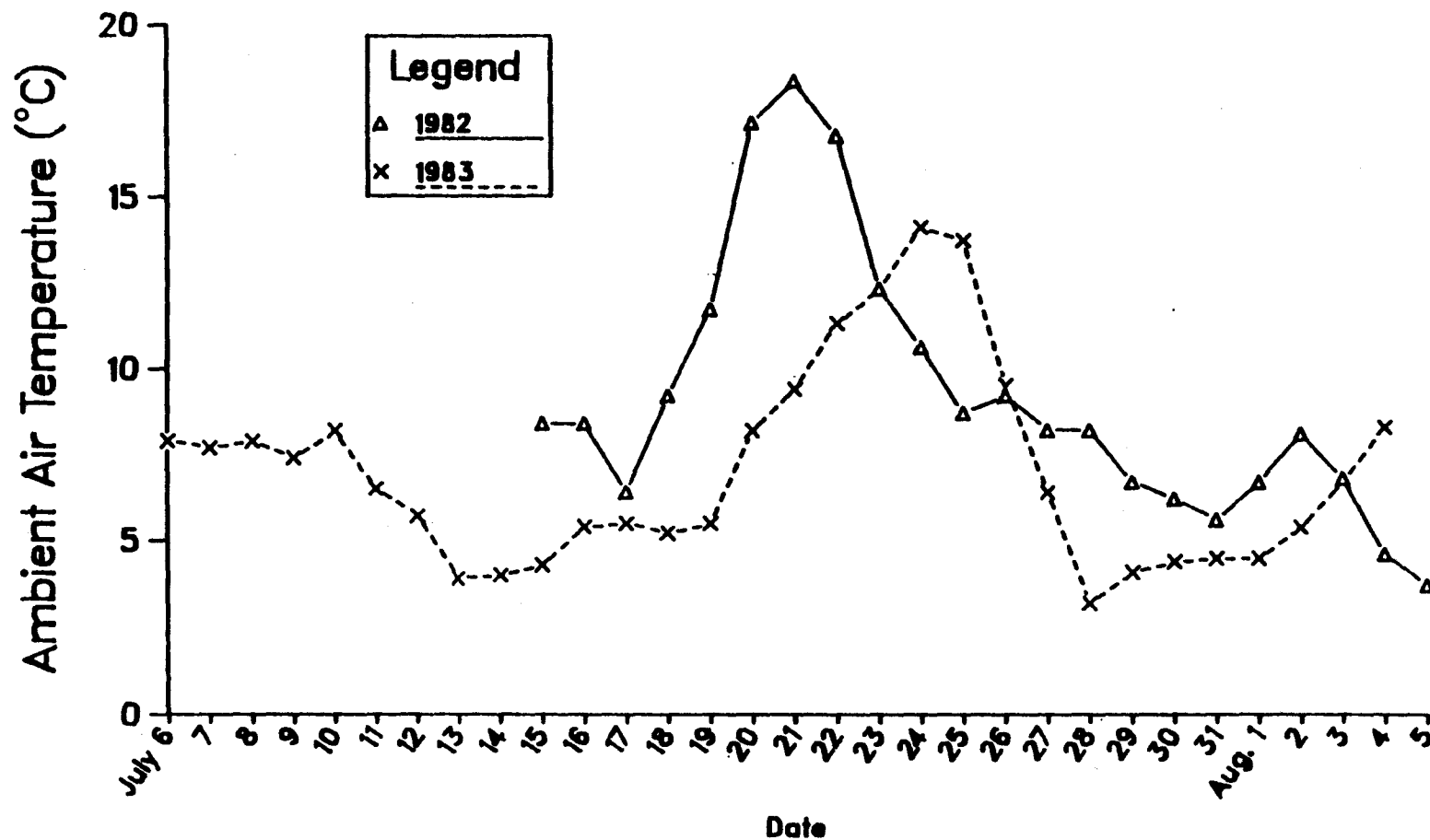


Figure 6. Three-day moving averages of current ambient shade air temperature near Milne Point, Alaska (n = 272, 1982; n = 455, 1983).

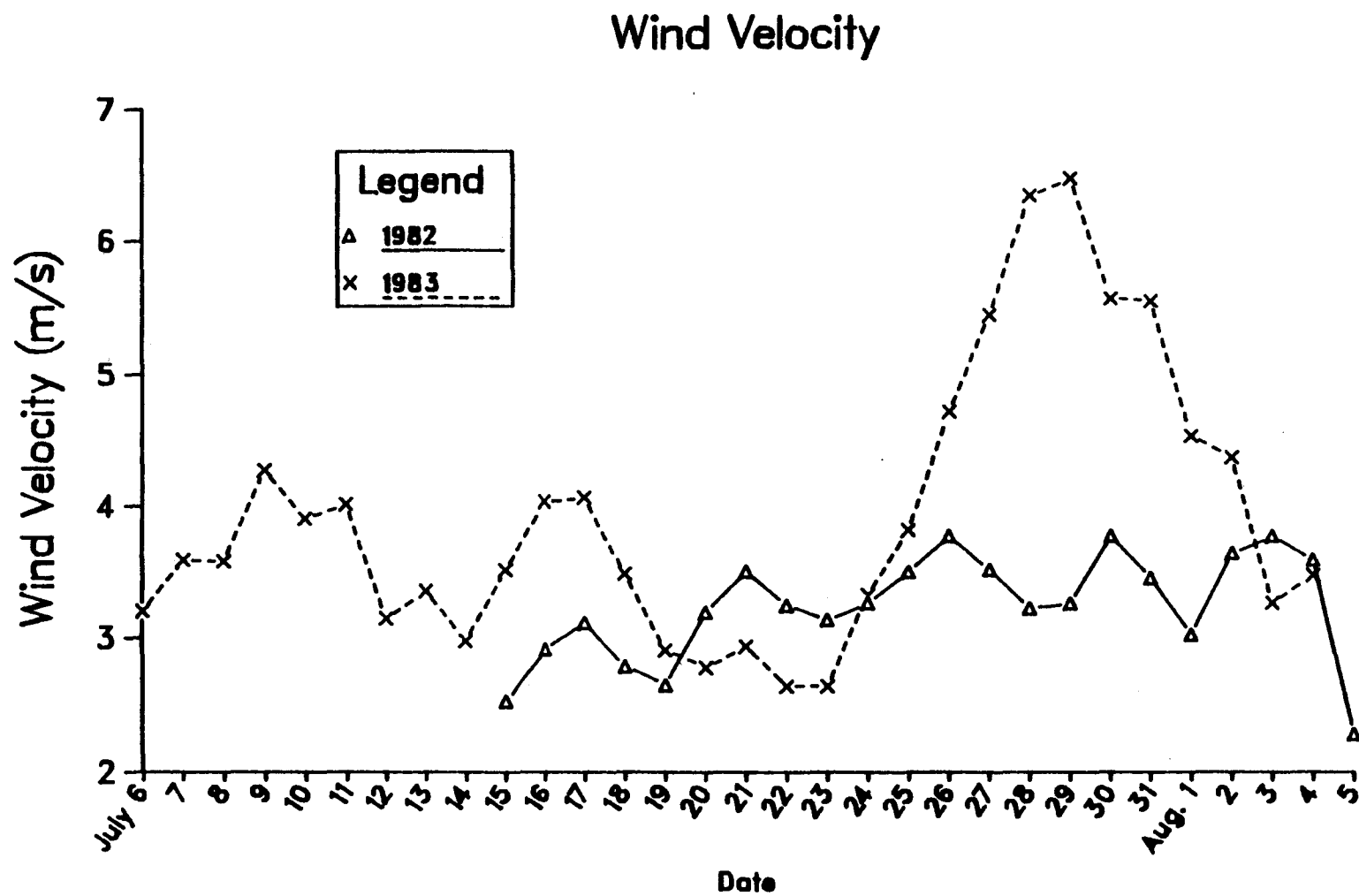


Figure 7. Three-day moving averages of wind velocity near Milne Point, Alaska (n = 272, 1982; n = 455, 1983).

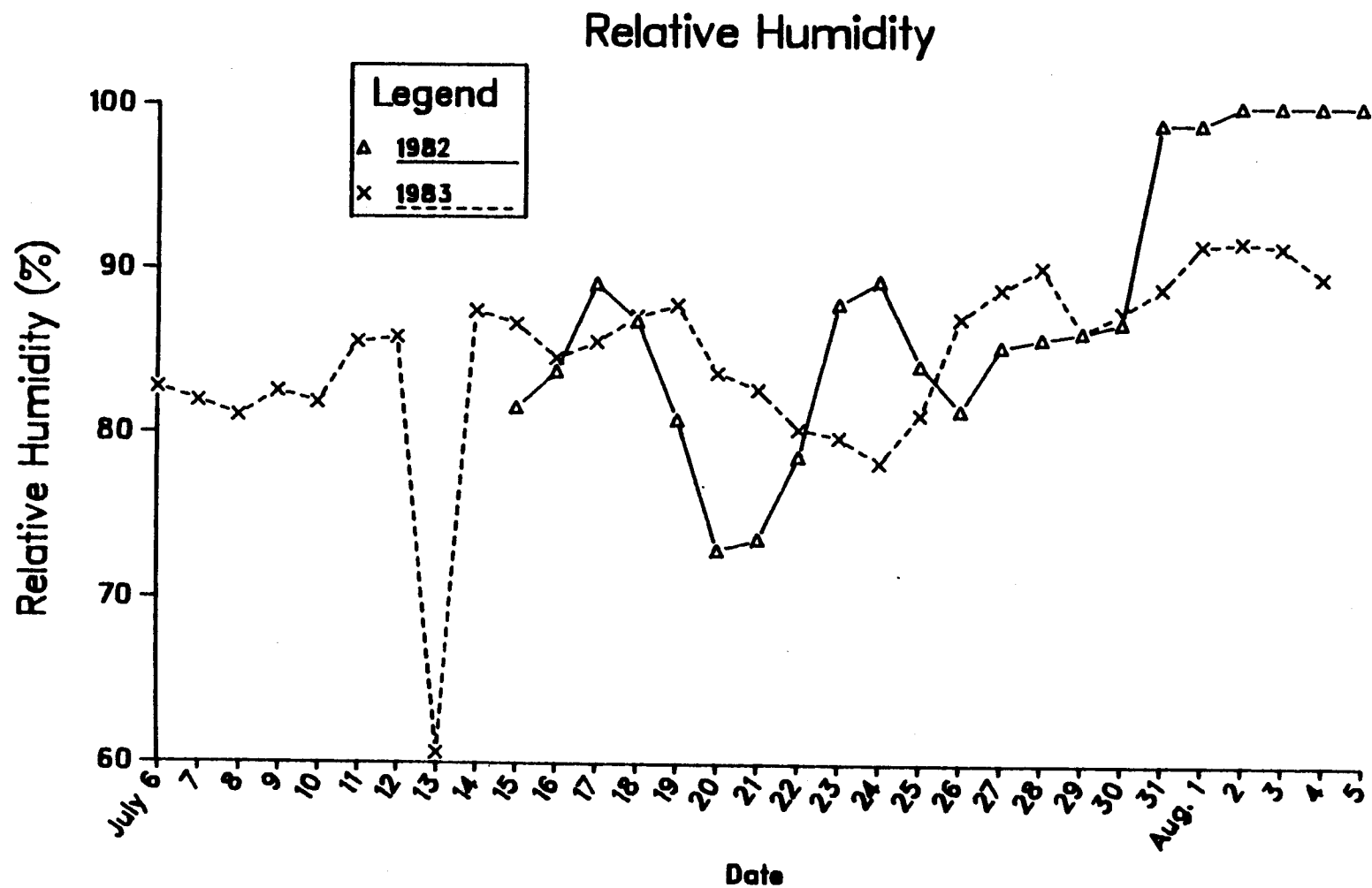


Figure 8. Three-day moving averages of relative humidity near Milne Point, Alaska (n = 220, 1982; n = 447, 1983).

Saturation Deficit

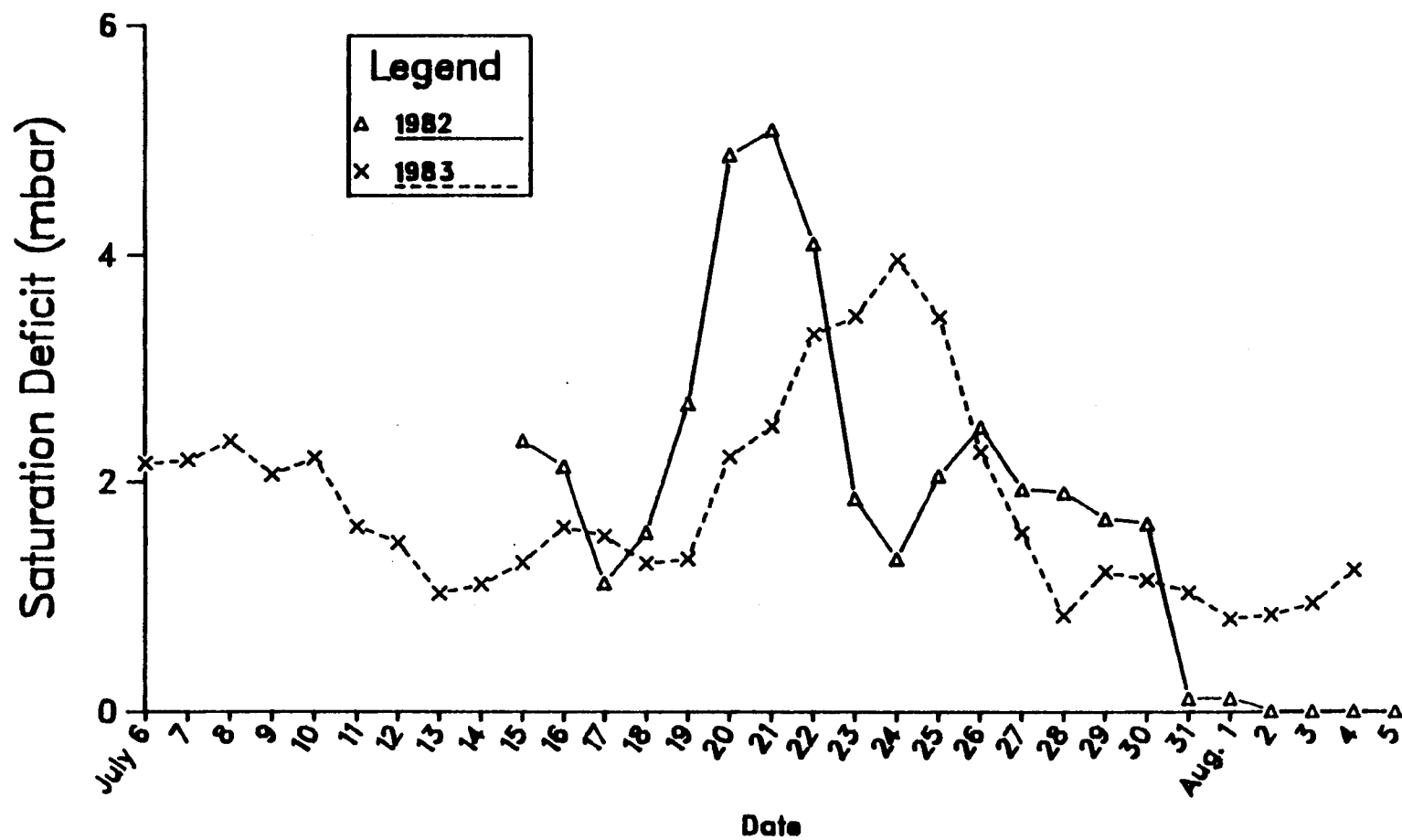


Figure 9. Three-day moving averages of saturation deficit near Milne Point, Alaska (n = 220, 1982; n = 447, 1983).

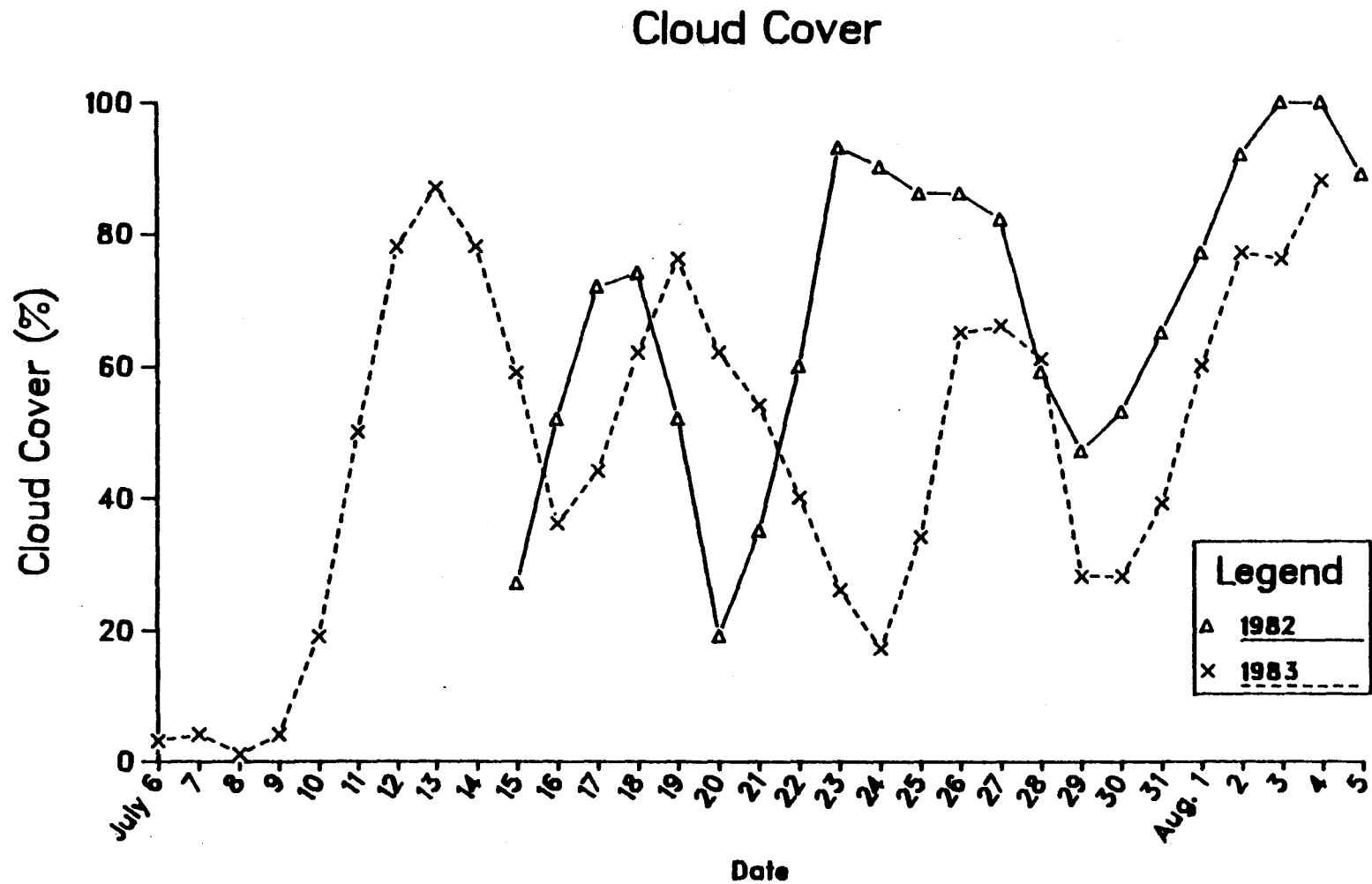


Figure 10. Three-day moving averages of cloud cover near Milne Point, Alaska ($n = 272$, 1982; $n = 455$, 1983).

Table 3. Median levels of weather parameters during periods when insects were present or absent, and the statistical significance of differences, for each index of insect activity.

Weather parameter	Mosquitoes (sweeps)				Mosquitoes (traps)				Oestrids (traps)			
	Present	Absent	K-S ^a P	M-W ^b P	Present	Absent	K-S ^a P	M-W ^b P	Present	Absent	K-S ^a P	M-W ^b P
Current temp. (°C)	12	5	<0.001	<0.001	10	6	<0.001	<0.001	12	6	<0.001	<0.001
Midrange temp. (°C)	11.5	5.5	<0.001	<0.001	9.0	5.5	<0.001	<0.001	11.5	5.5	<0.001	<0.001
Relative humidity (%)	74.5	92.0	<0.001	<0.001	80.0	89.5	<0.001	<0.001	75.5	93.0	<0.001	<0.001
Saturation deficit (mbar)	3.74	0.74	<0.001	<0.001	2.20	0.92	<0.001	<0.001	3.68	0.70	<0.001	<0.001
Wind direction (degrees)	103	114	<0.24 ^c		119	112	<0.35 ^c		122	123	<0.20 ^c	
Wind velocity (m/s)	2.69	3.87	<0.001	<0.001	3.02	3.72	<0.001	<0.001	3.16	4.04	<0.001	<0.001
Cloud cover (%)	10	100	<0.001	<0.001	40	90	<0.001	<0.001	0	100	<0.001	<0.001
n ^d	148	579			216	511			74	342		

^a P-value for the Kolmogorov-Smirnov test statistic; null hypothesis = "no difference in distributions between periods when insects were present and when they were absent"

^b P-value for the Mann-Whitney test statistic; null hypothesis = "no difference in median values between periods when insects were present and when they were absent"

^c P-value for the Chi-squared test statistic; null hypothesis = "no difference in median wind direction between periods when insects were present and when they absent;" wind direction measured to the nearest 45 degrees

^d sample sizes for relative humidity and saturation deficit, for periods when insects were present vs. absent, were 144 and 523 (mosquitoes/100 sweeps), 197 and 470 (mosquitoes per trap/hr.), and 68 and 305 (oestrids per trap/hr.), respectively

of each weather variable were significantly different among stations (Table 4). Multiple comparisons indicated that weather conditions at station 1 were least similar to conditions at the other stations, and that the similarity in weather between neighboring stations increased with distance from the coast (Table 5). I compared median values of weather parameters between coastal and inland stations (stations 1 and 2 vs. 3-5, respectively) during periods when mosquitoes were captured near the coast. There were no differences in weather conditions between the two sets of stations for any weather variable except relative humidity (Table 6). Weather conditions were generally cooler, windier, more humid, and less cloudy near the Beaufort Sea than in inland areas (Figures 11-14).

The proportion of samples in which insects were caught increased with distance from the coast (Figure 15), as did mean levels of mosquito activity (Figures 16-17). No such trends are apparent for oestrids (Figures 15 and 18). There were no differences among stations in median levels of mosquito or oestrid activity when all of the data were used (all medians = 0), or even when the data were restricted to periods when insects were active (Table 7). This indicates that weather conditions were usually unfavorable for flight. Thus, the relationships shown in Figures 16 and 17 were primarily influenced by the effects of maritime weather conditions on the occurrence, rather than prevailing level, of mosquito activity. The high percentage of days on which insects were caught results from brief periods of insect activity during warm, mid-day periods.

Table 4. Medians and ranges (in parentheses) of weather parameters for individual weather stations; 1982-83.

Weather parameter	Station 1	2	3	4	5	H ^a	P-value
Current temp. (°C)	4 (0-19)	7 (1-20)	7 (0-22)	7 (0-23)	7 (0-26)	51.47	<0.001
Maximum temp. (°C)	5 (1-19)	8 (0-24)	10 (2-24)	11 (0-28)	12 (1-27)	75.46	<0.001
Minimum temp. (°C)	2 (-2-14)	4 (0-18)	4 (-2-18)	3 (-4-20)	5 (-1-22)	49.86	<0.001
Midrange temp. (°C)	4 (0-15)	6 (0-20)	7 (2-21)	7 (0-22)	8 (2-24)	61.50	<0.001
Relative humidity (%)	93 (63-100)	87 (62-100)	86 (58-100)	84 (41-100)	86 (24-100)	41.07	<0.001
Saturation deficit (mbar)	0.6 (0-5.5)	1.1 (0-8.9)	1.5 (0-9.0)	1.7 (0-14.3)	1.4 (0-16.7)	38.24	<0.001
Cloud cover (%)	30 (0-100)	80 (0-100)	80 (0-100)	90 (0-100)	80 (0-100)	1.06	0.90
Wind direction (degrees)	135 (45-360)	135 (45-360)	135 (45-360)	135 (45-360)	135 (45-360)	32.27 ^b	0.25
Wind velocity (m/s)	4.5 (0.9-8.6)	3.5 (0.5-7.5)	3.4 (0.3-8.0)	3.2 (0-8.0)	3.4 (0.2-8.5)	30.84	<0.01
n	91	158	158	160	160		

^a Kruskal-Wallis statistic for the null hypothesis "no difference in medians among all stations"

^b two-sample Chi-squared test (Batschelet 1981) for the null hypothesis "no difference in median wind direction among all stations"; df=28

Table 5. Multiple comparisons of weather parameters between stations; 1982-83 ("*" indicates a significant difference; Kruskal-Wallis test; $P < 0.05$)^a.

Stations compared	Current temp. (°C)	Midrange temp. (°C)	Relative humidity (%)	Saturation deficit (mbar)	Wind velocity (m/s)
1 - 2	*	*	*	*	*
1 - 3	*	*	*		*
1 - 4	*	*	*	*	*
1 - 5	*	*	*	*	*
2 - 3				*	
2 - 4			*	*	
2 - 5		*	*	*	
3 - 4				*	
3 - 5				*	
4 - 5		*			

^a Kruskal-Wallis test statistics for the null hypothesis "no difference in medians among stations" is presented for each variable in Table 4

Table 6. Median values of weather parameters at coastal (stations 1 and 2) and inland (stations 3-5) sampling stations when mosquitoes were active (as determined by sweep counts) at stations 1 or 2.

Weather parameter	Stations 1-2	Stations 3-5	U ^a	P-value
Current temp. (°C)	11	13	802	0.64
Midrange temp. (°C)	11.5	12.5	657.5	0.08
Relative humidity (%)	78	72	1091	0.04
Saturation deficit (mbar)	2.76	4.43	699	0.17
Wind direction (degrees)	135	180	5.54 ^b	0.20
Wind velocity (m/s)	2.93	2.59	903	0.67
Cloud cover (%)	5	10	769.5	0.44
n	28	61		

^a Mann-Whitney test statistic for the null hypothesis "no difference in medians between coastal and inland stations" except where noted

^b two-sample Chi-squared test (Batschelet 1981) for the null hypothesis "no difference in median wind direction between coastal and inland stations"; df=3

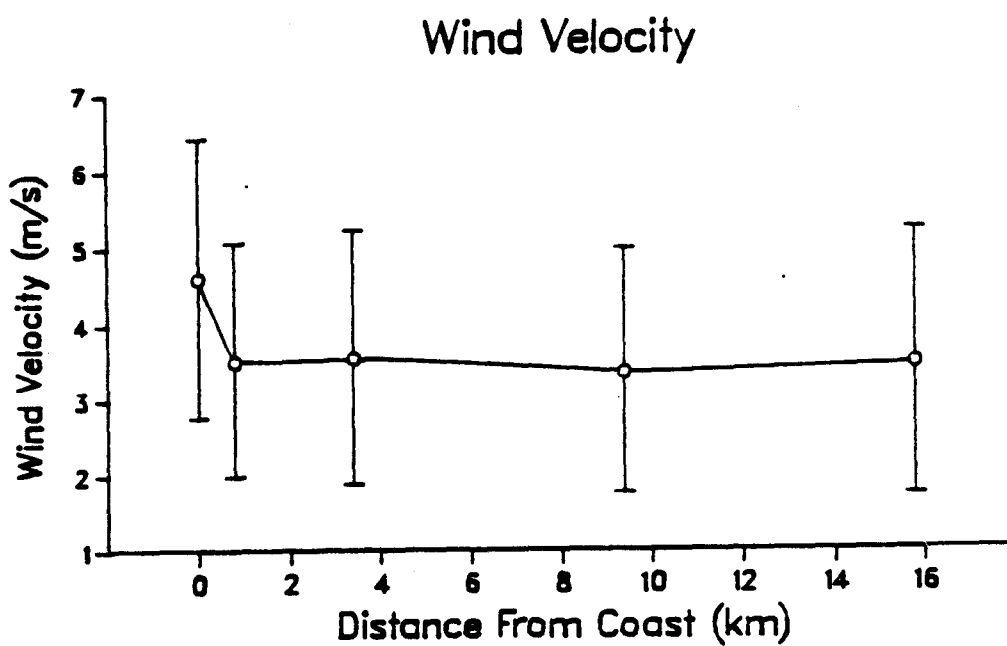
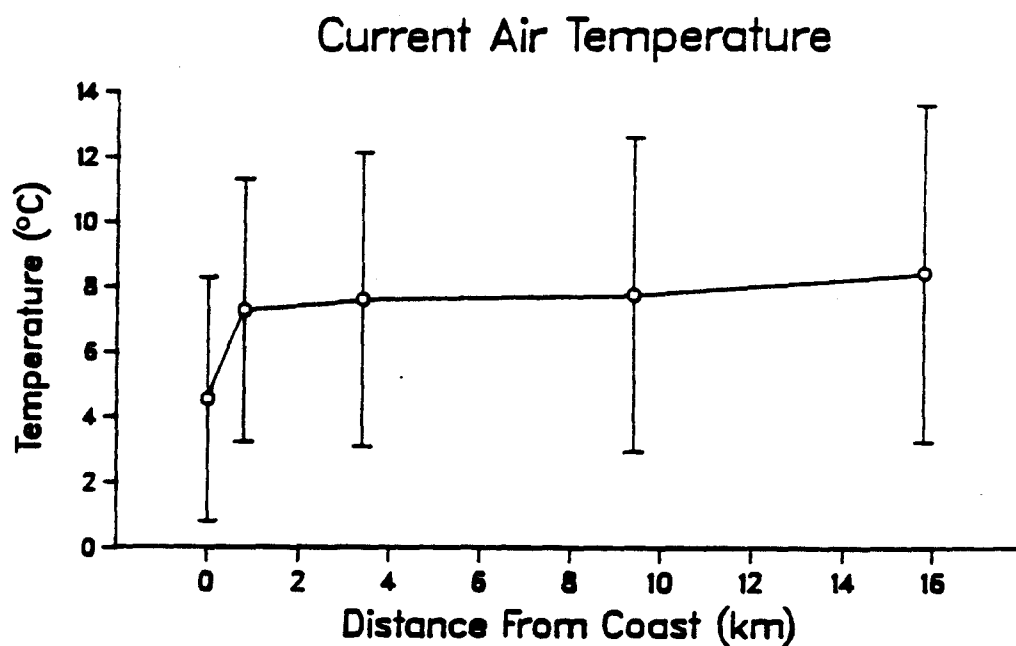


Figure 11. Mean (± 1 SD) current shade air temperature and wind velocity in relation to distance from the Beaufort Sea near Milne Point, Alaska; 1982-83 (sample sizes for stations 1-5 reported in Table 4).

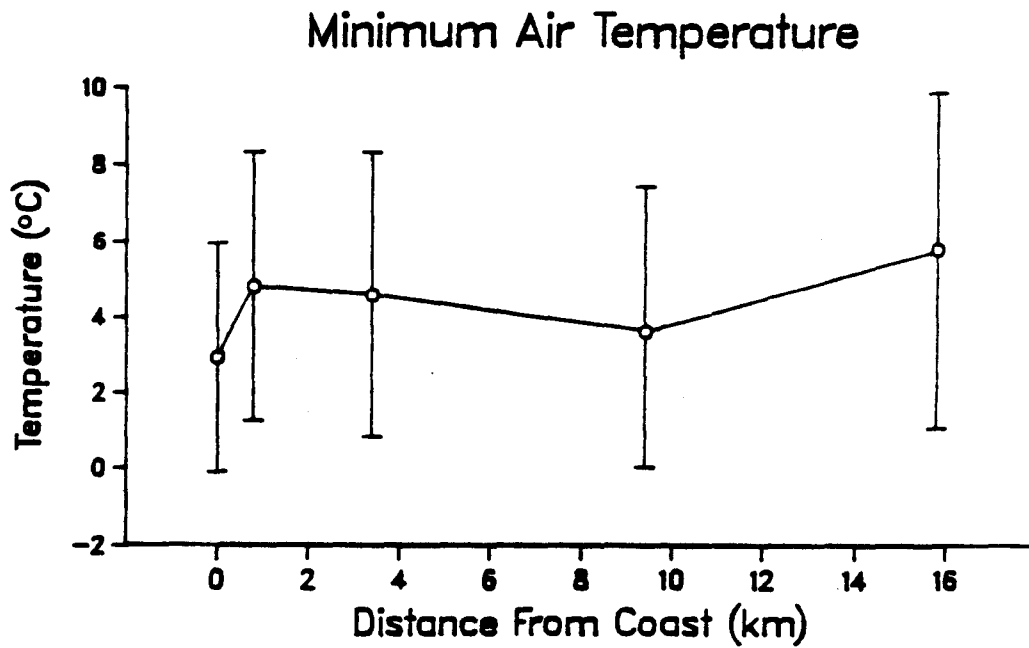
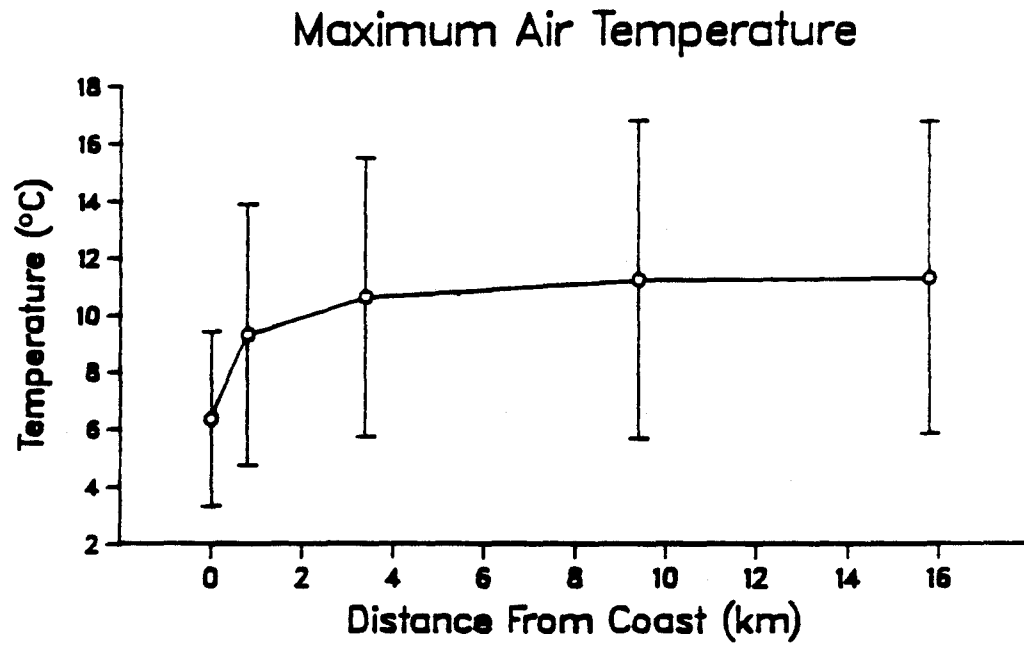


Figure 12. Mean (± 1 SD) maximum and minimum shade air temperature in relation to distance from the Beaufort Sea near Milne Point, Alaska; 1982-83 (sample sizes for stations 1-5 reported in Table 4).

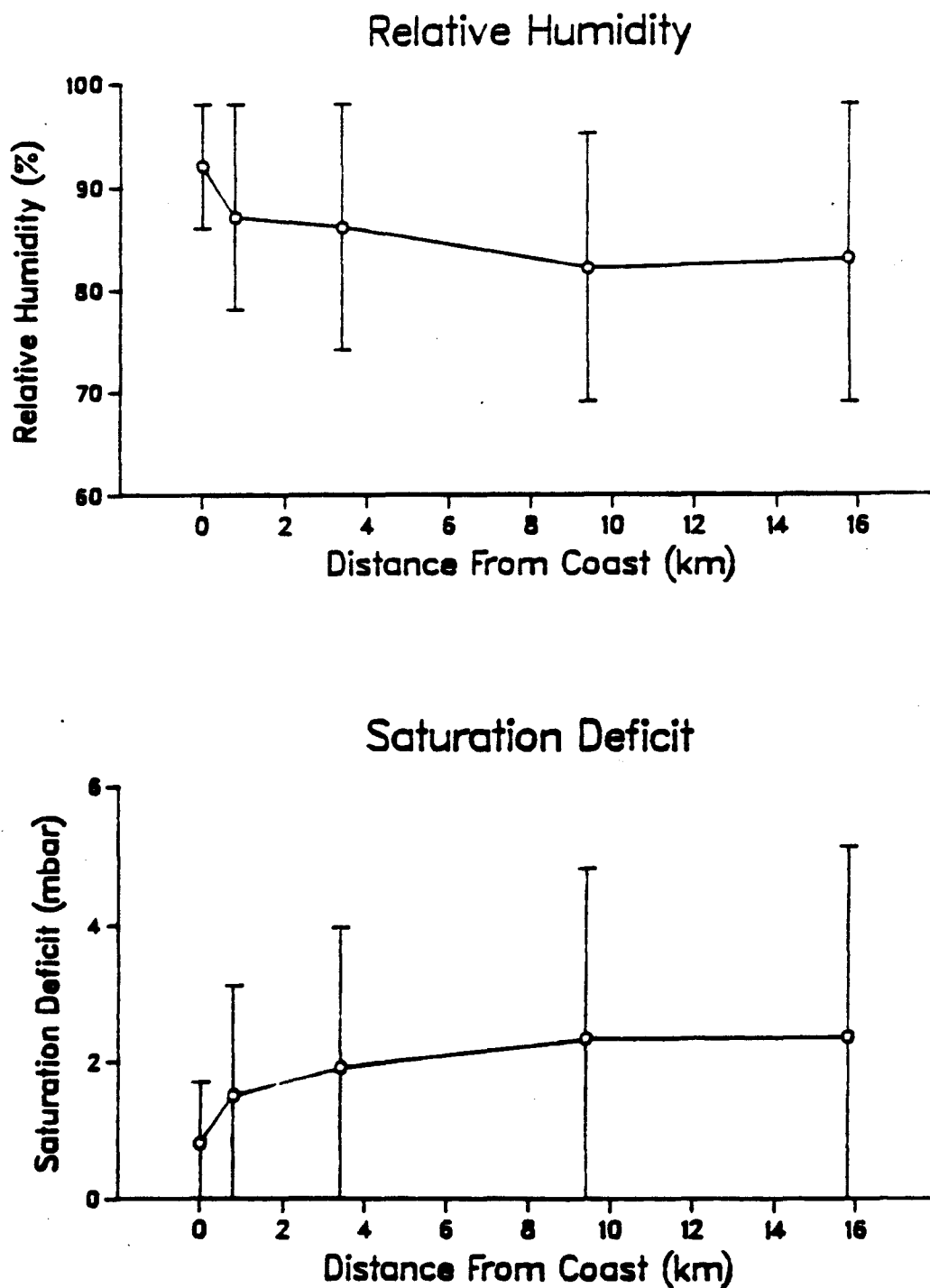


Figure 13. Mean (± 1 SD) relative humidity and saturation deficit in relation to distance from the Beaufort Sea near Milne Point, Alaska; 1982-83 (sample sizes for stations 1-5 reported in Table 4).

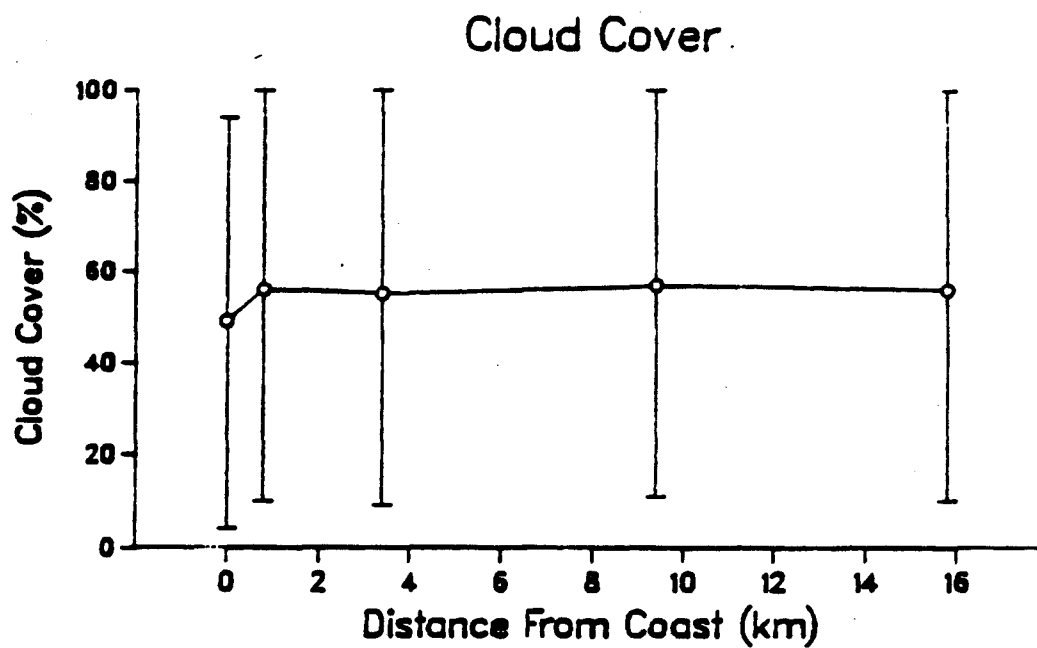


Figure 14. Mean (± 1 SD) cloud cover in relation to distance from the Beaufort Sea near Milne Point, Alaska; 1982-83 (sample sizes for stations 1-5 reported in Table 4).

Proportion of Samples in Which Insects Were Caught

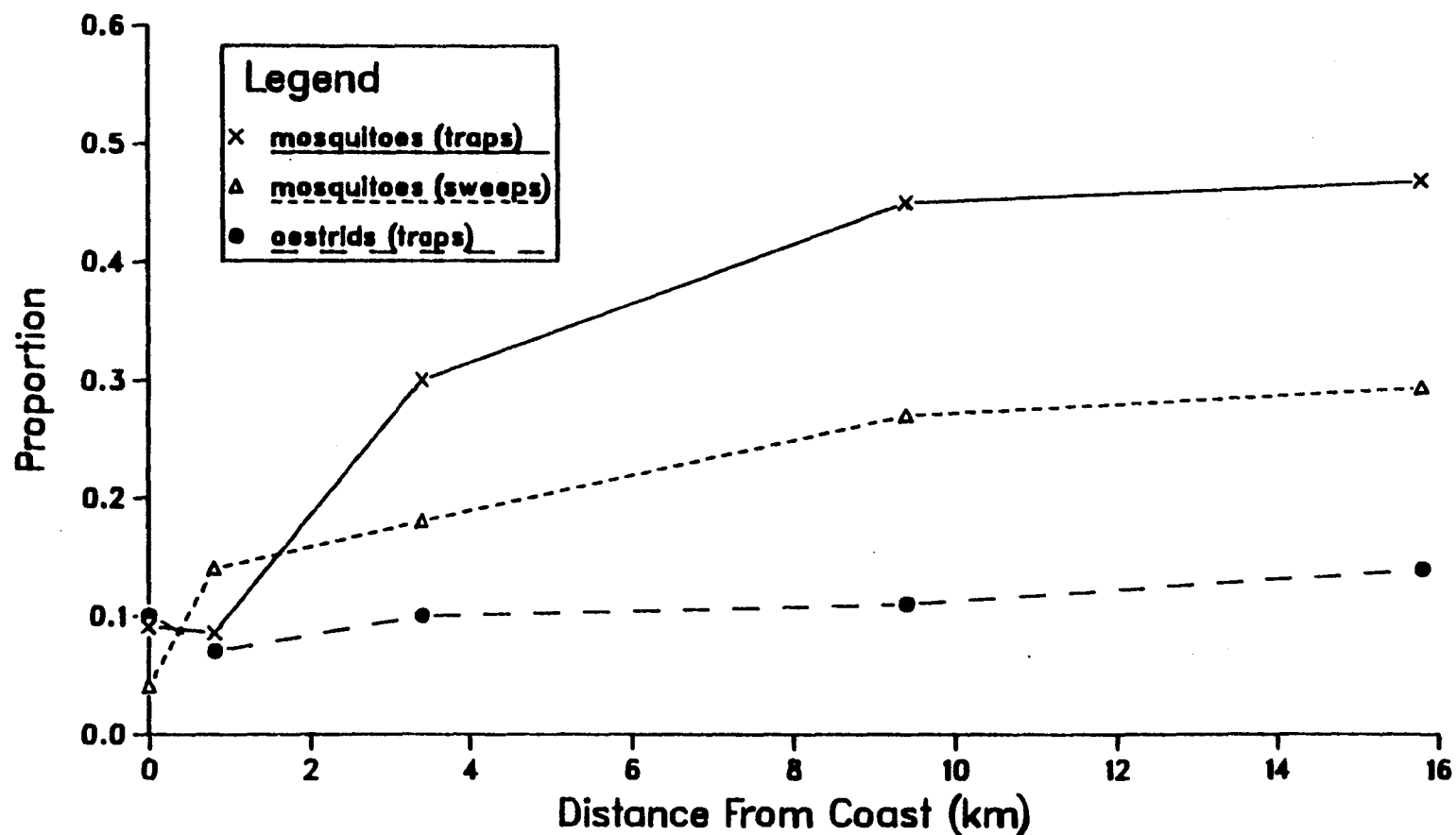


Figure 15. The proportion of samples in which mosquitoes and oestrids were caught in relation to distance from the Beaufort Sea near Milne Point, Alaska; 1982-83 (sample sizes for stations 1-5 are reported in Table 4).

Mosquito Activity (Sweeps)

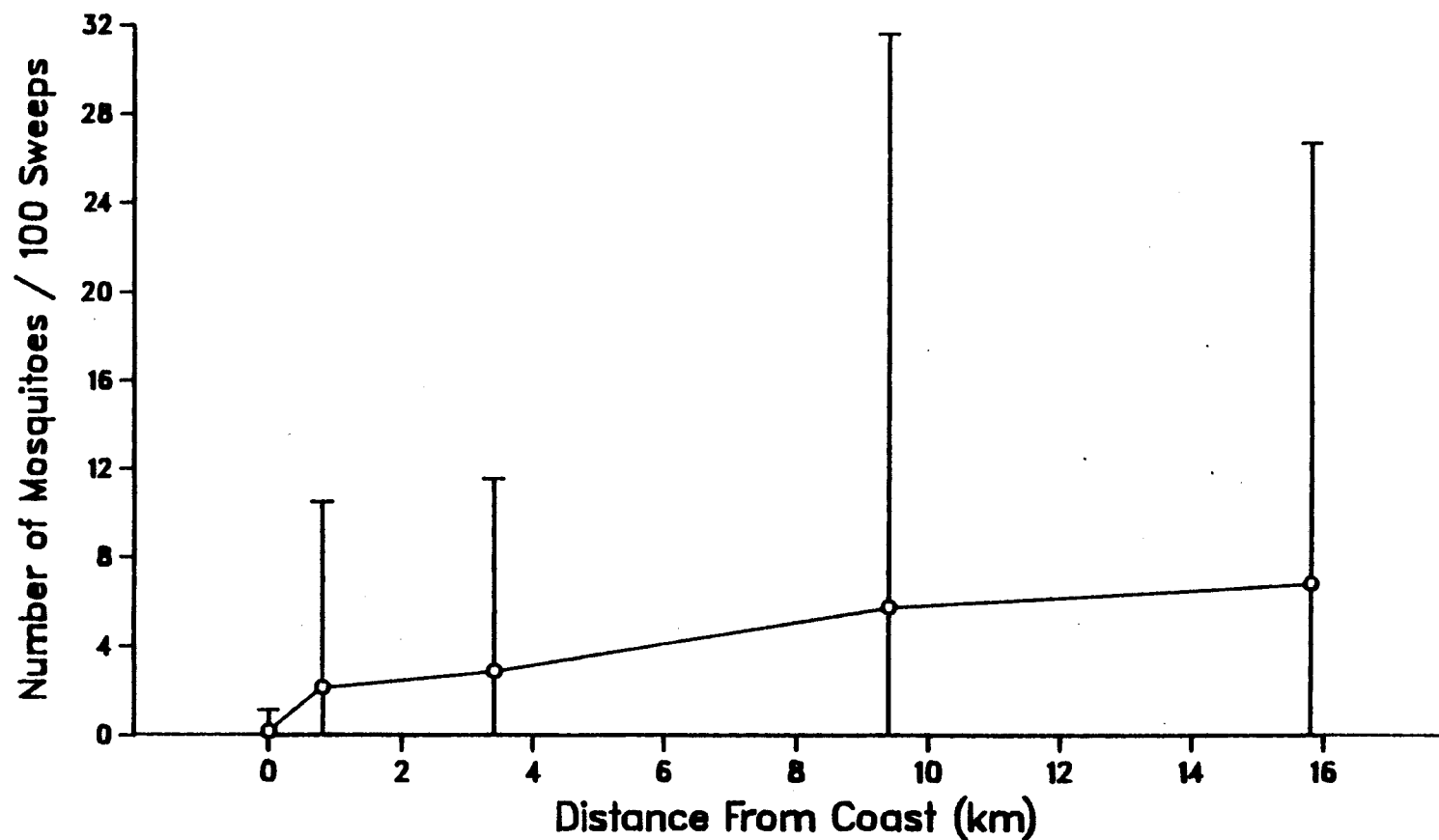


Figure 16. Mean (± 1 SD) number of mosquitoes captured per 100 sweeps in relation to distance from the Beaufort Sea near Milne Point, Alaska; 1982-83 (sample sizes for stations 1-5 reported in Table 4).

Mosquito Activity (Traps)

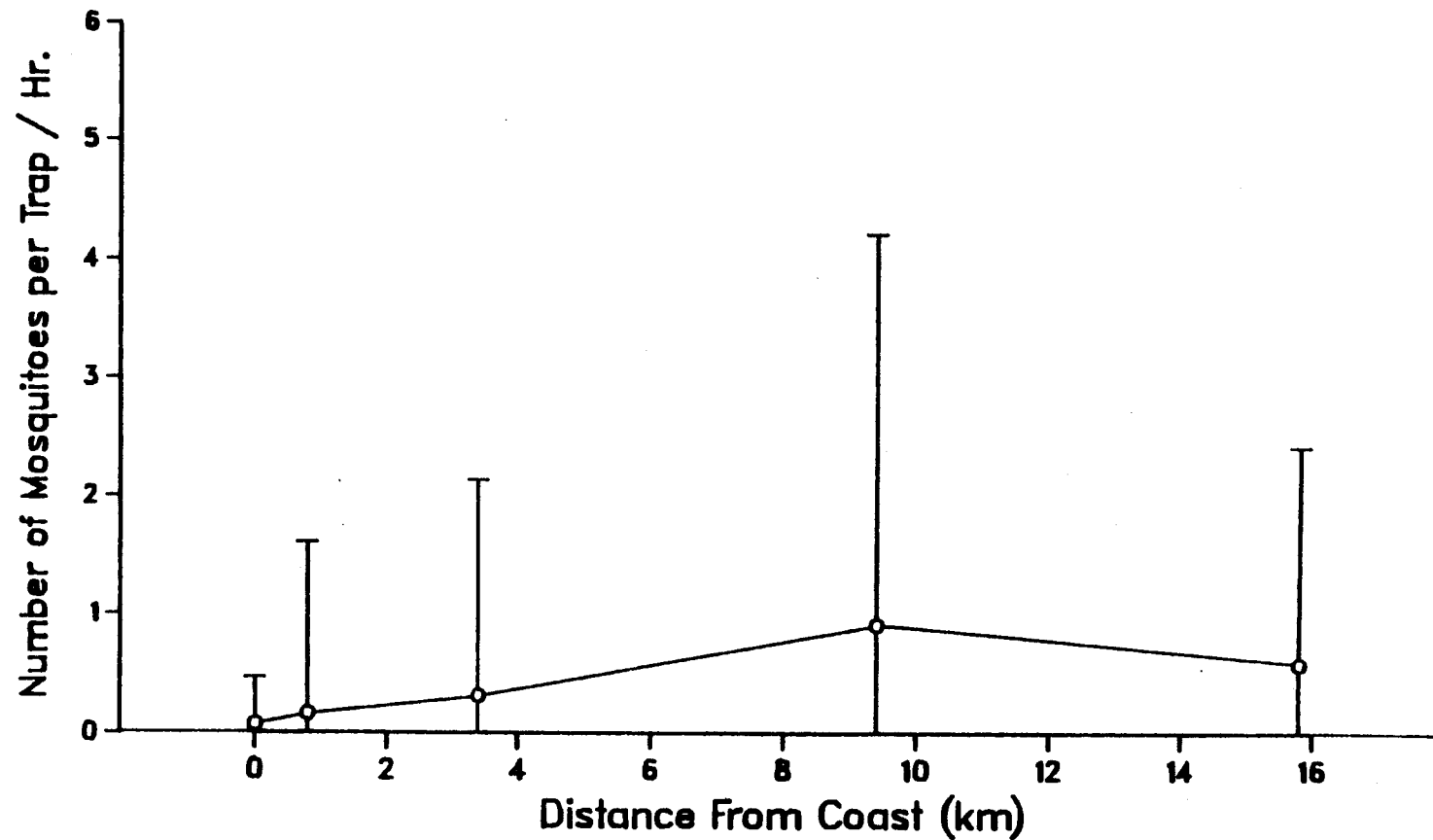


Figure 17. Mean (± 1 SD) number of mosquitoes captured per trap per hour in relation to distance from the Beaufort Sea near Milne Point, Alaska; 1982-83 (sample sizes for stations 1-5 reported in Table 4).

Oestrid Activity (Traps)

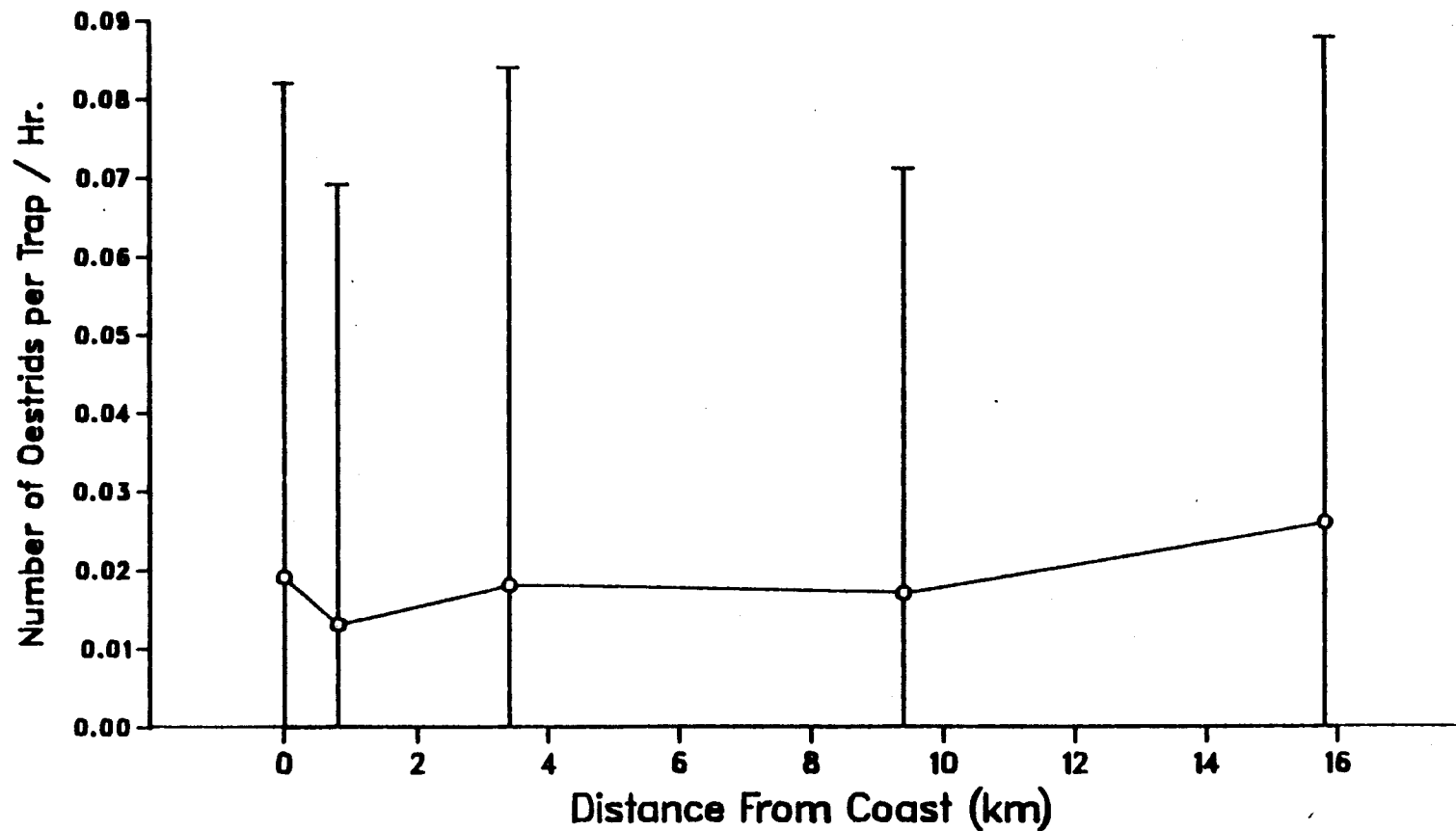


Figure 18. Mean (± 1 SD) number of oestrids captured per trap per hour in relation to distance from the Beaufort Sea near Milne Point, Alaska; 1982-83 (sample sizes for stations 1-5 reported in Table 4).

Table 7. Maximum and median levels of insect activity (for samples when insects were captured) at each sampling station; 1982-83.

Station	Mosquitoes (sweeps)		Mosquitoes (traps)		Oestrids (traps)	
	Median	Maximum	Median	Maximum	Median	Maximum
1	2	8	0.36	3.60	0.18	0.35
2	14	74	0.23	17.80	0.14	0.49
3	10	51	0.29	21.50	0.17	0.43
4	4	260	0.39	48.40	0.16	0.34
5	12	194	0.55	19.30	0.12	1.25
H ^a	7.24		4.67		4.62	
P-value	0.12		0.32		0.33	
n	148		216		76	

^a Kruskal-Wallis test statistic for the null hypothesis "no difference in median values among all stations"

Upper and lower thresholds of weather parameters for flight were similar among all measures of insect activity (Table 8). High ambient air temperature and atmospheric humidity never precluded insect activity. Mosquitoes and oestrid flies were caught across the entire range of cloud cover.

The median number of mosquitoes caught using sweeps conducted in the lee of the observers' vehicle (22, range 0-260, $n = 26$) was significantly greater than the median number of mosquitoes caught 50 m from the road (12, range 0-48, $n = 26$) (Mann-Whitney test, $0.025 < P < 0.05$). There was no difference in the median number of mosquitoes caught in the first vs. the second set of 50 sweeps (4 vs. 5; Mann-Whitney test, $P = 0.50$, n_1 and $n_2 = 26$).

Empirical models

Several trends are apparent in r^2 values for models predicting levels of insect activity from weather parameters (Table 9). The proportion of total variability in insect activity explained by weather parameters was usually lower when the data were restricted to cases when insects were present than when all cases were used. The high r^2 values for models using all cases, in comparison to models using only cases when insects were present, results at least partially from substantial disparities in sample sizes.

Pooling the data to create daily means of weather and insect activity for each station, and for each day (data pooled over all

Table 8. Thresholds of weather parameters for insect flight as determined by each index of insect activity; 1982-83.

Weather parameter	Mosquitoes (sweeps)		Mosquitoes (traps)		Oestrids (traps)	
	Lower ^a	Upper ^b	Lower ^a	Upper ^b	Lower ^a	Upper ^b
Current temp. (°C)	0	26	0	26	0	26
Maximum temp. (°C)	0	28	0	28	0	28
Minimum temp. (°C)	-1	22	-1	22	-4	20
Midrange temp. (°C)	0	25	0	25	0	25
Relative humidity (%)	24	100	41	100	41	100
Saturation deficit (mbar)	0	14.72	0	12.36	0	12.36
Wind velocity (m/s)	0	4.60	0	6.81	0	6.81
Cloud cover (%)	0	100	0	100	0	100
n ^c	727		727		727	

^a minimum value at which insects were caught

^b maximum value at which insects were caught

^c n = 667 for relative humidity and saturation deficit

Table 9. Coefficients of determination for multiple linear regression analyses estimating levels of insect activity^a, and the percentage of cases correctly classified for the presence of insects by discriminate analyses and logistic regression analyses (in parentheses); 1982-83.

Data set	Coefficients of determination for predicting levels of insect activity ^b						Percentage cases correctly classified for the presence of insects ^c		
	All cases			Cases when insects present					
	Mosq.'s (sweeps)	Mosq.'s (traps)	Oestrids (traps)	Mosq.'s (sweeps)	Mosq.'s (traps)	Oestrids (traps)	Mosq.'s (sweeps)	Mosq.'s (traps)	Oestrids (traps)
Individual samples (n)	0.43 (667)	0.21 (667)	0.22 (373)	0.29 (144)	0.24 (197)	0.08 (68)	85 (90) (667)	77 (78) (667)	84 (88) (373)
Daily station means (n)	0.58 (251)	0.32 (251)	0.30 (143)	0.38 (91)	0.40 (101)	0.14 (41)	85 (90) (251)	79 (79) (251)	80 (83) (143)
Overall daily means (n)	0.71 (55)	0.49 (55)	0.67 (31)	0.62 (33)	0.63 (35)	0.62 (17)	89 (93) (55)	76 (80) (55)	71 (87) (31)

^a log values used for each index of insect activity

^b weather parameters and their coefficients to predict daily mean levels of mosquito and oestrid activity are presented in Table 11

^c weather parameters and their coefficients to predict the presence of insects using logistic regression are presented in Table 10

^d Discussion section (Chapter 1) evaluates models using all days vs. models restricted to days when insects were present

stations), apparently damped the high variability in weather and insect parameters, and resulted in progressively higher r^2 values for models estimating levels of insect activity from weather parameters. However, pooling the data had little effect on the percentage of cases correctly classified by discriminant and logistic regression analyses for the presence or absence of insects. The percentage of cases correctly classified by discriminant and logistic regression analyses for the presence of insects, and r^2 values for models predicting levels of insect activity, were usually higher for sweep counts of mosquitoes than for trap counts of mosquitoes, or trap counts of oestrids.

Ambient air temperature was the most useful weather variable for predicting the presence of mosquitoes or oestrids using individual observations, while the log transformation of saturation deficit was the most important variable using data pooled by station, and by day (Table 10). Ambient air temperature and saturation deficit were also important variables for predicting levels of insect activity for periods when insects were active (Table 11).

Log transformations strengthened the relationships between indices of insect activity and weather parameters, and minimized the correlation between the variance of a dependent variable and size of an independent variable. However, I repeated the stepwise linear regression analyses using reciprocal values for daily averages of insect activity because it was not clear that mean levels of insect activity were linear functions of weather conditions. Reciprocal

Table 10. Weather variables (coefficients in parentheses) selected by stepwise logistic regression analyses to predict the presence of mosquitoes and oestrids (Tc = current air temperature ($^{\circ}\text{C}$); Tm = midrange air temperature ($^{\circ}\text{C}$); Wv = wind velocity (m/s); Wd = wind direction (degrees from true north); Cc = cloud cover (%); Lsd = log value of saturation deficit (mbar); Ldc = log value of distance from coast (km); Cnst = constant).

Data Set ^a	Mosquitoes (sweeps)	Mosquitoes (traps)	Oestrids (traps)
Individual observations	Tc (0.39) Wv (-1.42) Rh (-0.09) Ldc (1.23) Wd (-0.004) Cnst (4.72)	Tm (0.09) Ldc (1.99) Lsd (8.05) Rh (0.13) Wv (-0.23) Cc (0.006) Wd (-0.02) Cnst (-17.18)	Tc (0.19) Cc (-0.01) Wv (-0.25) Tm (0.12) Cnst (-4.37)
Cutpoints ^b n	0.542-0.558 667	0.375-0.392 667	0.658 373
Data pooled by sampling stations	Lsd (18.28) Wv (-1.34) Tm (0.23) Ldc (1.77) Wd (-0.004) Rh (0.24) Cnst (-27.91)	Lsd (22.92) Ldc (1.87) Rh (0.40) Tc (-0.22) Cnst (-42.25)	Lsd (14.96) Rh (0.22) Cnst (-26.10)
Cutpoints ^b n	0.592-0.608 251	0.342 251	0.258-0.275 143
Data pooled by day	Lsd (10.32) Tm (0.71) Cnst (-10.90)	Lsd (18.26) Rh (0.28) Ldc (-35.44) Cnst (0.00)	Lsd (7.74) Wv (-0.52) Cnst (0.00)
Cutpoints ^b n	0.258-0.292 55	0.208-0.458 55	0.508 31

^a Discussion section (Chapter 1) evaluates models using all days vs. models restricted to days when insects were present; the percentage of cases correctly classified by each model is presented in Table 9

^b insects are absent if the model produces a value < the cutpoint; the presence of insects is uncertain for values between the range of cutpoints

Table 11. Linear regression models to predict the average daily level of insect activity from daily means (all sampling stations combined) of weather parameters (Tc = current air temperature (°C); Tm = midrange air temperature (°C); Dc = distance from the coast (km); Wd = wind direction (degrees from true north); Wv = wind velocity (m/s); Cc = cloud cover (%); Rh = relative humidity (%); Sd = saturation deficit; Cnst = constant).

Data set ^a	Mosquitoes (sweeps) ^b	Mosquitoes (traps) ^c	Oestrids (traps) ^d
All days	Tc (0.06) Sd (0.10) Wd (-1.00) log Wv (-0.94) Cnst (-0.06)	Tm (0.04) log Dc (-0.59) Cnst (0.16)	Sd (0.12) Cnst (-0.02)
S.E.E ^e	0.26	0.14	0.01
n (days)	55	55	55
Days when insects present	log Tm (3.21) Wv (-0.22) Cnst (-2.31)	Tm (0.06) Sd (-0.16) Cc (1.00) log Dc (-1.66) log Rh (-7.44) Cnst (5.51)	Sd (0.01) log Cc (-0.01) Cnst (0.02)
S.E.E ^e	0.30	0.14	0.01
n (days)	33	35	17

^a Discussion section (Chapter 1) evaluates models using all days vs. models restricted to days when insects were present; coefficient of determination (r^2 value) for each model is presented in Table 9

^b log (number of mosquitoes/100 sweeps)

^c log (number of mosquitoes per trap/hour)

^d log (number of oestrids per trap/hour)

^e standard error of the estimate

transformations are appropriate when variances of dependent variables are proportional to independent variables, and the means of dependent variables fall on a curve (Neter and Wasserman 1974). Multiple linear regression models predicting levels of insect activity using reciprocal transformations of the independent variables resulted in lower r^2 values than those obtained using log transformations for all days, and for days when insects were caught.

I conducted two canonical correlation analyses to investigate the relationship between the set of variables that described weather, and the three indices of insect activity (data pooled over all samples and stations by day). For the first analysis, raw values for each index of insect activity were used; for the second analysis, log transformations of these parameters were employed. Both analyses showed a significant canonical correlation between the set of variables describing weather, and the three indices of insect activity (Table 12). However, a higher proportion of the total variability in insect activity was explained by the first pair of canonical variables (0.74 vs. 0.55) when log transformations of insect activity were used instead of raw values.

I included both the raw and log values of weather variables in the initial canonical correlation analysis using log values of insect activity. Surprisingly, the correlations between log values of the individual weather parameters and the canonical variable describing insect activity were no stronger than corresponding correlations with raw values of weather variables. However, when both the raw and log

Table 12. Test results for the selection of canonical variables for weather variables and indices of insect activity (data pooled over all samples and stations by day, and restricted to days when insects were present; n = 31).

Null hypothesis	Raw values of insect activity				Log values of insect activity			
	Chi-squared	df ^a	P-value	r ^{2b}	Chi-squared	df ^a	P-value	r ^{2b}
No linear relationship	51.71	30	0.008	0.55	81.23	30	<0.001	0.74
Two canonical variables no better than one canonical variable for describing the relationship between weather factors and insect activity.	14.03	18	0.73	0.19	17.54	18	0.48	0.24
Three canonical variables no better than two canonical variables for describing the relationship between weather factors and insect activity.	4.02	8	0.86	0.08	4.47	8	0.81	0.09

^a degrees of freedom

^b squared canonical correlation coefficient; indicates the proportion of total variability in the relationship between weather factors and indices of insect activity explained by the canonical variables

values of weather parameters were included in the analysis, two pairs of canonical variables were significant, and 92% of the total variability in insect activity was explained. When only raw values of weather parameters were used in the analysis, 74% of the total variability in insect activity was explained, and only one pair of canonical variables was significant.

The canonical correlation analyses show that maximum and midrange ambient air temperatures, and saturation deficit, were most highly correlated with indices of insect activity. Sweep counts of mosquitoes were correlated most strongly with weather parameters, and both measures of mosquito activity were more closely correlated with weather than trap counts of oestrids (Table 13).

Table 13. Correlations between the original variables and canonical variables for weather parameters (including distance from the coast) and indices of insect activity (data pooled over all samples and stations by day, and limited to days when insects were present; $n = 31$).

Original variable	r^a	r^2^b	P-value ^c	Coefficients for canonical vars.
Distance from coast (km)	0.04	0.06	0.33	-0.02
Current temp. (°C)	0.89	0.59	<0.001	-0.08
Maximum temp. (°C)	0.94	0.66	<0.001	-1.11
Minimum temp. (°C)	0.84	0.54	<0.001	-1.17
Midrange temp. (°C)	0.93	0.65	<0.001	2.50
Relative humidity (%)	-0.80	0.47	<0.001	-0.01
Saturation deficit (mbar)	0.90	0.60	<0.001	0.26
Wind direction (degrees)	-0.09	0.04	0.58	-0.001
Wind velocity (m/s)	-0.47	0.20	0.01	-0.21
Cloud cover (%)	-0.44	0.20	0.01	0.002
Mosquito activity _d (no./100 sweeps)	0.98	0.72	<0.001	1.75
Mosquito activity _d (no. per trap/hr.)	0.74	0.49	0.01	1.98
Oestrid activity _d (no. per trap/hr.)	0.54	0.28	0.17	-8.12

^a correlation between the original variable and its canonical variable

^b squared multiple correlation between the original variable and all variables in the other set

^c P-value for squared multiple correlation coefficient

^d log values of insect activity used

Discussion

Relationships between weather and insect activity

Differences between 1982 and 1983 in the distributions of weather parameters and indices of insect activity were probably an artifact of large sample sizes rather than an indication of biologically significant variability. The magnitude of differences between years in median levels of individual weather parameters was small in relation to their respective ranges. Also, the dispersion of data around median values was not substantially different between years, even for relative humidity and saturation deficit which exhibited significant differences in distributions not attributable to disparities in the location of medians.

The absence of a simple linear relationship between any combination of a weather parameter and an index of insect activity is not surprising. To my knowledge, all investigations of weather-insect relationships have shown insect activity to be a function of at least two weather factors (Hocking et al. 1950; Gjullin et al. 1961; Thomson 1973 as reported by Thomson 1977; Curatolo 1975; White et al. 1975, 1981; Roby 1978). Air temperature and wind velocity have been identified as important determinants of insect activity (Thomson 1971; White et al. 1975), although there is no consensus regarding which other weather factors are most influential.

The measure of insolation used in this study did not reflect the diel periodicity of this variable, or show differences in light intensity attributable to changes in cloud cover. Reports regarding the effects of insolation on mosquito activity do not all agree (e.g., Gjullin et al. 1961; Hocking et al. 1950). Without exception though, sunlight has been found to strongly affect the activity of oestrids (Skjenneberg and Slagsvold 1968; Kelsall 1975; White et al. 1975; Downes et al. 1985). The omission of a direct measure of insolation from the final analyses was somewhat ameliorated by the inclusion of cloud cover; however, this latter variable did not reflect the circadian periodicity of light cycles. Also, the effects of cloud cover on incoming solar radiation were confounded by the type(s) and altitude of clouds, and the angle of incidence for sunlight.

I also omitted maximum and minimum air temperatures from the final model-selection processes to avoid obscuring any significant relationships between insect activity and weather parameters with redundant measures of temperature, and to minimize the effects of multicollinearity among weather factors (Neter and Wasserman 1974). I retained current and midrange temperatures because the periods over which these measures were recorded best agreed with sweep and trap counts, respectively. Also, "F to enter" statistics for maximum and minimum temperatures were usually low in initial stepwise linear regression analyses. However, models predicting the presence of insects, and their levels of activity, may have been more sensitive

to threshold effects of temperature on insect activity if I had included maximum temperature as a potential independent variable.

I calculated saturation deficit in response to the report by Hocking et al. (1950) that dessication is a principal factor limiting mosquito activity, and that relative humidity fails to show this effect. In contrast to the report by Hocking et al. (1950), the activity of mosquitoes, and oestrids, was positively related to saturation deficit. This was probably because the abundance of surface water in the area maintained chronically high levels of atmospheric humidity. Humidity, even at the lowest levels observed during this study, probably remained above lower critical levels for insect flight. Regional differences in prevailing levels of atmospheric moisture may be responsible for the disparity between my results and those of Hocking et al. (1951).

Seasonal patterns of activity of alate mosquitoes and oestrids generally agreed with the range of dates reported in the literature (Hadwen and Palmer 1922; Hadwen 1927; Savel'ev 1968; Curatolo 1975; White et al. 1975, 1981; Roby 1978). Mosquitoes appeared two to four weeks before oestrids were consistently observed, although oestrids were caught as early as 4 July (1982). The appearance of oestrids on 4 July supports the hypothesis that oestrids are active during early summer (Boertje 1981); however, oestrid activity is certainly low during this time. Nose bots did not appear before warbles as reported by Savel'ev (1968) and Skjenneberg and Slagsvold (1968). In 1982, both species of oestrids were first caught on 25

July; in 1983, warbles were caught six days before bots. This lag in date of emergence for bots may have been due to low trap counts for oestrids.

In both years, the regular sampling scheme was terminated before mosquitoes or oestrids completely disappeared. The infrequent capture of mosquitoes or oestrids during the last week of sampling, and the low levels of activity when they were present, suggest that the period of peak insect activity was over before sampling ceased during each year. Data collected during late July and early August (Figures 4-6), and opportunistic observations made between 19-26 August of each year, support other reports that oestrids remain active later into summer than mosquitoes (Roby 1978). Oestrid pupae or imagoes may be better adapted to survive periods of unfavorable weather than mosquitoes, and thus retain the capacity to capitalize on the few marginally suitable days for activity that occur during autumn. However, since mosquitoes can be active within 20 km of the Beaufort Sea as late as 2 September (W. Smith, personal communication), the extended period of low and infrequent oestrid activity, as compared to mosquitoes, may be attributable to a wider range of weather conditions suitable for flight than a superior ability to survive inclement conditions. Although my results indicate that there was little difference between mosquitoes and oestrids in thresholds for flight, this may have been attributable to the insensitivity of traps to low levels of insect activity. In other words, oestrids were probably active during periods of less

favorable weather than mosquitoes were, but I was unable to detect their presence at such low levels of activity.

The peak in sweep counts of mosquitoes that occurred on 14 July 1982 was not indicated by trap counts for reasons unknown. With that single exception, peak trap counts of mosquitoes lagged one day behind peaks in sweep counts during both years. An explanation of this one day lag requires an understanding of the components that determine the number of adult insects caught per sample; these are: (1) size of the insect population, (2) the fraction of the population that is flying, and (3) the total time spent capturing insects during each sample.

Johnson (1969) suggested that it was possible to discern between the first two components of total catch by manipulating the period over which samples are pooled. Johnson proposed that long-term (ca. 3-5 d) moving averages of insect samples reflect the population (numeric) response by insects to prevailing weather conditions; he implied that short-term changes in weather have no net effect on population size since favorable periods of short duration are negated by brief unfavorable intervals. Conversely, the number of insects captured during any single sample of short duration (ca. 1 h) is highly influenced by the proximal effects of weather conditions on the proportion of the population that is active when the sample is collected. The difference between the number of insects caught in any one sample of short duration and the associated moving average represents the functional response of insects to current weather

conditions.

The flaw in this logic lies in the dependence of the long-term, numeric response of insects to weather, on the short-term measure of insect activity. For example, if insects are active and the total catch varies over time, some proportion of the change in total catch can always be attributed to both the functional and numeric responses of insects to weather conditions even if the population size remains constant. Similarly, the relative contribution by each component of total catch would vary with the interval over which the moving average was determined.

Conceptually, Johnson's (1969) logic regarding the functional and numeric components of total insect catch is sound, but the lack of independence between the measures he used to distinguish between these components is a serious shortcoming. It may be possible to separate the functional and numeric responses of insects to weather using two independent samples collected over long and short time intervals, respectively. This would shift the emphasis from the period of time over which the data were pooled to the duration of each sampling period. Superimposing plots of these variables through time could then indicate the relative contribution to total catch made by each of these components. Smoothing functions would not affect the contribution by each type of response so long as each component was treated similarly.

Traps sampled 6-12 h periods, a considerably longer period of time than the 100 s required to conduct a sweep count. Thus, trap

counts probably reflected the population response of mosquitoes to prevailing weather conditions to a greater extent than did sweep counts. The one day lag of peak trap counts behind peak sweep counts may reflect the time required to warm small larval rearing ponds and stimulate the emergence of adult mosquitoes. The extremely low volume of water (ca. 0.4 m^3) and shallow nature (ca. 0.1 m) of many small pools in which mosquito larvae were observed suggests that water temperature could quickly change in relation to air temperature. Also, since species of mosquitoes adapted to tundra regions show no lag between the time of emergence and flight (Hocking et al. 1950), a rapid numeric response by mosquitoes to favorable weather conditions indeed seems likely.

Adult mosquitoes are capable of dispersing 40-80 km over a four to six week period (Gjullin et al. 1961); intuitively, such movements could be facilitated via the physical transport of mosquitoes by breezes below velocities that would preclude flight. However, the independence of sweep and trap counts of mosquitoes with wind direction, and a similar report that neither on- nor offshore winds influenced the number of mosquitoes captured in Manitoba (Hocking et al. 1950) indicates that wind is probably not an important mode of transport for mosquitoes in coastal tundra regions. This may be because breezes in tundra areas, especially near the coast, tend to occur above threshold limits for flight. Wind velocities were typically far above the 0.25 m per s threshold which reportedly reduces mosquito activity by 75%, and were also far above

the 1-2 m per s cruising speed reported for mosquitoes (Snow 1976; Bidlingmayer et al. 1985). Even allowing for the higher tolerance of tundra-dwelling mosquitoes to wind (Gjullin et al. 1961), it is obvious that wind velocities were consistently above levels that limit flight. Also, since air temperatures in the study area were usually only marginally favorable for flight, and because wind has a proportionately greater effect on insect activity at temperatures approaching lower threshold limits for flight (Gjullin et al 1961), wind probably functioned more to preclude the activity of insects altogether than to influence levels of activity, or affect the direction of flight (Snow 1976).

I suspect that wind from the south had a profound effect on insect activity by raising ambient air temperature. This effect was not evident in my results because I recorded wind direction over a short period (60 s). Wind from the south had no effect on insect activity unless it prevailed long enough to move warm, inland air masses to the coast; however, onshore winds quickly lowered ambient air temperature, and hence insect activity.

Sweeps and traps showed at least two peaks in mosquito activity during 1982, and one peak in 1983 (Figures 3-5). The unimodal distribution and high peak level of mosquito activity in 1983 probably occurred because conditions of each weather factor conducive to flight (e.g., high air temperature and low humidity) coincided during 1983, but were asynchronous in 1982 (Figures 6-10). At least three species of Aedes occur near Prudhoe Bay (A. cataphylla, A.

nigripes, and A. impiger; MacLean 1975). The multiple peaks in mosquito activity during 1982 may be due to the sequential emergence of different mosquito species (Hocking et al. 1950); however, this is unlikely (MacLean, personal communication). The single occurrence of weather conditions favorable for insects in 1983 may have severely limited the activity of one or more species of mosquitoes (e.g., species that emerge early or late in summer), and disproportionately facilitated the activity of other species; or, it may have caused the concurrent emergence of several species.

Oestrid activity peaked within one day of peak sweep or trap counts of mosquitoes. Thus, weather conditions favorable for flight are similar between mosquitoes and oestrids, even though differences may exist in their respective tolerances to marginal weather conditions (Roby 1978; White et al. 1975).

In 1982, the relative magnitude of peaks in mosquito activity was reversed between sweep and trap counts (Figures 3-5). The primary peak in sweep counts of mosquitoes occurred on 20 July with a secondary peak during 24-25 July. Maximum trap counts of mosquitoes occurred during 25-26 July, while a less pronounced peak occurred on 21 July. If the difference between sweep and trap counts of mosquitoes reflects the proximal effects of weather on insect activity as suggested by Johnson (1969), then the high peak in sweep counts that corresponds with a secondary peak in trap counts indicates that a high proportion of small population was active during 20-21 July. This implies that weather conditions were

extremely favorable for flight at this time. Conversely, the high trap counts and relatively low sweep counts that occurred during 24-26 July suggests that a small proportion of a large population was active, perhaps in response to marginally suitable conditions for flight. Weather conditions certainly appear to have been more favorable for flight during the first, rather than second, peak in mosquito activity. However, the absence of any measure of population size makes it impossible to determine whether reversals in primary and secondary peaks between sweep and trap counts were attributable to functional and numeric responses of mosquitoes to weather, or merely an artifact of chance.

More mosquitoes and oestrids were captured on days of peak activity in 1983 than in 1982; also, mosquitoes and oestrids were caught on a greater proportion of days in the latter year. The higher proportion of days on which mosquitoes were captured was partially due to the higher level of trapping effort expended in 1983 as compared to 1982. In 1983, trap data were collected to allow direct comparisons of trap catches between years. The 1983 subsample of trap data collected with the same sampling intensity as in 1982 shows that mosquitoes were caught, by traps or sweeps, on 26 of 33 days (73%), while oestrids were caught on 13 of 33 days (39%). This represents a 12% decrease (85 vs. 73%) in the proportion of days that mosquitoes were caught at the 1982 level of trapping effort during 1983; there was no difference in the proportion of days on which oestrids were captured between the two levels of sampling

effort in 1983. Even so, the proportion of days when mosquitoes were captured during 1983 remained higher than that for 1982 (73 vs. 64%), even after eliminating disparities between years in trapping effort. More importantly, this indicates that the level of trapping effort expended in 1982 was probably inadequate to accurately reflect mosquito activity, and raises the possibility that even the higher trapping effort employed in 1983 may have been inadequate for estimating mosquito activity. Even so, mosquitoes were active on a considerably higher proportion of days than reported by White et al. (1981), and Thing and Thing (1983), but these proportions agree closely with the 60-61% reported by Thomson (1977) for Norway (Hardangervidda). Thomson also noted that there is considerable annual variation in the proportion of days when insects are active; this is reportedly due to long-term (i.e., annual) variability in precipitation (Gjullin et al. 1961).

Cumulative effects of slight differences between 1982 and 1983 in individual weather factors cannot explain differences in the frequency or magnitude of peaks in insect activity. In 1983, any benefit to insects from lower median cloud cover and atmospheric moisture was countered by lower ambient air temperature and higher wind velocity. Therefore, the high proportion of days when insects were active, and the high maximum levels of activity observed in 1983, were probably attributable to the concurrence and persistence of conditions favorable for insect emergence and flight (Taylor 1963; Kelsall 1975).

The pattern of low ambient air temperature, high wind velocity, and high atmospheric humidity near the coast is consistent with other reports regarding spatial patterns of weather on the Arctic Coastal Plain (Russell 1976; Moritz 1977; Haugen and Brown 1980). Kozo (1977) reported that the zone of maritime influence extends 37 km inland from the Beaufort Sea, and Russell (1976) indicated that the Beaufort Sea has a negative effect on insect activity up to 30 km from the coast. However, Figures 11-14 and 16-18 indicate that the area of functional importance to mosquitoes, oestrids, and hence caribou, is much narrower. The positive relationship between the proportion of days when mosquitoes were caught and distance from the coast supports this observation (Figure 15).

Weather conditions were indeed less favorable for insect activity near the coast than in inland areas (Table 5), but were more variable through time than through space (Figures 11-14). The slight difference in weather conditions within 1 km of the coast, in relation to the large temporal variability in weather, had a profound effect on the frequency of insect activity at the coast because weather conditions were rarely more than marginally favorable for flight, even in the southern portion of the study area. The difference in weather conditions between station 1 and stations 2-5 may have been attributable to annual differences in weather conditions since station 1 was not established until 1983. However, considering the between-year differences in weather conditions at stations 2-5, this seems highly unlikely.

The close similarity in weather parameters between coastal and inland stations when mosquitoes were active at stations 1 and 2 (Table 6) indicates that mosquitoes were active at the coast in response to a northward shift in favorable weather conditions from inland areas, rather than in response to regional changes in weather that affected all stations proportionately.

Oestrids were less affected by coastal weather conditions than mosquitoes (Figures 15-18). The relatively large body mass of oestrids, in comparison to mosquitoes, may act as a thermal reservoir, and undoubtedly counters the effects of wind. The presence of hair on the thorax probably retards heat loss as well. Strong flight capabilities, behavioral adaptations (e.g., basking, inhabiting sheltered areas, and limiting flight to within 1 m of the ground), the possible production of metabolic heat, and broad thresholds to initiate and maintain flight (Johnson 1969; Oke 1978) may also enable oestrids to harass caribou in coastal regions that are unsuitable for mosquitoes.

Mosquitoes rely on visual stimuli, local carbon dioxide gradients, and warm, moist, convective air currents to locate their hosts (White et al. 1975; Snow 1976). Anderson and Olkowski (1968) reported that adult Cephenemyia females are attracted by carbon dioxide, but do not respond to visual stimuli; however, it appeared that oestrids use visual cues to some extent in the final location of hosts. In any event, it is not clear whether oestrids are better able to "track" caribou to the coast than mosquitoes.

Thresholds of weather for mosquito activity were similar between sweep and trap counts (Table 8). Where discrepancies between threshold values do exist (e.g., for relative humidity, saturation deficit, and wind velocity), values identified using sweep counts are probably the most accurate since they sampled a smaller time interval. Similarly, current temperature should best reflect the lower critical temperature for mosquito or oestrid activity since it is based on an instantaneous measurement. Therefore, current temperature, and values identified using sweep counts of mosquitoes, are used for comparison with corresponding values in the literature.

Thresholds of weather identified for oestrid activity are probably inaccurate for two reasons. I was not able to detect oestrids on a point-in-time basis, and weather conditions varied within the 6- to 12-h between trap checks; therefore, up to 5-6 h could separate the time when oestrid activity ceased and when weather information was recorded. Also, traps probably failed to detect oestrids at low levels of activity (see also Chapter 2); if so, then the threshold values reported here are conservative.

The minimum air temperature at which both mosquitoes and oestrids were caught (Table 8) was substantially lower than the 6-8°C threshold reported for oestrids (Kummeneje 1980; White et al. 1981; Downes et al. 1985), and somewhat lower than the 4.4 C reported for mosquitoes of tundra regions (Gjullin et al. 1961). The maximum wind velocity at which mosquitoes were captured is similar to the 4.5 m per s reported by Gjullin et al. (1961). The upper limit of wind

velocity for oestrids (6.81 m per s) was well below the 8-9 m per s reported by Kelsall (1975); this may have been due to the synergistic effect of wind and ambient air temperature on oestrid activity in the study area.

As noted by Curatolo (1975), the strong correlation between atmospheric humidity and air temperature (Table 2) makes it difficult to separate their respective effects on insect activity.

Consistently high levels of humidity in the study area probably released mosquitoes and oestrids from the effects of dessication and enabled them to respond primarily to air temperature. Although minimum thresholds of relative humidity and saturation deficit are reported for mosquitoes and oestrids (Table 8), they represent the lower range of these variables recorded during the study rather than a functional limit for insect activity. Oestrids did not exhibit an upper tolerance to relative humidity, whereas Kelsall (1975) reported that oestrids were not active when relative humidity exceeded 89%. Cloud cover alone never precluded the activity of either mosquitoes or oestrids. The effects of clouds on insect activity are probably manifested through air temperature and insolation.

The significantly greater number of mosquitoes caught using sweep counts conducted in the lee of the observer's truck, as compared to sweeps conducted in the tundra, indicates that: (1) the truck provided a windbreak that allowed mosquitoes to closely approach the observer, (2) the heat and human odors associated with the vehicle attracted mosquitoes, or (3) the truck was an effective

visual attractant for mosquitoes (Day and Edman 1984; Bidlingmayer et al. 1985). If the vehicle did act as an attractant, I doubt that its presence altered the relationship between mosquito activity and any weather factor except possibly wind velocity. Even so, groups of caribou probably have a similar wind-break effect on mosquito activity. However, the effects of the truck on the activity of insects cannot be directly extrapolated to the effects of caribou groups since the truck created a highly artificial situation. The most serious shortcoming of this capture technique lies in its unfeasibility for remote regions where similar objects may not be available.

The absence of a significant difference in the number of mosquitoes caught between the first and second sets of 50 sweeps suggests that: (1) mosquitoes quickly reached an upper level of aggregation around the person collecting the sample; (2) the 2-5 minutes separating the first and second sets of sweeps were insufficient to allow mosquitoes to aggregate; or (3) sweep counts conducted in the tundra failed to show actual differences in the number of mosquitoes present.

Empirical models

Several assumptions for multiple linear regression analysis were not met during the modeling process. Frequency distributions, and the third and fourth powers of variance for each parameter, indicated

that all variables exhibited skewness or kurtosis. This was corroborated by the stronger correlations obtained using rank vs. linear correlation coefficients, and by the higher percentage of cases correctly categorized for the presence of mosquitoes or oestrids using logistic regression vs. discriminant analyses. Since the variables were not distributed normally, median values would probably have provided better estimates of average insect activity when the data were pooled over stations and samples; however, deriving median values for entire data sets was unfeasible with the statistical software available.

Durbin-Watson statistics (Neter and Wasserman 1974) indicated that individual observations of weather parameters and insect activity were serially correlated. However, pooling the data over all samples and stations by day made the effects of autocorrelation nonsignificant for models discriminating between the presence and absence of insects, and models predicting levels of insect activity.

Multicollinearity among weather variables was evident at all levels of the analyses. This was indicated by the large standard errors associated with regression coefficients for weather parameters selected by stepwise multiple linear regression processes to estimate levels of insect activity, and the marked change in regression coefficients with the addition or deletion of independent variables (Neter and Wasserman 1974). In addition, the rank correlations between weather factors (Table 2) indicate strong interrelationships (see also Curatolo 1975; Roby 1978). Multicollinearity among weather

factors renders the regression coefficients for individual weather parameters meaningless in a biological sense (Neter and Wasserman 1974). Thus, the effects of weather on the activity of insects can be evaluated only in terms of the entire set of variables included in the model. However, multicollinearity does not preclude fitting an accurate line through a linear relationship, nor does it prevent making inferences about that relationship within the range of values observed.

The high r^2 values obtained using data pooled by day over all stations, as compared to individual measurements and even daily means of weather and insect parameters for each station, undoubtedly stem in part from the inverse relationship between accuracy of prediction and generality of the model. The tendency for r^2 values to increase with progressive pooling of data may have a biological basis as well. Individual measurements of weather parameters were instantaneous estimates of climatic conditions at each station, conditions that continuously changed through space and time. Insects were probably less responsive to changes in weather conditions than the instruments used to measure these factors; therefore, insects may have responded to prevailing weather conditions on a more regional basis than measured by instantaneous samples. This is not to say that mosquitoes or oestrids were incapable of responding to weather over time periods shorter than 24 h, or over regions smaller than the study area. The high r^2 values for models based on regional daily means of weather and insect parameters may indicate the level of

analysis at which the responsiveness of mosquitoes and oestrids to weather agreed with my ability to show changes in these variables.

Coefficients of determination for models predicting levels of insect activity were usually lower when the data were restricted to periods when insects were present than when all cases were used (Table 9). This disparity in r^2 values between the two modeling approaches (i.e., using all cases vs. only cases when insects were present to predict levels of insect activity) is probably the result of differences in sample sizes. The two-stage approach discriminating between the presence and absence of insects, and then predicting the level of insect activity when insects were present, is more plausible than using all cases to predict levels of insect activity despite differences in r^2 values. Beyond threshold conditions for flight, weather did not affect the number of airborne mosquitoes or oestrids (i.e., the level of insect activity reached a lower asymptote of zero). Predicting levels of insect activity for periods when insects were present focused on the range of conditions in which insects responded to changes in weather. Therefore, the two-stage approach predicting the presence of insects, and then their level of activity when insects were present, is probably "best." Estimates of insect activity are most reliable when used with data pooled over all samples and stations by day.

Several probable sources of residual error for multiple linear regression models predicting levels of insect activity from weather parameters (e.g., some behavioral and physical attributes of insects)

have been previously noted. Other potential sources of error include: (1) effects due to the rate and direction of changes in weather factors (Taylor 1963); (2) deviations from average levels of precipitation on an annual basis (Gjullin et al. 1961); (3) the age structure of insect populations (Johnson 1969); (4) the effects of barometric pressure (Burnett and Hays (1974); and (5) local suitability of habitat for larval and adult insects.

The tendency for both the raw and log values of individual weather parameters to enter initial multiple linear regression models suggests that trap counts of mosquitoes and oestrids approached exponential relationships with certain weather variables, but had linear components as well. There is no evidence to indicate that such a response is biologically impossible. However, the increase in percentage of total variability explained by these unorthodox models must be evaluated against the possibility of merely fitting a mathematical model to this particular data set. The accuracy of each type of model should be determined using an independent set of data.

Results of the canonical correlation analyses are consistent with the relationships shown for individual weather parameters and estimates of insect activity. Sweep counts of mosquitoes were more highly correlated with weather parameters than either trap counts of mosquitoes, or trap counts of oestrids; measures of ambient air temperature and atmospheric humidity were the dominant weather factors influencing insect activity. The relationship between ambient air temperature and atmospheric humidity may have been strong

enough to cause relative humidity and saturation deficit to be significant even if temperature was actually the primary factor driving insect activity.

CHAPTER 2. EFFECTS OF INSECT HARASSMENT ON THE DISTRIBUTION AND BEHAVIOR OF CARIBOU

Introduction

The CAH is a distinct subpopulation of caribou that ranges between the Canning and Colville Rivers (Cameron and Whitten 1979). In 1983, the CAH numbered approximately 13000 caribou, of which 5000-6000 occurred in the vicinity of the study area (W. Smith, unpublished data). Throughout July and early August, CAH caribou inhabit the Arctic Coastal Plain and exhibit daily, insect-induced movements between coastal insect-relief terrain and inland foraging areas (White et al. 1975, 1981; Thomson 1977; Roby 1978).

During summer, caribou in northern Alaska are harassed by a variety of alate insects (Chapter 1). The effects of these insects on the distribution and behavior of reindeer (R. t. tarandus) and caribou have been widely documented (e.g., Pruitt 1960, Skoog 1968; Skjennneberg and Slagsvold 1968; Thomson 1977; Thing and Thing 1983). However, most of these reports have been largely qualitative, and have mainly described temporal patterns of insect abundance throughout summer (e.g., Savel'ev 1968), general trends in the size and movements of Rangifer groups in response to insect harassment (Reimers 1977), and behavioral reactions of individual reindeer and caribou to insect attack (Hadwen 1922; Hadwen and Palmer 1927).

Recently, more rigorous examinations of caribou response to insect harassment have been reported (Curatolo 1975; White et al. 1975, 1981; Russell 1976; Thomson 1977; Roby 1978; Wright 1979, 1981). However, with the exception of work conducted by Helle and Aspi (1983) on simuliid and tabanid parasites of Finnish reindeer, and current investigations being conducted by Pank et al. (1984) and Nixon (personal communication) in northern Alaska and Canada, no examination of insect-caribou ecology has employed quantitative estimates of insect activity. Instead, qualitative, categorical estimates of insect activity have been used to examine the effects of insect harassment on caribou. These estimates have often been determined in part from the behavior of caribou themselves (e.g., Curatolo 1975) which has limited an evaluation of the relative effects of harassment by each type of parasite on the overall and individual responses of caribou.

The objective of this portion of the study was to determine the effects of harassment by mosquitoes and oestrids on the distribution and behavior of barren-ground caribou on the Arctic Coastal Plain of Alaska. Levels of insect activity and measures of caribou response are plotted through time. Hypotheses are tested using quantitative estimates of insect activity and caribou response. Correlations between sets of variables describing insect activity, weather factors, and caribou response are examined. Descriptive observations regarding the behavior of attacking oestrids and responses by caribou are included.

Methods

Site characteristics, access, sampling periods, and measurements of weather and insect activity are described in Chapter 1. Sweep net counts of mosquito activity are used in all analyses unless specified otherwise.

Two types of surveys were used to monitor the distribution and behavior of caribou: (1) standard surveys and, (2) grid surveys. Standard surveys were conducted to determine the distribution of caribou along the entire westernmost section of the Milne Point road system (Figure 2), and to provide a large sample of observations for describing the distribution and behavior of caribou. Grid surveys were conducted to determine the rate of travel for caribou groups, and to provide detailed information on the behavior of individual caribou within groups. In addition, aerial reconnaissance flights of the study area were conducted by fixed-wing aircraft roughly each week.

Standard surveys were conducted along the entire Milne Point road system daily between 1100 and 1400 h, and between 1900 and 2200 h. Surveys were conducted by 1 or 2 observers in a pickup truck at speeds less than 48 km per hour. For each group of caribou sighted (group defined as one or more caribou separated by < 300 m), the vehicle was stopped at a point approximately perpendicular to the center of the group, and the caribou were observed using binoculars or a spotting scope. The following variables were recorded for each

group of caribou observed: (1) date, (2) time, (3) road location (km), (4) total number of caribou, (5) number of adults (caribou > 12 months old), (6) number of calves (caribou < 12 months old), (7) number of caribou of unknown age, (8) predominant activity of the group (lying, standing without feeding, feeding, walking without feeding, trotting, running, nursing-licking), (9) direction of travel (degrees from true North to the nearest 45 degrees), and (10) group density (estimated average distance between individuals; 4 subjective categories: < 3 m, > 3 to < 15 m, > 15 to < 50 m, > 50 to < 300 m).

Data used to examine the effects of insect harassment on the distribution of caribou in relation to the coast were limited to observations recorded along the westernmost section of the Milne Point road system. Observations of caribou that overtly reacted to a human disturbance were excluded from all analyses. Likewise, groups with individuals whose age could not be determined were excluded from examinations regarding the proportion of calves in caribou groups.

Nine grids were established along the road. Each grid was 200 m wide and extended 1000 m from the road. Grid boundaries were marked with 1-l cans painted fluorescent orange and wired to steel stakes 1.3 m above ground. Markers were spaced at 200-m intervals. Grids were spaced along the road in three sets; each set consisted of three grids. Sets of grids were spaced near the northern, middle, and southern regions of the study area, and were roughly centered on sampling stations 3-5 (Figure 2).

Grids were surveyed four times daily: twice in conjunction with

standard surveys, at 1500-1600 h, and 1700-1800 h. Opportunistic observations of caribou within grids were also used. The following variables were recorded for each group of caribou observed within a grid: (1) date, (2) time, (3) total number of caribou, (4) number of adults, (5) number of calves, (6) the locations that the leading caribou of a group entered and exited a grid, (7) the elapsed time between grid entry and exit for the leading caribou of a group, and (8) the number of caribou observed in each of 8 behavior categories (see above) during 1 instantaneous scan (Altman 1974). The net straight-line distance (m) traveled within a grid was calculated using Pythagorean Theorem, and the rate of travel (m per s) within a grid was calculated from distance and elapsed time. Caribou that were standing or lying were observed for 5 minutes before 0 m traveled was assigned.

The distributions of all caribou response variables (distance from the coast, rate of travel, proportion of calves in maternal groups, proportion of groups in constructive activity, direction of travel, group density, and group size) were skewed despite attempts at normalization. Thus, Kruskal-Wallis, Spearman rank correlation, and contingency table tests were used to analyze the data. Differences in the distribution of data were compared using the Kolmogorov-Smirnov test.

Insect activity and caribou response were plotted through time to provide a graphic overview of caribou-insect relationships. Hypotheses were tested regarding the individual and combined effects

of harassment by mosquitoes and oestrids on each caribou response. Canonical correlation analysis (Morrison 1967; Thompson 1984) was used to examine the relationship between the set of variables describing insect activity (sweep and trap counts of mosquitoes, and trap counts of oestrids), and the set of variables describing caribou groups (group size, composition, and density). This analytical technique was also used to investigate the relationship between insect activity and all caribou response parameters as well as the combined effects of insect harassment and weather factors on caribou responses. Alpha levels (P-values) ≤ 0.05 were considered statistically significant.

Insects were often inactive, or active at levels too low to measure. Also, caribou were frequently not in proximity to weather stations when insects were captured. Therefore, observations of caribou were pooled to increase sample sizes for quantitative comparisons; data sets are described in Table 14. Data set 1 retained spatial differences in caribou response and insect activity, but sacrificed some resolution through time by using observations of caribou near sampling stations with corresponding measurements of insect activity that were closest in time. Thus, for data set 1, observations of caribou may have been made up to 3 h from the time when insect activity was measured, although this disparity was usually less than 2 h.

Some analyses required subsampling data set 1; for example, the analysis of caribou group density necessitated that groups contain at

Table 14. Descriptions of data sets used to examine the responses of caribou to insect harassment.

Data set	n	Caribou response variables	Description
1	202	Group size Proportion of calves in maternal groups ^a Group density Predominate group activity Direction of travel Distance from the coast	Observations of caribou groups made during standard surveys within 300 m south of sampling station 1, 500 m north or south of station 2, or 1 km north or south of stations 3-5, and measurements of insect activity that correspond in space and time. Sample unit is caribou group.
2	509	Same as for data set 1 (above)	Observations of caribou groups made during standard surveys, and the means of insect activity over all sampling stations. Sample unit is caribou group.
3	52	Same variables as for data sets 1 and 2 (above) Group rate of travel	Daily means of caribou response variables pooled over all standard survey observations, and the daily means of insect activity pooled over all stations; rate of travel taken from grid survey observations. Sample unit is caribou group.
4	67	Group rate of travel Proportion of caribou/group in constructive activity ^b	Daily means of caribou response variables for each grid, and the daily means of insect activity at the corresponding sampling station. Sample unit is caribou group for examining rate of travel, and individual caribou for examining activity.

^a maternal group defined as any group containing calves

^b constructive activity defined as feeding, lying, standing while ruminating, and nursing

least two caribou. To compensate for this further reduction in sample sizes, I created a second data set from the original standard survey data that included observations of caribou along the entire road system (vs. only those in proximity to sampling stations as for data set 1) with the daily mean level of insect activity over all stations combined (data set 2, Table 14).

Sample sizes for grid surveys were also small (102 groups of caribou over all grids for both years combined). Thus, daily means of caribou response were determined for each group of grids and used with daily mean levels of insect activity at the corresponding station (data set 4, Table 14). Caribou rate of travel (from grid survey data) was included with the other response parameters (from standard survey data) when conducting the canonical and Spearman rank correlation analyses. Therefore, variables from both data sets were expressed as daily averages to achieve a common denominator in time (data set 3, Table 14). All Spearman rank correlation coefficients were determined using data set 3 (Table 14).

When using standard survey data to examine caribou activity through contingency table analysis, I first analyzed the data on the basis of caribou groups since only the predominate activity of groups was recorded. I then repeated the analysis after weighting each group of caribou according to its size. This in effect changed the analyses from a "per group" to a "per caribou" basis. However, weighting groups by size ignores within-group variability in caribou activity, and undoubtedly magnifies the lack of independence between

observations of caribou. Therefore, P-values associated with these contingency table tests should be viewed with caution.

Most analyses were performed using BMDP statistical software (Dixon 1981, 1983). Contingency tables tests and rank correlations involving circularly distributed variables (e.g., direction of travel) follow Batschelet (1981). Multiple comparisons using the Kruskal-Wallis technique were programmed in FORTRAN after Conover (1980). When two proportions are compared, the Z statistic is reported rather than the Chi-squared statistic (Zar 1974). Computer-assisted operations were performed on a Honeywell 66/40, or a VAX 11-785 (VMS 4.1) computer.

Results

Quantitative analyses

Three-day moving averages of insect activity (Figures 3-5) and responses by caribou (Figures 19-23) show that high levels of insect activity generally correspond with: (1) short average distance of caribou groups from the Beaufort Sea, (2) large group size, and (3) relatively low proportion of groups in constructive activity. The distribution and behavior of caribou coincides more closely with temporal changes in sweep counts of mosquitoes than with trap counts of mosquitoes, or trap counts of oestrids.

There was at least one significant difference in the median distance of caribou from the Beaufort Sea among days when: (1) insects were absent (14.6 km, $n = 1419$), (2) mosquitoes were present (6.8 km, $n = 7870$), (3) oestrids were present (2.2 km, $n = 141$), or (4) both parasites were present (4.0 km, $n = 4663$) (Kruskal-Wallis test, $P < 0.001$; $n = 14093$, data set 2, Table 14). Multiple comparisons indicate that all pairwise contrasts, except 3 vs. 4, were significantly different (Kruskal-Wallis test, $P < 0.05$). Similar results were obtained when the analyses were conducted using caribou group as the sample unit. On a daily basis, distance of caribou groups from the coast was negatively correlated with sweep counts of mosquitoes, trap counts of mosquitoes, and trap counts of oestrids (Table 15).

Distance of Caribou From the Coast

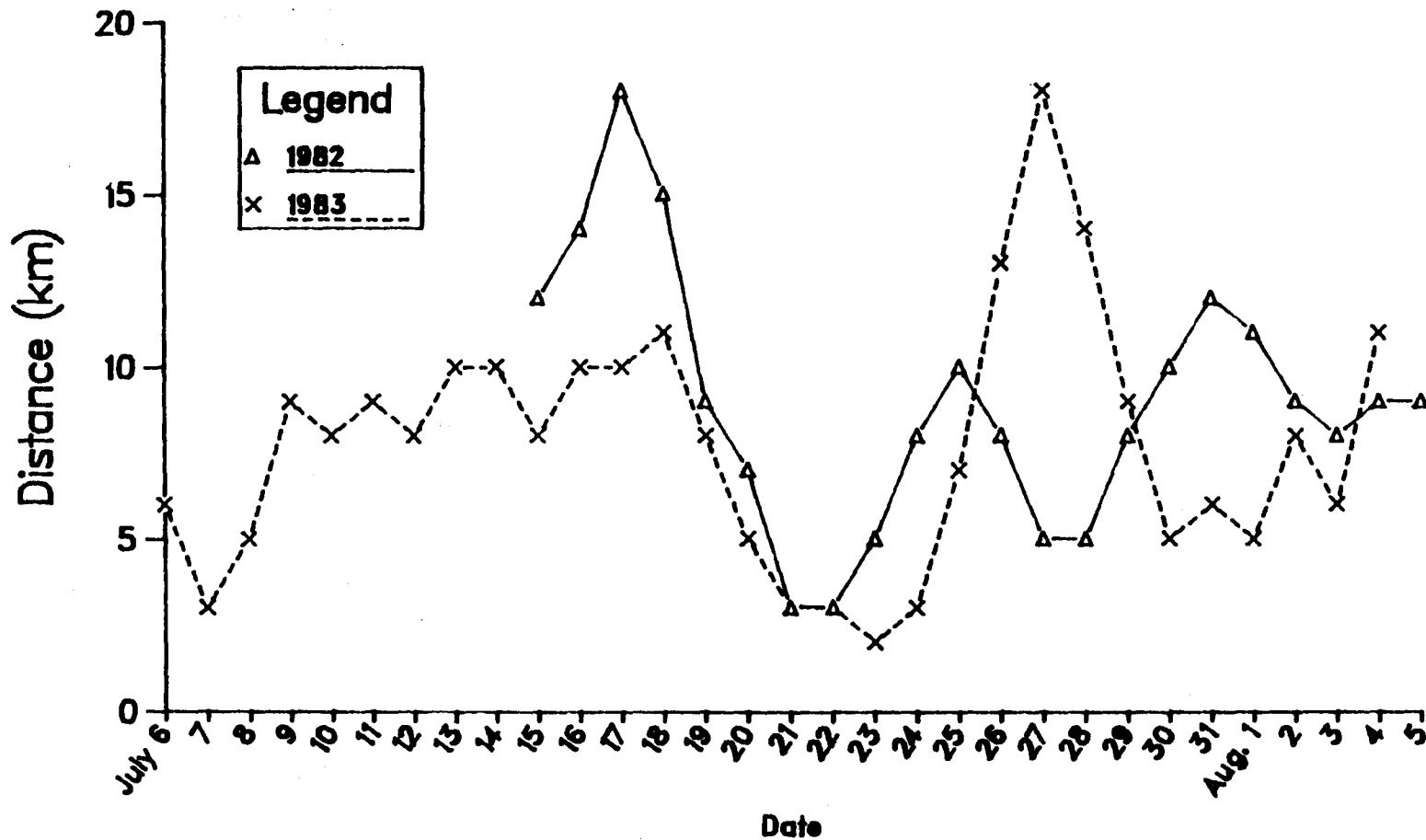


Figure 19. Three-day moving averages of distance of caribou from the Beaufort Sea near Milne Point, Alaska (n = 2085, 1982; n = 12008, 1983).

Caribou Group Size

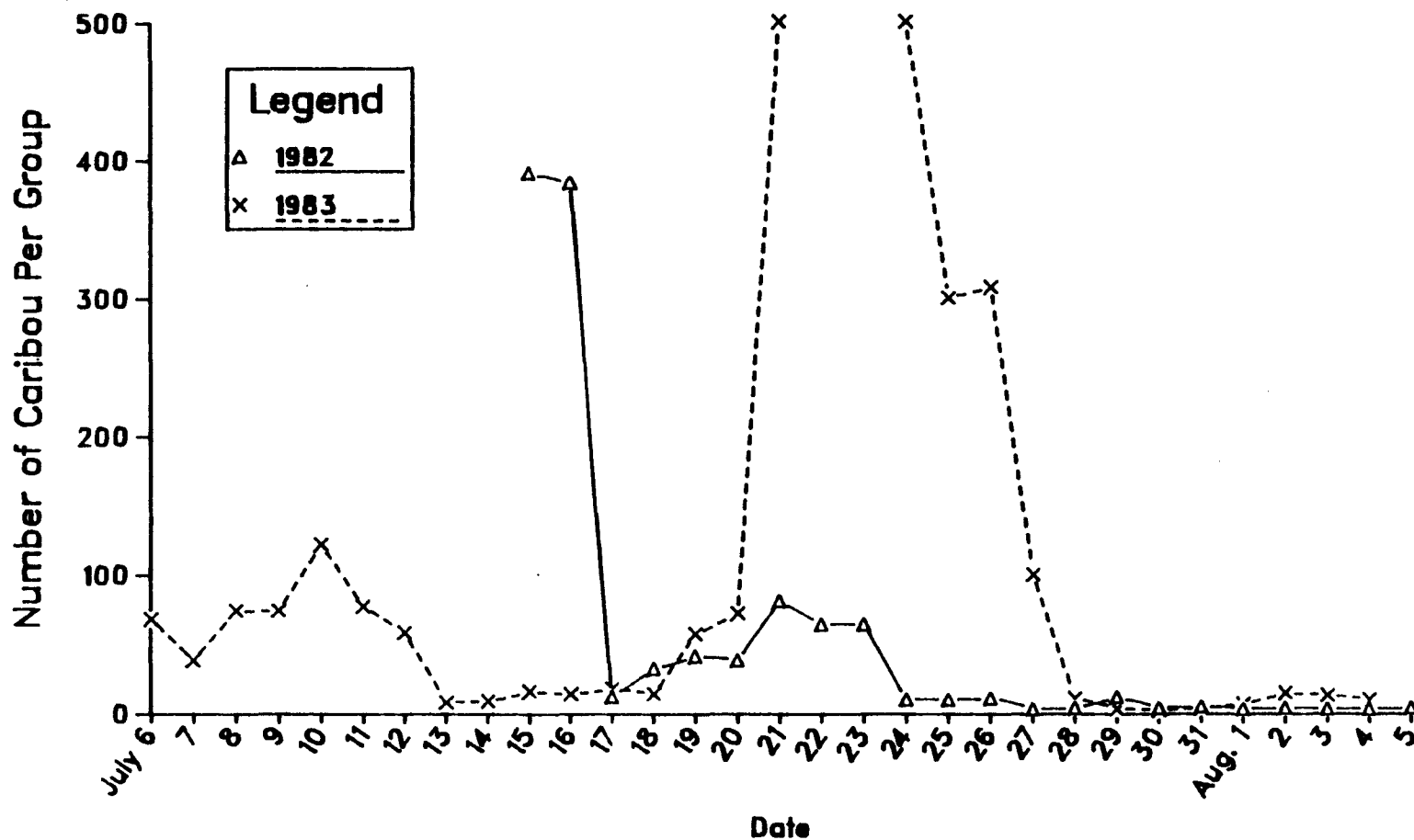


Figure 20. Three-day moving averages of caribou group size near Milne Point, Alaska (n = 255, 1982; n = 254, 1983).

Proportion of Groups in Constructive Activity

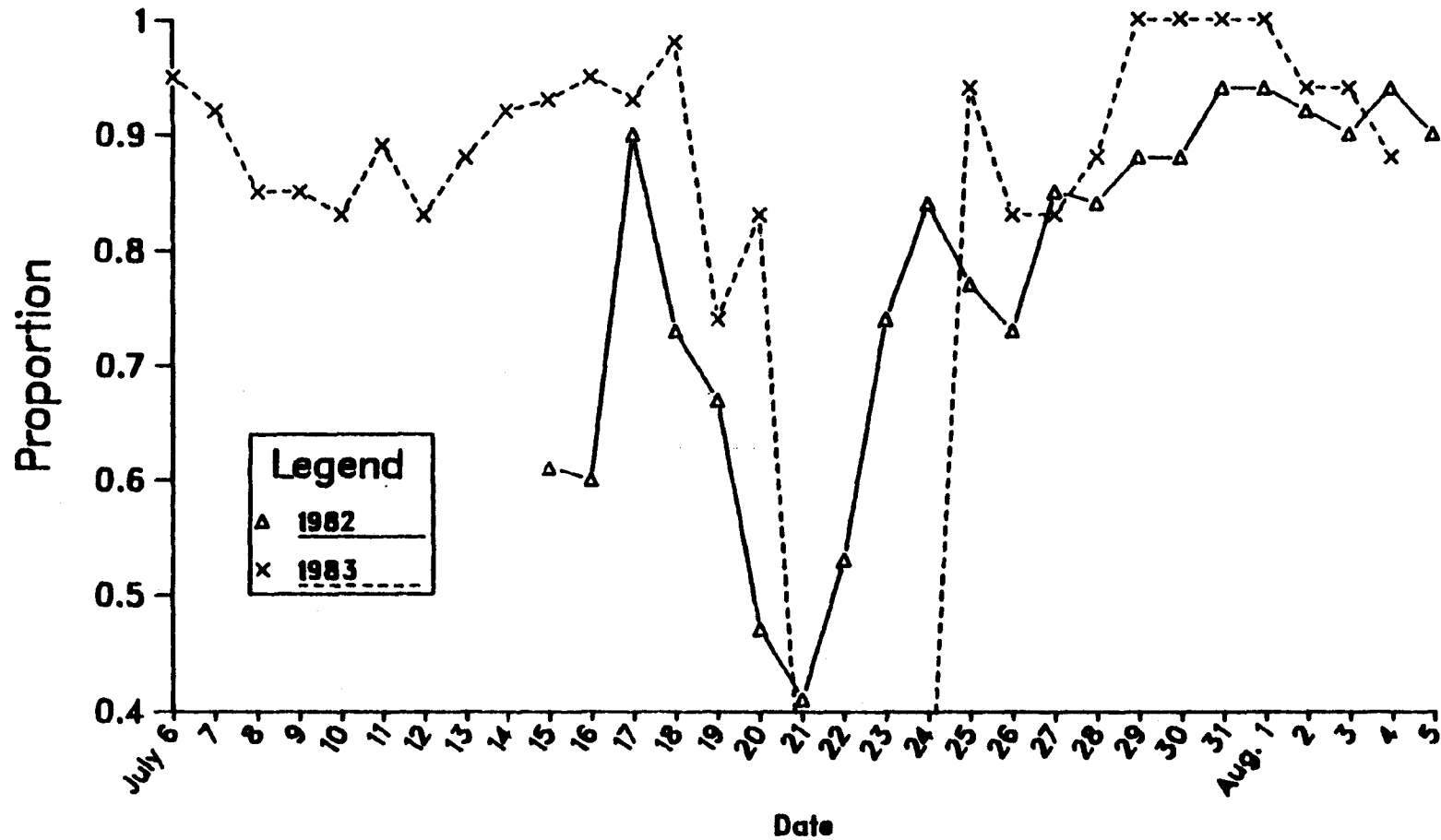


Figure 21. Three-day moving averages of the daily proportion of caribou groups in constructive activities (feeding, lying, or nursing) near Milne Point, Alaska ($n = 255$, 1982; $n = 254$, 1983).

Proportion of Calves Per Group of Caribou

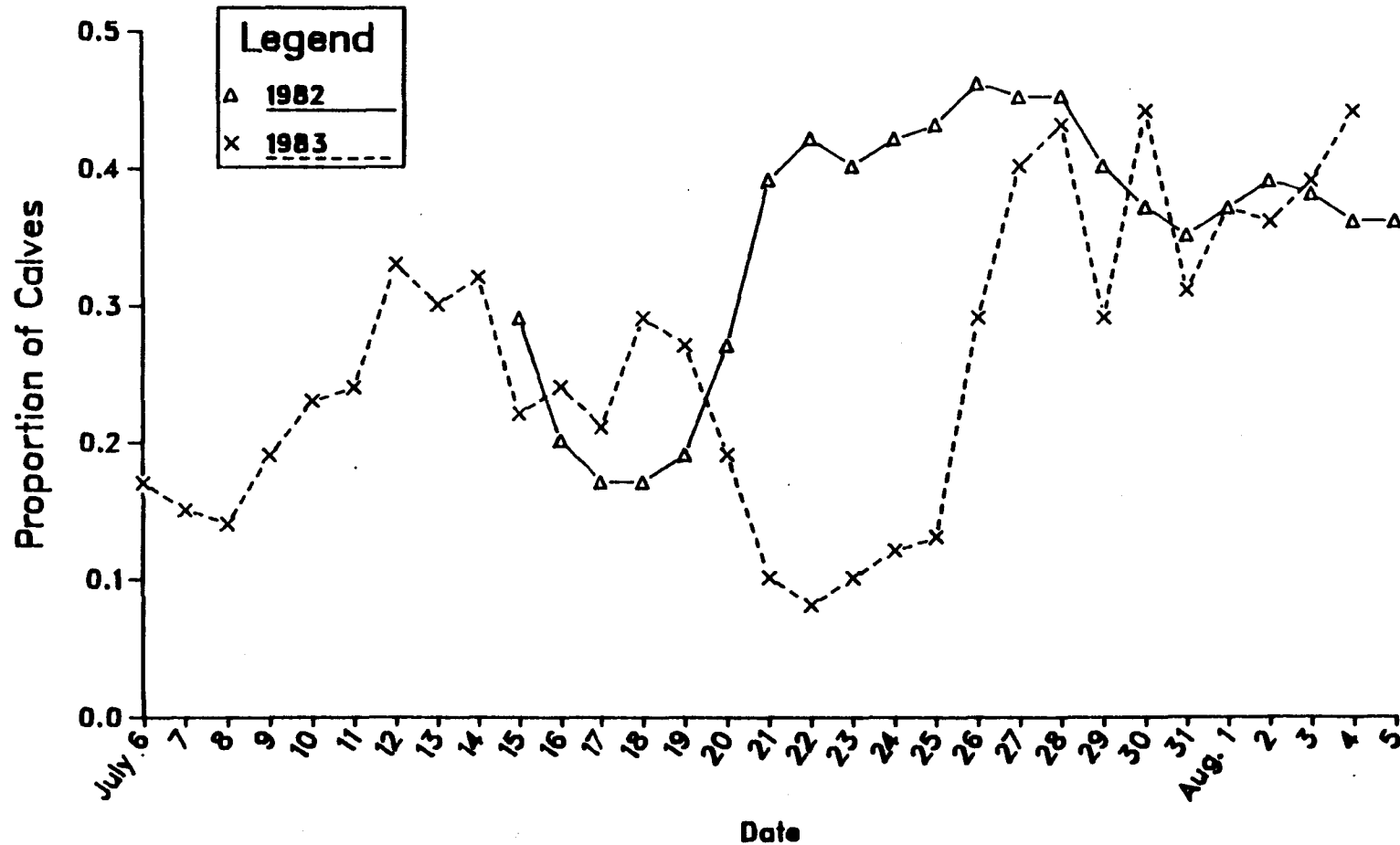


Figure 22. Three-day moving averages of the proportion of calves per group of caribou (for groups containing calves) near Milne Point, Alaska ($n = 106$, 1982; $n = 149$, 1983).

Density of Caribou Groups

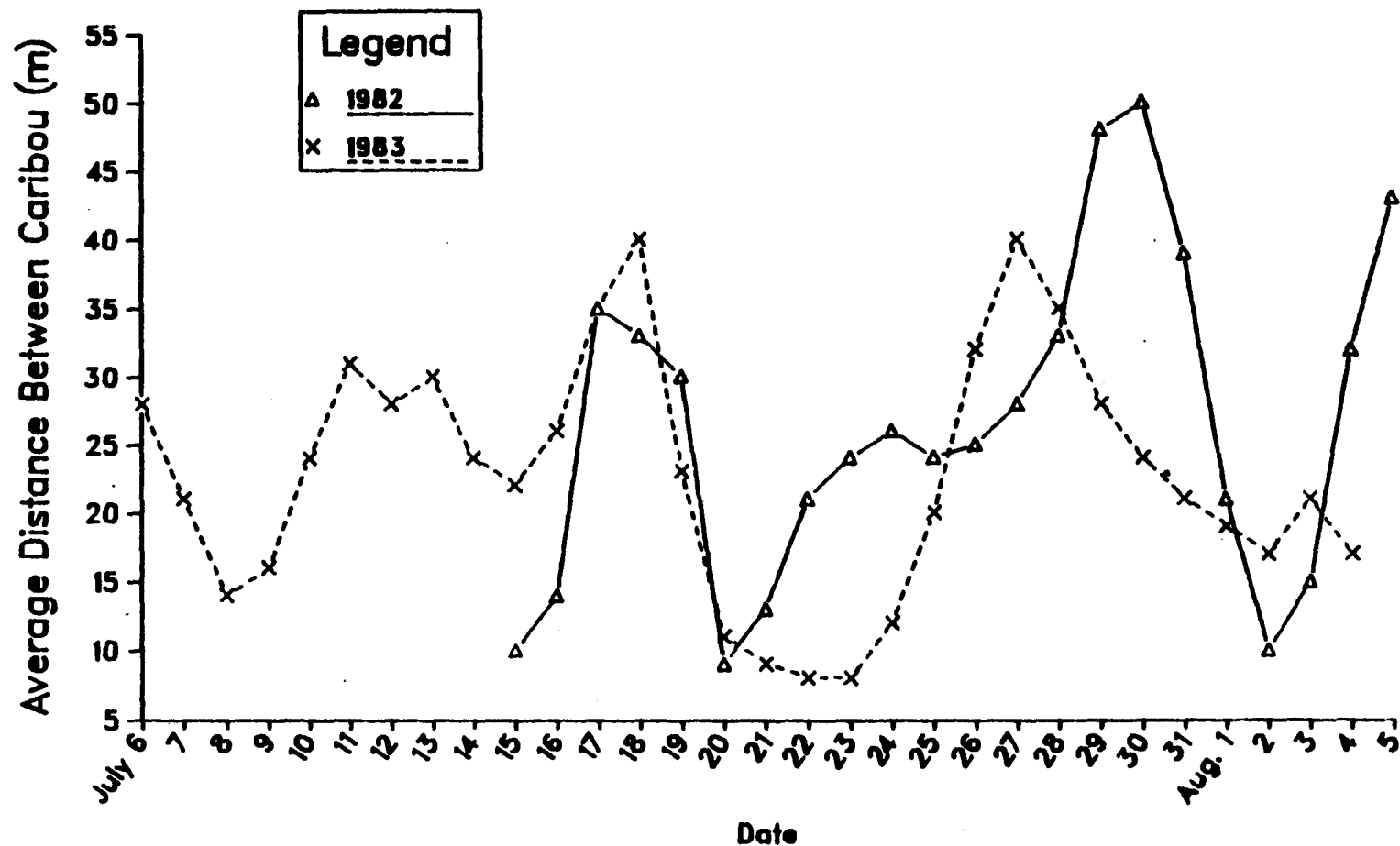


Figure 23. Three-day moving averages of the distance between caribou within groups near Milne Point, Alaska (n = 183, 1982; n = 204, 1983).

Table 15. Spearman rank correlation coefficients^a between daily means of insect activity and caribou response parameters; 1982-83 (data set 3; Table 14).

	Dist. from coast	Group size	Prop. calves	Group density	Prop. groups const. activity	Rate of travel	Mosq. act. (sweeps)	Mosq. act. (traps)	Oestrid act. (traps)
Dist. from coast (km)	1.0								
Group size (no. caribou)	-0.20	1.0							
Proportion calves in maternal groups ^b	0.20	-0.33	1.0						
Group density ^c (m)	0.21	0.07	-0.07	1.0					
Proportion groups in constructive act. ^d	-0.05	0.38	0.17	-0.24	1.0				
Rate of travel (m/s)	0.04	0.10	0.22	-0.31	0.41	1.0			
Mosquito activity (no./100 sweeps)	-0.45	0.32	-0.21	-0.41	-0.44	0.44	1.0		
Mosquito activity (no. per trap/hr.)	-0.29	0.11	0.07	-0.01	0.10	0.18	0.37	1.0	
Oestrid activity (no. per trap/hr.)	-0.32	-0.09	0.21	0.06	-0.07	-0.13	0.12	0.54	1.0

^a $|r| > 0.27$ is significantly different from 0 at $P < 0.05$; $|r| > 0.36$ is significantly different from 0 at $P < 0.01$ (two-tailed test; $n = 52$)

^b maternal group defined as any group containing calves

^c average distance between caribou within each group

^d constructive activity defined as feeding, lying, and nursing

Initially, I examined the relationship between insect harassment and caribou activity using data from grid surveys with individual caribou as the sample unit ($n = 1606$; data set 4, Table 14). The same proportion of caribou (0.34) was observed in nonconstructive activities (standing, walking, trotting, or running) when insects were present, and when they were absent. However, a significantly greater proportion of caribou was in extreme avoidance activities (trotting or running) when insects were present than when they were absent (0.25 vs. 0.16, $Z = 3.98$, $df = 1$, $P < 0.001$). Inspection of the grid survey data suggests that the activity of individuals within groups was most synchronous when insect attack was severe and all caribou were engaged in avoidance responses; it was least synchronous when insect attack was light to moderate. When insects were absent, group members tended to engage in similar activities, but this synchrony was far from complete.

To increase the sample size, I re-examined the effects of insect harassment on caribou activity using data set 1 (Table 14). Each group was weighted by the number of caribou that it contained. Contingency table analysis indicated that the presence of insects had a significant effect on the relative number of caribou observed lying, feeding stationary, feeding while walking, standing, or walking-trotting-running (Table 16A). Fewer caribou were observed feeding (irrespective of walking) than expected when insects were present. Also, more caribou were observed lying when insects were present than when they were absent; this was the greatest single

Table 16. Contingency tables showing the observed and expected numbers of caribou engaged in five activities in relation to the presence of mosquitoes or oestrids.

(A) Using data set 1 (Table 14)

		Lying	Feeding (stationary)	Feeding (moving)	Standing	Walking, trotting, running	Total
Insects	Absent	observed	283	738	3083	7	941
		(expected)	(649)	(641)	(2942)	(8)	(812)
	Present	observed	506	41	494	3	47
		(expected)	(140)	(138)	(635)	(2)	(176)
	Total		789	779	3577	10	988
							6143

Chi-squared = 1398 df = 4 P < 0.001^a

(B) Using data set 2 (Table 14)

		Lying	Feeding (stationary)	Feeding (moving)	Standing	Walking, trotting, running	Total
Insects	Absent	observed	83	678	387	0	273
		(expected)	(90)	(243)	(604)	(2)	(482)
	Present	observed	1099	2531	7573	20	6083
		(expected)	(1092)	(2966)	(7356)	(18)	(5874)
	Total		1182	3209	7960	20	6356
							18727

Chi-squared = 1024 df = 4 P < 0.001^a

^a the significance of the Chi-squared statistic should be viewed with caution due to the large sample size, and because the gregarious nature of caribou probably causes the assumption of independent observations to be violated

effect of harassment on caribou activity based on the contribution of each component (or cell) to the overall Chi-squared statistic.

However, due to the lack of independence in the activity of caribou within groups, the relative size and direction of differences between observed and expected values are probably more meaningful than P-values.

Since some of the above results appeared to contradict many published reports regarding the effects of insect harassment on caribou, I repeated the analysis using data set 2 (Table 14). Again, insect activity had a significant effect on the number of caribou observed in the five activities noted above (Table 16B). This was mainly a result of the tendency for caribou to feed without walking, and secondarily to not walk, trot, or run, when insects were absent. I further classified days of insect activity into days when mosquitoes were present, oestrids were present, or both insects were present, to discern between the effects of mosquitoes and oestrids on caribou activity. The relative number of caribou observed in the five activities noted previously was significantly different among the three categories of insect activity (Table 17). This was because caribou: (1) fed while walking (at the expense of feeding without walking) when both insects were present, (2) bedded when both insects were present, and (3) walked, trotted, or ran when only mosquitoes were present. Significantly more caribou were observed standing when oestrids were present than when they were absent ($X^2 = 34.3$, $df = 1$, $P < 0.001$; $n = 20429$). However, even when insects were present,

Table 17. Contingency table showing the observed and expected numbers of caribou engaged in five activities in relation to the presence of mosquitoes or oestrids (data set 3; Table 14).

		Lying	Feeding (stationary)	Feeding (moving)	Standing	Walking, trotting, running	Total
Mosquitoes present	observed	1057	2363	3307	3	3934	10664
	(expected)	(671)	(1554)	(4665)	(20)	(3754)	
Oestrids present	observed	15	52	39	6	41	153
	(expected)	(10)	(22)	(67)	(0)	(54)	
Both insects present	observed	27	128	4290	23	2169	6637
	(expected)	(418)	(967)	(2904)	(12)	(2336)	
Total		1099	2543	7636	32	6144	17454
Chi-squared = 3012		df = 8		P < 0.001 ^a			

^a the significance of the Chi-squared statistic should be viewed with caution due to the large sample size, and because the gregarious nature of caribou probably causes the assumption of independent observations to be violated

less than 1% of all caribou observed were standing.

Spearman's rank correlation indicated a positive relationship between the daily proportion of caribou groups in nonconstructive activities (as above) and sweep counts of mosquitoes (Table 15). This proportion was significantly different among days when insects were absent, mosquitoes were present, oestrids were present, or both insects were present (Table 18). Multiple comparisons showed significant differences in this proportion between periods when mosquitoes were present and all other periods (Kruskal-Wallis test, $P < 0.05$). Contingency table analyses also indicated that significantly more groups of caribou were observed in predominately nonconstructive activities than expected when insects were present (Tables 19A and 19B).

Initial contingency table analysis indicated that significantly more caribou were observed traveling when insects were absent than when they were present ($\chi^2 = 416$, $df = 1$, $P < 0.001$; $n = 6143$, data set 1, Table 14). However, when I repeated the analysis using data set 2 (Table 14) to increase the sample size, significantly fewer caribou than expected were observed traveling when insects were absent, while more caribou were observed than expected traveling when both parasites were present ($\chi^2 = 533$, $df = 3$, $P < 0.001$; $n = 18727$). More caribou were observed stationary than expected when oestrids were present, but this effect was not as pronounced as those noted above.

Rate of travel by groups of caribou was positively correlated

Table 18. The daily proportion of caribou groups in predominately nonconstructive activities (walking, trotting, or running without feeding, or standing in a head-low posture) among four categories of days determined by the presence of mosquitoes and oestrids (data set 3; Table 14).

Category ^a	Median proportion ^b	Range	n
(1) No insects	0.07	0 - 0.35	13
(2) Mosquitoes only	0.15	0 - 1.00	20
(3) Oestrids only	0.02	0 - 0.20	5
(4) Mosquitoes and oestrids	0.18	0 - 0.33	11

^a the median proportion of groups in nonconstructive activities was significantly different among categories (Kruskal-Wallis H = 8.17; P = 0.04)

^b multiple comparisons (Kruskal-Wallis test; P < 0.05) indicate significant differences in median proportions of groups in nonconstructive activities between categories 1 and 2, 2 and 3, and 2 and 4 (as above)

Table 19. Contingency tables showing the observed and expected numbers of caribou groups observed in predominately constructive (feeding, lying, or nursing) vs. nonconstructive (walking, trotting, or running without feeding, or standing in a head-low posture) activities in relation to the presence of mosquitoes or oestrids.

(A) Using data set 1 (Table 14)

		No insects	Mosquitoes only	Oestrids	Total
Constructive activity	observed	133	14	9	156
	(expected)	(129)	(17)	(10)	
nonconstructive activity	observed	34	8	4	46
	(expected)	(38)	(5)	(3)	
Total		167	22	13	202
Chi-squared = 3.97		df = 2	P < 0.10 ^a		

(B) Using data set 2 (Table 14)

		No insects	Mosquitoes only	Oestrids only	Oestrids and mosquitoes	Total
Constructive activity	observed	107	187	37	69	400
	(expected)	(100)	(187)	(33)	(80)	
Nonconstructive activity	observed	18	48	5	31	102
	(expected)	(25)	(48)	(9)	(20)	
Total		125	235	42	100	502
Chi-squared = 12.28		df = 3	P < 0.01 ^a			

^a see footnote ^a, Table 16

with sweep counts of mosquitoes (Table 15). There was a significant difference in median rate of travel among days when insects were present (0.50 m per s; $n = 25$) vs. absent (0.30 m per s; $n = 42$) (Mann-Whitney test, $P = 0.03$). Caribou traveled most rapidly when mosquitoes were present (0.85 m per s; $n = 20$) while the increased tendency of caribou to remain stationary when oestrids were present (see above) reduced the median rate of travel (< 0.25 m per s; $n = 5$). Rate of travel was more variable when mosquitoes were present than when they were absent. This variability in rate of travel may have been attributable to distance of caribou from the coast, since caribou rate of travel sometimes decreased when mosquito-harassed groups came within 1-3 km of the Beaufort Sea. There were insufficient observations of caribou within grids when oestrids were present to adequately compare the effects of mosquitoes vs. oestrids on caribou rate of travel.

Contingency table analyses indicated that the direction traveled by caribou that were more than 0.8 km from the coast was significantly affected by the presence of insects (Table 20). This was due to the tendency for caribou to travel north or east when insects were present, and to travel south when insects were absent. The median direction of travel for caribou (as determined through interpolation; Batschelet 1981) was 86 degrees when insects were present, and 195 degrees when insects were absent.

There was no circular rank correlation between daily mean direction of travel by caribou groups and daily mean wind direction

Table 20. Contingency table showing caribou direction of travel in relation to the presence of insects; 1982-83 (includes only those caribou observed >0.8 km from the coast; data set 1, Table 14).

Direction of travel ^a		N	NE	E	SE	S	SW	W	NW	Total
Insects	Absent	observed	268	4	129	235	774	24	648	708
		(expected)	(349)	(4)	(352)	(259)	(651)	(28)	(552)	(594)
	Present	observed	148	1	291	73	2	9	10	0
		(expected)	(67)	(1)	(68)	(49)	(125)	(5)	(106)	(114)
	Total		416	5	420	308	776	33	658	708
										3324
Chi-squared = 1399			df = 7		P < 0.001 ^b					

^a median direction of travel (as determined through interpolation; Batschelet 1981) when insects absent = 195 degrees; when insects present = 86 degrees

^b see footnote ^a, Table 16

when all days were used ($r = 0.18$, $P > 0.10$, data set 3, Table 14). This correlation was still not significant when the data were restricted to days when mosquitoes and oestrids were present, ($r = 0.30$, $P < 0.10$, $n = 38$), nor when the data were further restricted to days when only mosquitoes were present ($r = 0.32$, $P < 0.10$, $n = 29$).

There was a significant difference in the median size of caribou groups when insects were absent, mosquitoes were present, oestrids were present, or both insects were present (Table 21). Multiple comparisons among these four categories indicated that median group size was significantly larger when mosquitoes alone were present than when oestrids, or mosquitoes and oestrids, were present. Group size was most variable when mosquitoes, or mosquitoes and oestrids, were present. On a daily basis (data set 4, Table 14), group size was positively correlated with sweep counts of mosquitoes (Table 15).

Contingency table analyses indicate that there was no difference in the density of caribou groups among days when insects were absent, mosquitoes were present, oestrids were present, or both insects were present using data set 1 ($\chi^2 = 2.15$, $df = 3$, $P = 0.54$; $n = 154$) or data set 2 ($\chi^2 = 1.32$, $df = 3$, $P = 0.72$; $n = 353$). The average distance between caribou within groups was roughly 10 m (range 1-300 m). However, on a daily basis (data set 3, Table 14), group density was negatively correlated with sweep counts of mosquitoes (Table 15).

Initially, the proportion of calves in maternal groups (defined as groups containing calves) was not significantly different among days when insects were absent ($n = 95$), mosquitoes were present ($n =$

Table 21. Median values and ranges for group size of caribou in relation to the presence of mosquitoes and oestrids; 1982-83 (data set 2; Table 14).

Category ^a	Median	Range	n
No insects	5	1-112	126
Mosquitoes only	8	1-2000 ^b	239
Oestrids only	2	1-33	42
Mosquitoes and oestrids	2	1-1500 ^b	102

^a median group size was significantly different among categories (Kruskal-Wallis $H = 38.10$; $P < 0.001$)

^b upper value is an approximation since these groups could not be accurately counted

9), oestrids were present ($n = 4$), or both insects were present ($n = 3$) (Kruskal-Wallis test, $P = 0.42$; data set 2, Table 14). I repeated the analysis using data set 2 (Table 14) to increase the sample size for periods when insects were active. This reanalysis showed a significant difference in the median proportion of calves per group when: (1) insects were absent (0.33, $n = 70$), (2) mosquitoes were present (0.24, $n = 121$), (3) oestrids were present (0.39, $n = 22$), and (4) both insects were present (0.33, $n = 42$) (Kruskal-Wallis test, $P < 0.001$). Multiple comparisons indicated that this proportion was significantly lower when mosquitoes were present than at any other time (Kruskal-Wallis test, $P < 0.05$).

Canonical correlation analysis indicated that the set of variables describing caribou group structure (group size, composition, and density) was correlated ($r^2 = 0.42$) with the set of variables describing insect activity (sweep and trap counts of mosquitoes, and trap counts of oestrids) ($\chi^2 = 27.38$, $df = 9$, $P = 0.001$; $n = 52$, data set 3, Table 14). Group size and density were the most important variables for describing the structure of caribou groups in response to insects, while sweep counts of mosquitoes was the best estimator of insect harassment as it affected caribou group structure (Table 22).

Canonical correlation analysis showed a significant relationship between the set of variables for insect activity (as above) and all caribou response variables (distance of groups from the coast, group size, group density, group composition, proportion of groups in

Table 22. Correlations between the original variables and canonical variables for parameters describing caribou groups (group size, density, and calf composition), and indices of insect activity (data set 3; Table 14).

Original variable	r^a	r^{2b}	P-value ^c	Coefficient for canonical var.
Group size (no. caribou)	-0.74	0.24	0.004	-0.003
Proportion calves in maternal groups ^d	0.44	0.08	0.25	2.39
Group density ^e (m)	0.73	0.23	0.005	0.03
Mosquito activity (no./100 sweeps)	-0.87	0.32	<0.001	-0.15
Mosquito activity (no. per trap/hr.)	-0.10	0.01	0.95	0.15
Oestrid activity (no. per trap/hr.)	0.09	0.01	0.96	11.81

^a correlation between the original variable and its canonical variable

^b squared multiple correlation between the original variable and all variables in the other set

^c P-value for squared multiple correlation coefficient

^d maternal group defined as any group containing calves

^e determined through interpolation from four categories of group density (see Methods; Chapter 2)

predominantly nonconstructive activities, rate of travel, and whether traveling north or east). Two canonical variables were significant in describing this relationship (Table 23). Mosquito activity (as determined by sweeps) was the major component of the first canonical variable for insect activity, and was the most important measure of insect activity as it affected caribou. The second canonical variable for insect activity largely reflected trap count information, of which oestrid activity was least important for describing caribou response. The first canonical variable for caribou response mainly reflected caribou rate of travel and the proportion of groups in constructive activities (i.e. feeding, lying, or nursing); the second canonical variable for caribou response mainly reflected group size (Table 24).

Adding the daily means (all stations combined) of weather factors (current ambient air temperature, midrange temperature for the period between weather measurements, relative humidity, saturation deficit, wind direction, wind velocity, and cloud cover) to the daily mean levels of insect activity did not substantially increase the strength of the relationship between caribou response variables and weather-insect parameters (Table 25). Mosquito activity (as determined by sweeps) was still the most important variable for describing the response of caribou to insect harassment, but measures of relative humidity, saturation deficit, current temperature, and midrange temperature were next in importance. The most important parameters of caribou response were the proportion of

Table 23. Test results for the selection of canonical variables describing insect activity, and all responses by caribou (data set 3; Table 14).

Null hypothesis	Chi-squared	df	P-value ^a	r ² ^b
No linear relationship	79.46	21	<0.001	0.90
Two canonical variables no better than one canonical variable for describing the relationship between insect activity and all responses by caribou.	23.69	12	0.02	0.53 ^c
Three canonical variables no better than two canonical variables for describing the relationship between insect activity and all responses by caribou.	5.40	5	0.37	0.20

^a P-value for Chi-squared statistic

^b squared canonical correlation coefficient

^c indicates that 53% of the variability in the relationship between caribou and insects not explained by the first pair of canonical variables is explained by the second pair of canonical variables; thus, 95% of total variability in this relationship is explained by the two canonical variables

Table 24. Correlations between the original variables and canonical variables describing insect activity, and all responses by caribou (data set 3; Table 14).

Original variable	r^a				Coefficients for canonical vars.	
	1st ^b	2nd ^c	r^2 ^d	P-value ^e	1st ^b	2nd ^c
Distance from coast (km)	-0.44	-0.37	0.26	0.04	-0.02	-0.009
Group size (no. caribou)	0.30	0.85	0.47	<0.001	0.002	0.007
Group density ^f (m)	-0.34	0.05	0.19	0.12	0.003	0.005
Proportion calves in maternal groups ^g	0.15	0.15	0.03	0.81	0.47	2.61
Proportion groups in const. act. ^h	-0.79	0.28	0.60	<0.001	-2.07	0.73
Rate of travel (m/s)	0.85	-0.35	0.71	<0.001	0.65	-0.36
Direction of travel ⁱ	0.14	-0.12	0.09	0.48	0.05	0.06
Mosquito activity (no./100 sweeps)	0.97	-0.20	0.87	<0.001	0.26	-0.13
Mosquito activity (no. per trap/hr.)	0.44	0.89	0.59	0.01	0.77	2.84
Oestrid activity (no. per trap/hr.)	-0.02	0.48	0.27	0.32	-4.73	-1.79

^a correlation between the original variable and its canonical variable

^{b,c} first and second canonical variables, respectively

^d squared multiple correlation between the original variable and all variables in the other set

^e P-value for squared multiple correlation coefficient

^f determined through interpolation from four categories of group density (see Methods; Chapter 2)

^g maternal group defined as any group containing calves

^h constructive activities defined as feeding, standing and ruminating, lying, and nursing

ⁱ direction limited to two categories; toward the north and east, or toward any other direction

Table 25. Test results for the selection of canonical variables for weather-insect parameters, and all responses by caribou^a.

Null hypothesis	Chi-squared	df	P-value ^b	r ^{2c}
No linear relationship	117.32	70	<0.001	0.94
Two canonical variables no better than one canonical variable for describing the relationship between weather and insects, and all responses by caribou.	54.96	54	0.44	0.67
Three canonical variables no better than two canonical variables for describing the relationship between weather and insects, and all responses by caribou.	30.63	40	0.86	0.51

^a data set 3 (Table 14) with daily means of weather parameters (all stations combined)

^b P-value for Chi-squared statistic

^c squared canonical correlation coefficient

groups in nonconstructive activity, rate of travel, and whether traveling north or east (Table 26).

Descriptive observations

Due to time constraints in the field, I was unable to quantify individual behavioral reactions of caribou to insect harassment. Mosquitoes caused a set of reactions that were quite different from those elicited by oestrids. During early summer when mosquitoes were active and before oestrids had emerged, caribou would usually exhibit head shakes, ear and tail flicks, and body shakes similar to those used to shake water from their coat. When oestrids were active, these acts were complemented by head bobbing (distinguished from head shaking by an expansive vertical movement of the head and neck), grabbing mouthfulls of hair from the back and lumbar region, vigorous kicking and foot stamping, and violent twitching of the body. Oestrids frequently attacked caribou, and always stimulated stronger defense reactions than did mosquitoes. The low number of bots in the area (Chapter 1) precluded identifying many instances of attack by these parasites.

Some caribou, especially bulls, appeared to be less sensitive to human disturbances and structures when harassment by oestrids became severe. At such times, caribou sought the shade of pipelines and buildings, and were nearly oblivious to traffic and construction equipment. In fact, caribou occasionally sought gravel roads as

Table 26. Correlations between the original variables and canonical variables for weather-insect parameters, and all responses by caribou^a.

Original variable	r^b	r^2^c	P-value ^d	Coefficients for canonical vars.
Distance from coast (km)	-0.36	0.33	0.45	-0.01
Group size (no. caribou)	0.21	0.55	0.05	0.001
Proportion calves in maternal groups	0.21	0.25	0.67	0.81
Group density (n)	-0.31	0.44	0.18	0.005
Proportion groups in constructive activity	0.83	0.74	0.00	2.42
Rate of travel (m/s)	0.87	0.79	<0.00	0.65
Direction of travel	0.13	0.26	0.65	0.04
Current air temp. (°C)	0.72	0.71	<0.00	-0.04
Midrange air temp. (°C)	0.76	0.76	<0.00	0.02
Relative humidity (%)	-0.61	0.41	0.05	0.007
Saturation deficit (mbar)	0.77	0.64	<0.00	0.39
Wind direction (degrees)	0.15	0.20	0.56	-0.0005
Wind velocity (m/s)	-0.12	0.13	0.81	0.10
Cloud cover (%)	-0.17	0.10	0.91	0.01
Mosquito activity (no./100 sweeps)	0.96	0.88	<0.00	0.21
Mosquito activity (no. per trap/hr.)	0.36	0.59	0.00	0.08
Oestrid activity (no. per trap/hr.)	-0.04	0.30	0.2	-1.90

^a data set 3 (Table 14) with daily means of weather factors

^b correlation between the original variable and its canonical variable

^c squared multiple correlation between the original variable and all variables in the other set

^d P-value for squared multiple correlation coefficient

relief terrain from oestrids and were often reluctant to venture back onto the tundra even when vehicles approached. When vehicles approached at speeds less than 30 km per h, caribou often tried to outrun them for up to 1-2 km before leaving the road. These behavioral responses occurred infrequently each summer, and were never caused by mosquitoes alone.

Warble flies usually flew directly to caribou and attempted to land on them; however, they may approach caribou on the ground as well. While observing a group of about 5000 caribou that eventually surrounded me, I saw several warbles fly close to caribou and then immediately land on polygon ridges or tussocks within 2-3 m of their potential host. These caribou had been under severe harassment by oestrids for several days and were intent on foraging; they occasionally trotted or ran a short distance in response to oestrids, but usually tensed and stood motionless with their head lowered for 5-15 s before resuming feeding. I never witnessed a warble actually approach a caribou from the ground, but a warble did crawl up to me, turned around, and repeatedly touched my leg with its extended ovipositor. No eggs were released, presumably because the female failed to contact hair on my leg (Hadwen and Palmer 1922). A similar experience happened to my field assistant that day (J. Smith, personal communication). It may be a viable strategy for female warbles to land in the vicinity of caribou and then wait on elevated mounds where they can see, and where they can expect to encounter caribou. Alternatively, the warbles that landed on tussocks may have

been males if this area was an aggregation site, though this seems unlikely.

Discussion

Quantitative analyses

Rank correlation coefficients indicate the strength of the relationships qualitatively suggested by comparing Figures 3-5 and 19-23 (Table 15). Rank correlation coefficients between caribou responses and trap counts of mosquitoes were consistently weaker than those for sweep counts. This suggests that traps were inferior to sweeps for monitoring mosquito activity, at least at the respective levels of sampling effort expended during this study.

Traps were probably no more effective for estimating levels of oestrid activity than they were for estimating levels of mosquito activity. This suspicion is supported by the comparable strength of correlations for trap counts of mosquitoes and trap counts of oestrids with caribou responses (Table 15). Indeed, the abundance of oestrids in the study area was extremely low in relation to that for mosquitoes. Also, oestrids are more mobile and better adapted to locate hosts than mosquitoes (White et al. 1975; Roby 1978). Thus, the distribution of oestrids may be more highly influenced by the distribution of caribou than the distribution of mosquitoes. If so, the difficulty in trapping oestrids attributable to their low density is compounded by a patchy distribution.

Numerous reports indicate that oestrids have a pronounced effect on the distribution and behavior of caribou at both the individual

and population levels (Hadwen and Palmer 1922; Skoog 1968; Curatolo 1975; Roby 1978; Wright 1979; Boertje 1981). These effects might not necessarily be reflected in strong correlations between level of oestrid activity and degree of caribou response if caribou react to oestrids in a discrete manner (Roby 1978). Even so, I suspect that all of my results underestimate the effects of oestrids on the distribution and behavior of caribou because of the difficulty associated with capturing adult flies.

Neither sweeps nor traps appeared to detect mosquitoes or oestrids when they were present in low numbers. Traps captured mosquitoes on a greater proportion of days than sweeps (Figure 15); this was probably because traps sampled mosquitoes continuously, while sweeps were limited to only 1-2 minutes per sample. Sweeps were actually more sensitive to low levels of mosquito activity than traps per unit time sampled. This was probably because the person conducting the sweeps attracted mosquitoes. If traps were less sensitive to low levels of insect activity than sweeps, this effect was most pronounced for oestrids. Therefore, the comparative effects of mosquitoes and oestrids on the distribution and behavior of caribou using sweep and trap counts, to estimate their relative levels of activity should be viewed with caution.

The canonical correlation analyses indicating that sweep counts of mosquitoes were most highly correlated with caribou responses, while trap counts of oestrids were least important for describing these reactions, also suggest that traps were less effective than

sweeps for estimating mosquito activity. If sweeps and traps failed to detect mosquitoes or oestrids at low levels of activity, then all of my results may be biased toward high levels of insect activity.

Reports vary regarding the respective effects of harassment by mosquitoes vs. oestrids on the tendency for caribou to seek insect-relief terrain. This inconsistency is apparently due to regional differences in the types and extent of insect-relief terrain available to caribou, and to differences in the relative severity of mosquito vs. oestrid harassment (Skoog 1968; Bergerud 1974; Boertje 1981). Wright (1979, 1980) reported that mosquitoes had no effect on habitat selection of untended reindeer on the Seward Peninsula of Alaska, while oestrids caused them to use coastal beaches and mudflats since other sources of relief terrain were unavailable. Boertje (1981) reported that caribou in interior Alaska moved to windy, sparsely-vegetated uplands in response to oestrid attack. In contrast, Roby (1978) reported that mosquito harassment causes CAH caribou to move to the Beaufort Sea coast, and that there is little or no terrain available to this herd that affords relief from oestrids; Figures 15 and 18 support this hypothesis. This indirectly suggests that the dispersal and emigration of caribou from summering areas (August dispersal) is caused by the disappearance of mosquitoes with continued attack by oestrids during late summer (Kelsall 1968, 1975; Curatolo 1975; Roby 1978). White et al. (1975, 1981) and Russell (1976) did not distinguish between the effects of mosquitoes and oestrids on the tendency of CAH caribou to seek relief terrain,

but merely noted that insect harassment caused caribou to move to the coast.

My results indicate that both mosquitoes and oestrids cause caribou to move to the coast. Results of the Kruskal-Wallis test indicating that this effect was most pronounced for oestrids seem contrary to the absence of a correlation between trap counts of oestrids and distance of caribou from the coast. This may indicate that caribou respond to oestrids in a discrete manner by moving to the coast whenever oestrids are present. Caribou are less apt to encounter mosquitoes at the coast because weather conditions there are frequently not conducive to flight (Chapter 1). Also, the sparse, decumbent vegetation characteristic of portions of the Beaufort Sea coast may not provide adequate shelter in which mosquitoes can escape inclement weather (Skjenneberg and Slagsvold 1968; White et al. 1975). The inhospitable weather and sparse, decumbent vegetation characteristic of the coast did not appear to affect oestrids to the degree that they affected mosquitoes (Figures 15-18). Therefore, the tendency for caribou to move to the coast when harassed by oestrids may be a stereotyped response to any insect attack. However, I suspect that oestrids are active in inland areas more frequently than at the coast, but are usually present in low numbers. The insensitivity of traps to low numbers of insects obscured this effect.

Many reports indicate that insect attack causes caribou to increase the frequency of standing, walking, trotting, running, and

milling, and decrease the frequency of feeding, lying, and nursing (Hadwen and Palmer 1922; Espmark 1968; Skjenneberg and Slagsvold 1968; Baskin 1970; White et al. 1975, 1981; Thomson 1977; Thing and Thing 1983). The results obtained using data sets 1 and 3 (Table 14) to examine the effects of insect harassment on caribou activity are inconsistent with these reports; however, the results obtained using data set 2 (Table 14) are consistent with the literature. I suspect that the results obtained using data sets 1 and 3 did not agree with other reports partially because the individual sweep and trap counts used to estimate insect activity for these data sets were susceptible to site-specific aberrations in levels of insect activity. In addition, sweep counts were especially vulnerable to short-term variability in prevailing levels of mosquito activity. For data set 2, each index of insect activity was pooled over all stations and samples (morning, noon, and evening) to indicate the daily level of mosquito or oestrid activity within the study area. Sacrificing the ability to detect spatial and temporal differences in insect activity was apparently outweighed by the greater accuracy of daily estimates of insect activity over all stations.

The more plausible results obtained using data set 2, as compared to results based on data sets 1 or 3 (Table 14) may have had a biological basis in addition to the stochastic reason just discussed. For example, the ability of caribou to perceive and react to changes in mosquito harassment may have agreed more closely with the sensitivity of daily estimates of mosquito activity for the

entire transect than with individual sweep counts. As noted above, sweep counts essentially provided point-in-space and time estimates of mosquito activity; they were probably quite sensitive, at least above some minimum level of activity, to local and ephemeral perturbations in prevailing levels of mosquito activity. In contrast, any potential host traveling over the tundra stirs mosquitoes from the vegetation and quickly accumulates a trailing cloud of these insects. This reservoir of mosquitoes around caribou probably buffers local and short-term variations in mosquito harassment between areas they traverse. In other words, caribou may be capable of grading their intensity of response only to prevailing levels of insect attack over large areas (e.g., the study area). This argument applies to the ability of caribou to respond to oestrids as well; however, since traps sampled periods 6-12 h long, the temporal component of variability would be less pronounced. Alternatively, caribou may have, in fact, been more sensitive to local and ephemeral changes in insect activity than I could measure. If so, the more plausible results obtained using data set 2 vs. 1 or 3 may merely indicate a coincidence in my ability to measure levels of insect activity and caribou response.

Results of the caribou activity examinations based on data sets 1 and 3 (Table 14) may also have contrasted with the literature because these data sets comprised only a small number of groups which made them vulnerable to the vagaries of observing a few very large groups of caribou behaving differently than most other groups. For

example, in the contingency table test presented in Table 16A, 491 of the 506 caribou observed lying when insects were active were contained in only two groups. The larger number of caribou groups for data set 2 apparently damped the effects of these large groups on the results.

It is tempting to interpret the significant rank correlation between sweep counts of mosquitoes and the daily proportion of groups in nonconstructive activities, and the absence of such a correlation for trap counts of oestrids (Table 15), as further evidence that caribou graded their response to the level of harassment by mosquitoes but reacted in a discrete manner to the presence of oestrids. However, the low proportion of groups in predominately nonconstructive activities when oestrids alone were present (Table 18) again raises the suspicion that trap counts failed to accurately estimate oestrid activity.

Results of the initial contingency table analysis based on data set 1 (Table 14) suggesting that caribou traveled most when insects were absent contradict most reports regarding caribou under insect attack (Russell 1976; Skjenneberg and Slagsvold 1968; Curatolo 1975; Geller and Borzhanov 1975; White et al. 1975, 1981; Roby 1978; Fancy 1986). Indeed, traveling as an insect-avoidance response is reportedly more important for caribou that inhabit flat, open areas (e.g., the Arctic Coastal Plain) than it is for caribou inhabiting mountainous regions because flat areas provide little insect-relief terrain (Skoog 1968; Bergerud 1974; Roby 1978).

In contrast, the results regarding caribou movements and activity obtained using data set 2 (Table 14) are consistent with the literature. During this study, caribou responded to oestrid harassment by standing motionless in a head-low posture, and by running; running was by far the most prevalent response. Occasionally, when oestrid attack was severe, lone caribou responded by alternately sprinting short distances (< 2 km) in panic, and then abruptly lying for a brief period (< 60 s) (Espmark 1968). The behavior of these caribou suggested that lying was mainly an attempt to evade the attacking flies rather than a consequence of overheating (Nikolaevskei 1968; Thomson 1977) or fatigue.

The greater tendency for caribou to travel in response to mosquito harassment, in comparison to harassment by oestrids, is also reflected in the examination of caribou rate of travel. The median rate of travel when mosquitoes and oestrids were present agrees closely with the 0.50–0.52 m per s rates of travel reported for reindeer and caribou under insect attack (Geller and Borzanov 1975; White et al. 1975; Wright 1979). The higher median rate of travel that I observed when mosquitoes alone were present is roughly comparable to the 0.93 m per s rate of travel that Curatolo (1975) reported for caribou under low levels of insect attack, but is substantially lower than the 1.53 m per s he reported for periods of severe attack. These disparities may indicate functional differences between populations in the response of reindeer or caribou to insect attack that are attributable to regional differences in the types and

availability of insect-relief habitat, or to the total and relative severity of harassment by mosquitoes vs. oestrids. Alternatively, they may be the result of using means vs. medians to express average rate of travel, unequal sample sizes, or differences in periods and distances over which these rates were determined.

Although inland movements by caribou were usually less directed, slower, and more relaxed than insect-induced movements toward the coast (see also Russell 1976), the cessation of insect attack occasionally caused rapid movements by caribou as well. On several occasions following long bouts (> 3 days) of insect harassment, I observed caribou trotting and running inland with only cursorial feeding through areas they typically used for foraging when insects were absent. This suggests that the quality or quantity of forage is substantially higher in inland areas than at the coast, and that caribou are most intent upon reaching these inland areas after expending considerable energy avoiding insects in coastal areas (Fancy 1986), and foregoing opportunities to feed (see also White 1983). Additionally, caribou may have been fleeing areas of high density, where the availability of food is reduced through intraspecific competition (Baskin 1970) and trampling, as much as racing toward areas having inherently better forage.

I was unable to quantitatively evaluate reports that oestrids cause caribou movements to be directed downwind (Roby 1978), or to become erratic (Espmark 1968; Curatolo 1975) since only 86 of 534 caribou observed more than 0.8 km from the coast were present when

oestrids were active. Aberrant movements by caribou seemed to occur most often when harassment by oestrids was severe. The contingency table analysis indicating that caribou traveled north and east when insects (i.e., essentially mosquitoes) were present agrees with reports that mosquitoes cause caribou to travel into the wind, as prevailing winds in the study area are from the northeast (Haugen and Brown 1980). This effect of mosquito harassment on the direction of caribou movements is suggested by the weak correlation between caribou direction of travel and wind direction. This correlation may have been weakened by caribou modifying their direction of travel to reach coastal areas as quickly as possible (White et al. 1975), and to negotiate real and perceived barriers, e.g. large lakes and roads. However, reindeer move into the wind even during periods when insects are absent (Thomson 1977; personal observation); therefore, insect harassment may merely reinforce this trait rather than act as a causative agent itself.

My results agree with other reports indicating that reindeer and caribou aggregate in response to mosquito attack (Espmark 1968; Baskin 1970; Skogland 1974; Roby 1978; Helle 1979); similar observations have been reported for many other species (Freeland 1977; Duncan and Vigne 1979; Waage 1979; Collins and Urness 1983). In addition to these empirical examinations, theoretical and experimental investigations leave little doubt that aggregations provide caribou near the center of groups some relief from mosquito attack (Baskin 1970; Helle and Aspi 1983). Groups could afford

relief from mosquitoes by overwhelming them with a superabundance of hosts and, perhaps most importantly, by denying mosquitoes adequate space to maneuver and locate areas of exposed skin, especially when group members become tightly packed. Milling behavior (Skoog 1968) may be an attempt by caribou near the unprotected periphery of a group to reach its center.

Results of my quantitative analyses suggest that oestrid attack causes caribou groups to fragment (see also Curatolo 1975; Roby 1978; Calef and Heard 1980; Helle 1981). However, the data on which these results are based may have been biased because often, when oestrids reached detectable levels of activity, mosquito activity was also severe and the large groups of caribou that formed at the coast were not visible from the Milne Point road. At these times, caribou were often either alone or in very small groups, and appeared to be "stragglers" that had not yet reached insect-relief terrain. For example, few caribou were observed during road surveys between 20-23 July 1983 when insect activity peaked for that year (Figures 3-5). At that time, aerial reconnaissance flights revealed that essentially all CAH caribou west of the Sagavanirktok River were aggregated into a large group that remained on the coast between the Kuparuk River delta and western margin of the Prudhoe Bay development complex.

Observations of this group on the afternoon of 22 July 1983 suggest that oestrids do not always cause caribou groups to disperse. On this day, no mosquitoes were present at the coast, but they were extremely bothersome more than 3-5 km inland; oestrids were present

inland and at the coast. This suggests that oestrid attack may complement mosquito harassment and maintain the coherence of aggregations that form in response to mosquito harassment, or even cause caribou to aggregate. Groups rarely fragmented even during severe harassment by oestrids, and when individual caribou did break out of a group, they usually returned very quickly. Most panic behavior was displayed by caribou that were alone or in very small groups. Boertje (1981) also reported no apparent reduction in the mean group size of an interior Alaskan caribou herd during the oestrid season, but noted that this was probably attributable to the accessibility of insect-relief sites on their summering grounds.

The mechanisms by which caribou aggregations alleviate mosquito harassment (swamping mosquitoes with a superabundance of potential hosts, and denying them room to maneuver) would also seem to apply to oestrid attack. Even if oestrids "clump" in response to the distribution of caribou groups and thus increase their probability of finding hosts (Cumming 1975), the above constraints on ovi- or larviposition could outweigh this apparent benefit to oestrids.

If oestrid attack does not induce group formation by caribou, then August dispersal may result solely from a reduction in the intensity or frequency of mosquito harassment below some threshold level necessary to keep caribou near the coast. However, if oestrid harassment does cause caribou to aggregate as I suspect (in contrast to my quantitative results; see also Wright 1979; Boertje 1981), then the inland dispersal of caribou during August results from a

reduction in the activity of both mosquitoes and oestrids. This would allow caribou to move south while foraging, or in response to endogenous factors (White et al. 1981). This hypothesis is supported by the concurrent disappearance of mosquitoes, oestrids, and caribou from the study area during late July and early August of 1982 and 1983. Even if oestrids do not cause caribou to aggregate, it is difficult to attribute August dispersal to oestrid attack in the absence of mosquito harassment since oestrids caused caribou to move to the coast.

Thomson (1977) reported that August dispersal is probably related to intense foraging for mushrooms rather than to patterns of insect harassment, and Luick (1977) stated that searching for mushrooms can lead to the rapid dispersal of reindeer (see also Skoog 1968; Boertje 1981). Central Arctic Herd caribou may not necessarily be searching for mushrooms when they disperse inland during late summer and early autumn, but forage-related movements certainly could affect August dispersal.

Other factors affected the size of caribou groups besides the presence of mosquitoes and oestrids. These factors were: (1) level of insect harassment (at least for mosquitoes); (2) the duration of alternating periods of insect harassment and abatement; (3) the type and availability of insect-relief terrain; (4) the presence of barriers to movements; (5) human disturbance; and (6) number of caribou in the area.

Effects of the first two factors noted above on caribou group

size may be related. The positive relationship between caribou group size and level of mosquito harassment (Table 15) could indicate a graded, functional response of caribou to mosquito attack, or it may reflect a correlation between these parameters that is determined by time and weather. Levels of mosquito harassment may depend more upon the duration of weather conditions favorable for activity than upon the exact level of these weather factors once they are within threshold limits for flight, at least to the point where mortality equals or exceeds the emergence of adults (Taylor 1963). If so, then time required to recruit mosquitoes into the population, and to enable dispersed caribou to coalesce, may be responsible for this correlation. This did not appear to be the case though, as large groups of caribou formed much faster when insect harassment was severe than when it was moderate or low; the hypothesis presented above would suggest that rate of increase in group size would be independent of level of attack. Nevertheless, extended periods (> 1 day) of mosquito harassment resulted in the formation of large groups, while long periods without insects resulted in small groups, because caribou tended to be, or become, widely dispersed. Short periods (< 12 h) of insect harassment or abatement generally resulted in minor changes in the average size of caribou groups, the outcome depending upon whether most groups were large or small when the presence of insects changed.

The limited diversity of insect-relief terrain near Milne Point, and on the Arctic Coastal Plain in general (Roby 1978), may cause CAH

caribou to form larger aggregations than caribou inhabiting areas where relief habitat is patchy and abundant. The area near Milne Point is devoid of riparian gravel bars, auffs, and large pingos that could provide respite from insects. Maritime weather conditions near the coast make this area the sole source of insect-relief habitat available to caribou in this area (Chapter 1). The width of this coastal band of relief habitat probably varies with weather patterns that are mainly determined by wind direction. I suspect that winds from the south move inland weather conditions north, and allow levels of insect activity in coastal areas to approximate levels of activity in southern areas (Chapter 1). Onshore breezes have the opposite effect. Insect-relief terrain appears to be limited to that area within 3 km of the Beaufort Sea; however, the area within 1 km of the coast appears to be of highest functional importance to caribou.

The continuous nature of the coastline also facilitates the formation of large caribou groups by acting as a barrier to northerly movements, and by relaxing spatial constraints on the maximum size of groups that can form there. Although use of specific areas along the coastline by caribou was partially opportunistic, points, river deltas, sand dunes, and mud flats were used most intensively (see also White et al. 1975, 1981; Roby 1978; Wright 1979; Boertje 1981). Site-specific areas of insect relief may explain the formation of groups numbering more than 5000 caribou, the theoretical size at which any additional reduction in insect harassment gained by

increasing the size of a group is outweighed by increased competition for food (Baskin 1970).

Roads and associated activity sometimes funneled caribou into areas near intersections and temporarily halted caribou movements, especially during the relatively relaxed movements inland that followed the disappearance of insects. This caused caribou to accumulate in some areas. Similar effects of natural obstacles, e.g. large rivers, have also been reported (Kelsall 1968; Wright 1979). Traffic occasionally had the opposite effect on group size by fragmenting large groups that were crossing roads (see also Smith and Cameron 1985).

The number of caribou in the vicinity of Milne Point certainly imposed an upper limit on the maximum size that caribou groups could attain in the study area. This should be considered when comparing the effects of insect harassment on caribou among different herds.

Unlike many studies (reviewed by Hamilton 1971), my results do not unequivocally show that insect harassment causes the density of caribou groups to increase. In light of the extensive literature addressing this phenomenon and my empirical observations, the positive correlation between caribou group density and level of mosquito attack (Table 15) seems more plausible than results of the contingency table analysis indicating that group density is not affected by the presence of insects, particularly in light of the high tolerance of Rangifer to close contact by conspecifics during summer (Thomson 1977). As noted above, mosquitoes and oestrids

probably lack adequate space to maneuver and locate anatomical sites of attack on caribou near the center of densely packed groups. It has also been suggested that the "steam of sweat" that rises from tightly bunched groups of reindeer may also reduce levels of mosquito harassment (Itkonen 1948 as reported by Helle and Aspi 1983; Mezenev 1971 as reported by Helle 1979). This seems unlikely though, since the odors and carbon dioxide that emanate from caribou groups probably attract mosquitoes and oestrids (White et al. 1975; Roby 1978). Even so, group density is strongly influenced by social factors, activity (e.g., traveling vs. grazing or lying), and other disturbances (Thomson 1977). These factors may obscure the effects of insects on caribou group density.

The low proportion of calves in maternal groups when mosquitoes were present indicates that the tendency for caribou to aggregate when harassed by insects prevails over the tendency for maternal and nonmaternal caribou to segregate. This is an indirect effect of insect harassment rather than a defense reaction itself. Thomson (1977) reported similar observations for CAH caribou, and contrasted this behavior with wild reindeer in Norway.

Before discussing specific results of the canonical correlation analyses, it is important to note that this analytical technique does not distinguish dependent and independent sets of variables for examining functional relationships. Instead, the canonical variables are created to maximize the canonical correlation between linear combinations of two sets of variables. Thus, canonical correlation

analysis does not generate predictive models; rather, it shows the strength of a relationship between two sets of variables, and indicates the relative importance of each original variable in describing this relationship. This does not imply that responses by caribou are actually determined by other stimuli, e.g. weather factors, and are merely correlated with levels of insect harassment. The literature indicates that caribou respond to weather-mediated insect attack (Thomson 1971, 1977; Curatolo 1975; Russell 1976; Roby 1978). I make this distinction to point out that the coefficients obtained from this analysis are not meaningful for predicting an overall response by caribou to some combined level of insect activity.

Each canonical correlation analysis indicated that sweep counts of mosquitoes were more strongly correlated with caribou responses than trap counts of either mosquitoes or oestrids. This supports the recurrent suspicion that the trapping effort expended during this study was inadequate to estimate the activity of mosquitoes or oestrids (Chapter 1).

The canonical correlation analysis examining the relationship between variables describing caribou group structure (group size, composition, and density) and measures of insect activity further suggests that the inverse relationship between the proportion of calves in maternal groups and level of insect activity results from the tendency of caribou to aggregate during insect attack. These values also indicate that group density and group size are of

comparable importance in describing the effects of insect harassment on caribou group structure (Table 24). This suggests that the contingency table analysis indicating group density is not affected by insect attack is misleading.

Adding all remaining caribou response variables (proportion of groups in nonconstructive activities, rate and direction of travel, and distance from the coast) to those describing caribou group structure had two effects on the canonical correlation analysis. It greatly increased the strength of the correlation between the two sets of variables, and it added a second pair of significant canonical variables to the model. It is not surprising that the strength of the correlation between insect activity and caribou response increased because more information regarding these reactions was provided by the additional variables; however, adding random numbers to parameters describing caribou groups would also increase the strength of the canonical correlation merely through chance patterns of association. It is surprising that group density did not significantly contribute to describing the overall response of caribou to insect harassment in light of the rank correlation and canonical correlation analyses discussed above (Tables 15 and 22, respectively). Group density was weakly correlated with the proportion of groups in nonconstructive activity, and significantly correlated with caribou rate of travel (Table 15). Therefore, the high P-value obtained for group density in this analysis does not necessarily indicate that the tendency for groups to become more

dense with increasing mosquito activity was of no biological importance. Instead, it probably reflects a redundancy between group density and rate of travel, and perhaps with the proportion of groups in nonconstructive activity.

Caribou rate of travel and the proportion of groups in nonconstructive activity were the primary components of the first canonical variable for caribou response; the first canonical variable for insect activity reflected sweep counts of mosquitoes. The second pair of canonical variables mainly incorporated caribou group size and trap counts of mosquitoes into the model. The factor that seems to distinguish each pair of canonical variables is the plasticity of the original variables through time. Sweep counts changed more rapidly than trap counts of mosquitoes because of the different length of time that each capture technique sampled (100 s vs. 6-12 h); caribou rate of travel and activity could change almost instantly, while changes in average group size occurred more slowly as widely dispersed caribou coalesced (see also Thomson 1977). Thus, the first canonical variable for insect activity could be interpreted as expressing short-term fluctuations in levels of mosquito attack attributable to the immediate effects of weather, while the second canonical variable reflected changes in prevailing levels of mosquito activity. Similarly, these respective canonical variables for caribou response could be interpreted as expressing highly responsive behavioral reactions to insect attack, and a less responsive reaction at the group level.

The canonical correlation between weather-insect parameters and caribou responses was not substantially stronger than that for caribou responses and insect activity alone (Tables 24 and 26). However, adding weather variables to measures of insect activity made the second pair of canonical variables nonsignificant, and incorporated the effects of these abiotic factors into the model. This can be interpreted two ways: (1) caribou respond directly to weather factors; or, (2) the high degree of accuracy and precision associated with measurements of weather parameters in relation to estimates of insect activity (i.e. sweep counts of mosquitoes), combined with the strong correlations between sweep counts of mosquitoes, ambient temperature, and atmospheric humidity (Chapter 1), provided a better estimate of mosquito activity than sweep counts alone. Although the two interpretations are not mutually exclusive, I suspect that the nonsignificance of the second canonical variable is an artifact of these strong correlations between weather and insect activity rather than the result of a direct response by caribou to weather. With the exception of wind velocity and direction (Thomson 1977), weather factors are not thought to directly affect the distribution and behavior of caribou as much during summer as in winter; their principal effect on caribou during summer is reportedly expressed through weather-mediated insect attack (Curatolo 1975; White et al. 1975, 1981; Roby 1978). Since mosquito and oestrid harassment ensued almost immediately after conditions became favorable for flight, and because caribou would gain little from

predicting the cessation of insect attack, they would have little need or opportunity to assess current weather conditions and anticipate forthcoming harassment. Also, if caribou do exploit weather cues and begin to aggregate and travel rapidly toward the coast before insects become bothersome (i.e., there is a biological reason why weather factors significantly contributed to describing the relationship between weather-insect parameters and caribou response), these weather parameters should enter the model via a separate canonical variable since they reflect a different type of information (probability of future harassment) than sweep counts of mosquitoes (present level of harassment).

Lags between time-of-emergence for female mosquitoes and when they began to actively seek a blood meal may have affected my estimates of their effects on caribou. Hocking et al. (1950) reported that even though Aedes spp. that inhabit tundra regions tend to fly soon after emergence, up to seven days may pass before females begin to search for hosts. Therefore, sweep counts may have provided a better index of mosquito activity than mosquito harassment. My own experience as a donor of blood meals to mosquitoes suggests that lags between mosquito emergence and harassment had little effect on my results.

Lags between the time when insects became inactive and when caribou ceased their avoidance responses may have had a more serious effect on my results than the lags noted above. This effect varied among the different types of responses exhibited by caribou, and with

the duration of insect attack. Unfortunately, I could not quantitatively examine these effects through time-series analyses because the periods between measurements of insect activity, and between caribou surveys, were too long to reflect these lags. I suspect that time lags introduced an unmeasured source of variability into my results that weakened the measurable effect of insect harassment on caribou response. Nevertheless, insect harassment was the dominant force affecting the distribution and behavior of caribou near Milne Point during July and early August.

Descriptive observations

My impression that the immediate, behavioral reactions of individual caribou to oestrids were stronger than the responses elicited by mosquitoes concurs with other reports (Hadwen and Palmer 1922; Roby 1978; Wright 1979). This seems ironic considering that caribou probably do not realize any immediate benefit from avoiding oestrids. It is unlikely that female oestrids cause any discomfort during ovi- or larviposition since female warbles merely attach rows of eggs to individual caribou hairs, and female bots spray first stage larvae into caribou nares without physically making contact (Skjenneberg and Slagsvold 1968). However, the extremely close approach of female bots to the nares of caribou must be disconcerting; also, caribou may associate warbles and bots with other biting flies, e.g. tabanids, that cause discomfort. Thus,

there there are several possible explanations for the intense response of caribou to oestrids: (1) caribou are disturbed by the sound and close approach of female oestrids, (2) caribou associate oestrids with other insects that cause pain, (3) caribou associate any discomfort caused by the endoparasitic larvae with attacks by adult female flies, much as rats (Rattus norvegicus) learn to avoid certain foods (Alcock 1979; Garcia et al. 1974), (4) caribou have evolved stereotyped responses to oestrid attack based on an association between insects and pain, or (5) caribou have evolved avoidance responses to minimize the physiological costs imposed by endoparasitic oestrid larvae.

I doubt that merely the sound and close approach of female oestrids would elicit the intense responses typically exhibited by caribou under oestrid attack. Also, many reports suggest that reindeer, and other cervids, are capable of distinguishing different types of insect pests by the sound of their wingbeats (Hadwen and Palmer 1922; Espmark 1968; Collins and Urness 1983). Caribou may associate attacks by female warbles with subsequent discomfort caused when first stage larvae penetrate the skin, but this seems unlikely. Warble eggs require 3-7 days to hatch (Hadwen 1927; Brejev and Brejeva 1946; Skjenneberg and Slagsvold 1968); this seems too long for caribou to make such an association. The potential for irritation from bot fly larvae seems greater than for warble larvae since even first stage bot larvae possess strong mouth hooks (Skjenneberg and Slagsvold 1968). Even so, although caribou

frequently "blow" immediately after being attacked by a bot, they do not exhibit prolonged sneezing, blowing, or mucus production that would indicate continuous discomfort at other times during the summer. I suspect that the initial "blow" exhibited by caribou is an attempt to expel larvae from their nares, rather than a response to irritation or pain.

Oestrid larvae are capable of imposing substantial physiological costs on their hosts (Washburn et al. 1980; Dieterich 1985). Warble larvae create open fistulas through which they respire. Bot larvae possess strong mouth hooks that scrape the mucous membrane of the retropharyngeal pouch and stimulate the production of mucus on which they feed (Oldroyd 1964). Thus, both types of larvae eventually create sites of secondary infection for other pathogens.

Additionally, oestrid larvae cause dyspnea, allergic responses, and nervous disorders (Skjenneberg and Slagsvold 1968; Dieterich 1980; Dieterich and Haas 1981). Infestations by warble larvae can exceed 1000 per individual caribou (Hadwen and Palmer 1922; Savel'ev 1968; Zabrodin 1975; personal observation), and infestations of reindeer by bot larvae typically number 10-50 (personal observation). The cumulative effect of these parasites on their host is probably debilitating judging from the appearance of heavily parasitized reindeer and caribou, and can occasionally result (at least indirectly) in death. Therefore, it appears that the costs of endoparasitism by oestrid larvae probably exceed the disadvantages of avoiding adult flies, and thus confer a selective advantage to

caribou having avoidance characteristics. Examples of costs associated with oestrid avoidance include: energy demands resulting from avoidance responses (e.g., trotting and running) (Russell 1976; Fancy 1986), opportunity costs of reduced feeding (Thomson 1977; White 1983), cow-calf separation (Calef and Lortie 1975; personal observation); and traumatic injuries sustained while running aberrantly and milling.

In contrast to oestrids, mosquitoes can be extremely annoying to caribou since they do bite, and because they concentrate their attack on sensitive areas of exposed skin around the eyes, genitals, and anus. However, the potential threat to the health of caribou in northern regions seems less for mosquitoes than for oestrids, even considering that mosquitoes are the intermediate host for some internal parasites (e.g., Setaria yehi; Dau and Barrett 1981), and can remove up to 125 g of blood per reindeer per day when harassment is severe (Nikolaevskei 1968).

Thus, caribou probably avoid mosquitoes to reduce the annoyance caused by their bites (proximal explanation), and to minimize the long-term effects of blood-loss (ultimate explanation). However, it may not be necessary to invoke the latter explanation of mosquito avoidance if such responses are merely nonadaptive. Since caribou react less intensely to mosquitoes than to oestrids, and considering that caribou usually lose less than 125 g of blood to mosquitoes per day, caribou may be responding more to the proximal costs of mosquito attack than to ultimate, selective forces. If the intensity of

avoidance by caribou reflects the strength of the selective pressure exerted by a parasite (Skjenneberg and Slagsvold 1968), then the consequences of being parasitized by oestrids appears to be more severe than those associated with losing blood to mosquitoes.

Unlike other researchers (see above), I did not detect any difference in the type or degree of response by caribou to warbles vs. bots. This may have been because I focused on the response of caribou to insect attack at the population rather than individual level. Also, the scarcity of bots in the study area in relation to warbles (Chapter 1) limited the opportunity to observe and compare the responses of caribou to each type of oestrid. Nevertheless, caribou usually lowered their head near the ground when attacked by bots or warbles. Espmark (1968) attributed this type of response to harassment by bots and suggested that it was an attempt by reindeer to reduce access to their nares. Alternatively, I suggest that caribou may be attempting to silhouette the dark flies against the sky and improve their chances of detecting and avoiding them.

CONCLUSIONS

1. Sweep net counts are superior to trap counts in modeling mosquito activity from weather variables, and for estimating mosquito harassment as it affects the distribution and behavior of caribou.
2. Sticky traps may be an effective means of quantitatively estimating the activity of oestrids; however, trapping effort expended during this study was probably inadequate to detect oestrids at low levels of activity. This limited my ability to model oestrid activity as a function of weather, and to compare the effects of mosquitoes and oestrids on the distribution and behavior of caribou.
3. Ambient air temperature and saturation deficit affect the activity of mosquitoes and oestrids more strongly than other weather factors.
4. Weather conditions near Milne Point are usually unfavorable for mosquitoes and oestrids within 20 km of the Beaufort Sea, and are least favorable within 1-3 km of the coast.
5. Weather conditions mainly affect the occurrence rather than prevailing level of insect activity within 20 km of the coast.
6. Weather conditions are more variable through time than through

space; this necessitates general models to predict daily levels of insect activity from weather variables for that area within 20 km of the coast.

7. A two-stage approach discriminating between days when insects are present and absent, and then predicting levels of insect activity for days when insects are present, is more plausible for predicting insect activity than using all observations to predict levels of insect activity. Estimates of insect activity are most accurate when predictions are made on a daily basis for a large area.

8. Caribou inhabit coastal regions during periods of harassment by mosquitoes or oestrids; this effect is most pronounced when oestrids are present.

9. Harassment by mosquitoes and oestrids prevents caribou from lying; insect harassment also causes caribou to feed while traveling, and to walk, trot, and run without feeding. Caribou occasionally stand in a characteristic head-low posture when harassed by oestrids, but few caribou stand even when insects are bothersome.

10. Caribou rate of travel is positively correlated with level of mosquito activity.

11. Caribou travel north and east into prevailing winds, and

generally toward the coast, during periods of insect harassment; caribou travel south when insect harassment ends.

12. Mosquito harassment clearly causes caribou to aggregate; the effect of oestrid attack on caribou group size is equivocal. Oestrid attack may complement other factors that cause caribou to disperse and emigrate from coastal areas during August, but is probably not responsible for this phenomenon by itself. Instead, infrequent periods of low mosquito and oestrid activity that occur during late July and early August may simply eliminate the need for caribou to remain near coastal insect-relief terrain in late June and early July.

13. The tendency for caribou to aggregate in response to insect harassment reduces segregation between maternal and nonmaternal caribou.

14. The average distance between caribou within groups tends to decrease during insect attack; however, this response is highly variable at all times during summer.

15. Caribou rate of travel, and the proportion of groups in constructive activities, are most highly correlated with level of insect activity. Sweep counts of mosquitoes are more strongly correlated with caribou responses than trap counts of mosquitoes, or

trap counts of oestrids.

16. Adding weather variables to measures of insect activity does not increase the canonical correlation between responses by caribou and insect harassment. Caribou appear to respond to weather-mediated insect harassment rather than to weather factors themselves.

17. Caribou react more strongly to oestrid imagoes than to alate mosquitoes; this suggests that endoparasitic oestrid larvae impose a greater selective cost on caribou than do ectoparasitic mosquitoes.

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