MIGRATORY BEHAVIOR OF SEMIPALMATED SANDPIPERS
AT INLAND AND COASTAL STAGING AREAS

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MIGRATORY BEHAVIOR OF SEMIPALMATED SANDPIPERS AT INLAND AND COASTAL STAGING AREAS

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Cornell University, 1983

The behavior of Semipalmated Sandpipers (Calidris pusilla) was studied at staging areas along an inland, overland migration route (North Dakota) and a coastal, transoceanic route (New Brunswick). Birds were captured, measured, aged, individually marked, released, and censused daily throughout the autumn migratory season. Timing, direction, and size of flocks leaving the study sites were recorded.

Morphometric analysis showed that inland migrants originated in western, and coastal migrants in eastern, breeding populations. Birds arrived with little stored fat, and could deposit 1.3-2.5 g./day of fat, with the higher rates on the coast. Maximum fat deposits approximated fat-free weights at both sites. Adults departed at fat levels of 16-20 g.; juvenile birds showed a wider range. Coastal adults had slightly higher fat departure thresholds than inland adults. Regardless of fat levels, birds did not migrate without favorable meteorological conditions. Birds were seen for 15-25 days after capture in July, but only 8-12 days by September. The decline in length of stay started earlier on the coast.

Flocks departed both sites heading southeasterly, the normal migratory direction. Departing flocks were larger on the coast (mode 18-22) than inland (mode 3-7). Inland the vanishing bearings of larger flocks were less variable, though in the same mean direction, as those of smaller flocks. Flocks departed primarily during a two-hour period before sunset. On the coast, departures also occurred on rising tides. At both sites, changes in weather stimulated some departures at other times. Flocks departed with predominantly WNW surface winds. Tail-winds at departure were stronger, and side-winds weaker, on the coast. Since prevailing winds were equivalent at the two sites, the difference implied greater selectivity by coastal migrants.

Inland and coastal Semipalmated Sandpipers showed similar migratory behavior, when contrasted with passerines. Nevertheless, the eastern population showed significant differences in fat stores, flock size, and winds at departure, suggesting increased specialization for non-stop, overwater flight.

BIOGRAPHICAL SKETCH

David Berel Lank has always been interested in the motivation of human and animal behavior.

He was born on 13 August, 1951, in Rochester, New York--at home, due to his mother's disinclination to waste time at the hospital waiting around. He has no memories prior to the summer of 1969, when he attended the Woodstock festival, watched the first moon launch, and hitchhiked across the United States. He then started as an undergraduate at Columbia University just in time for The Riots. He studied psychology and anthropology, concluding that neither field could adequately explain human behavior. So he moved to a tree house in Vermont, to study a simpler world. At Marlboro College he learned to cross-country ski, which he greatly enjoys still, and became a vegetarian, which he does not enjoy still.

From Marlboro he journeyed to the Bay of Fundy to complete an undergraduate research project on migration. There he discovered the charms of the Semipalmated Sandpiper. In the ten years since, his life has been devoted to unlocking the mysterious secrets behind the marvelous journey made by these tiny creatures.

After graduation Dov spent a summer at the Itasca field biology station, during which time he talked his way into graduate school at the University of Minnesota. After an inconclusive study on sandpiper migration, he next talked his way into Cornell University.

There he continued his quest for the answer to life, the universe and everything. In Ithaca he discovered the perfect combination of rural living and urban sophistication that all of his generation is searching for. He ultimately found The Barn, the perfect dwelling place despite certain rural inconveniences, and proceeded to fill it with a family of Barnmates. He stretched out his doctoral career in an effort to remain in Ithaca indefinitely, but this life was rudely brought to an end by the offer of a job at the University of North Dakota.

In Grand Forks he spent two years as a pre-doctoral post-doc and a third teaching Ornithology. After three summers observing the intimate personal relationships of Spotted Sandpipers in northern Minnesota, he moved to Columbus, Ohio, where his wife is beginning a graduate program. His new life as a man of leisure has been shattered by the offer of a job teaching Animal Behavior and Evolution, which he can find no excuse for refusing.

ACKNOWLEDGEMENTS

The design, execution, and completion of this dissertation involved the support of many persons and institutions.

Members of my graduate committee, P. P. Feeny, E. Adkins Regan, J. Camhi, H. C. Howland, and my chairman, S. T. Emlen provided guidance during my career at Cornell and suggestions for improvements of earlier drafts of this dissertation.

At Kent Island, a field station of Bowdoin College, Norman Carlin, Reid Harris, and W. G. Kinsey helped capture, measure, and census birds. Beverly Greenspan, Timothy Rummage, and Richard Podolsky aided in the design and execution of field work. Myhron Tate, of Ingall's Head, Grand Manan, provided essential logistical support and lobsters. I thank W. J. Richardson and the National Research Council of Canada for providing time-lapse cameras for filming radar screens.

At Sibley Lake, Danny Svingen, Eric Molbert, and Greg Lambeth helped with the field work; Mrs. Svingen provided the lunch boxes. Ralph Molbert permitted access to his prairie land, provided that the cattle gates were closed. Robert M. Stewart helped select the study site and suggested successful techniques for trapping sandpipers. Bertha and Jake Schwartz provided hospitality during my stay in North Dakota.

The data analysis phase of this study was aided by Steve Worona, who generously wrote an original computer program that collated the

data from marking and censuses. Cavelle Brownie and Douglas Robson of the Cornell Biometrics Unit, developed methods for estimating emigration rates.

My graduate years at Cornell were enlivened and enriched by fellow graduates students, and especially by my Barnmates, Todd Hutchenson, Peter Wrege, and Connie Smith.

This dissertation was written while I was working with Lewis Oring, at the University of North Dakota. I appreciate his understanding attitude towards my dual responsibilities. The assistance of the personnel, and use of the facilities, of the UND computer center facilitated the preparation of this manuscript.

Cheers are due Steven T. Emlen, my advisor at Cornell, who kept faith through the frustrating moments of my predoctoral career. His balance of encouragement and criticism greatly improved the quality of the work.

My parents, Norman and Edith Lank, provided essential support and criticism, from the initial manufacturing of wing tags to the final editing and preparation of the manuscript.

Constance M. Smith entered my life when this project was begun. Along the way she has helped with nearly every aspect of the work, including tag making, field work, data analysis, preparation of figures, editing my ramblings, and providing encouragement to get the job done. Connie, I thank you, and offer my assistance with your own work.

Thanks are due the G. D. Harris Foundation for funding the purchase of a spotting scope. The bulk of the work was supported by grants BNS-7518905 and BNS-7813016 from the National Science Foundation.

CONTENTS

LIST OF TABLES

LIST OF FIGURES

DEDICATION

This thesis is dedicated to

my maternal grandmother, Sara Heller,

and my paternal grandfather, Dr. Harold H. Lank.

Chapter I

INTRODUCTION

1.1 THE BEHAVIORAL ECOLOGY OF BIRD MIGRATION

Annual migrations of birds were first addressed in an evolutionary context by A. R. Wallace (1874:459) who wrote:

> It appears to me probable that here, as in so many other cases, "survival of the fittest" will be found to have had a powerful influence. Let us suppose that in any species of migratory bird, breeding can as a rule be only safely accomplished in a given area; and further, that during a great part of the rest of the year sufficient food cannot be obtained in that area. It will follow that those birds which do not leave the feeding area at the proper season will suffer, and ultimately become extinct; which will also be the fate of those which do not leave the feeding area at the proper time. . . . The actual causes that determine the exact time, year by year, at which certain species migrate will of course be difficult to ascertain. I would suggest, however, that they will be found to depend on those climatal changes which most affect the particular species. The change of colour, or the fall, of certain leaves; the change to the pupa state of certain insects; prevalent winds or rains; or even the decreased temperature of the earth and water, may all have their influence. . . . The two areas should be carefully determined for a number of migratory birds; the times of their movements should be compared with a variety of natural phenomena likely to influence them; the past changes of surface, of climate, and of vegetation should be taken account of; and there seems no reason to doubt that such a mode of research would throw much light on, if it did not completely solve, the problem.

Wallace recognized that the timing of migration was a key determinant of the probability of survival, hence an area where natural selection could have clear, strong effects on behavior. Studies relating environmental variables to the timing of migration have been pursued with increasing technical sophistication for nearly 100 years, especially with regard to the effects of meteorological conditions (e.g. Cooke, 1885a, b, 1911, 1913; Trowbridge, 1902; Clarke, 1912; Bagg et al., 1950; Lack, 1960; Nisbet and Drury, 1968; Able, 1973; Richardson, 1978a), and we now know a good deal about the "actual" or proximal causes of day-to-day variability in numbers of migrants. While broad generalizations about proximal causes may be made, there is also, as Wallace predicted, diversity among species in the control of migratory behavior. For example, studies of a wide variety of species at numerous locations and at different seasons have found clear positive correlations between numbers of birds aloft and the strength of following winds (see Richardson, 1978a, for review). However, in coastal Louisiana in spring, both radar and visual studies showed no relationship between the initiation of migratory flight by passerines and the prevailing wind direction (Gauthreaux, 1971; Hebrand, 1971). Apparently, in this case, the higher energetic cost of headwind flight has not been sufficient to deter migration, and we may infer that other selective forces favor rapid movement out of coastal forests. At the behavioral level, this means that wind direction (or whatever closely correlated environmental feature the birds sense and respond to) has been "downgraded" in the migratory control system relative to its apparent importance to these same migrants later in the season at more northerly latitudes (e.g. Bellrose, 1967; Nisbet and Drury, 1968; Richardson and Gunn, 1971).

Examination of the selective forces operating in this unusual case, if possible, would provide insight into the evolution of migratory behavior. In the tradition of Wallace, such a study would involve consideration of the routes, distances, and timing of flights relative to environmental, physiological and social conditions. Uncovering selective pressures by relating these factors to migratory behavior defines the field I am calling the behavioral ecology of bird migration.

This study compares the behavior of two populations of the same species of small shorebird which make quite different migratory flights. One population migrates diagonally across central North America, and has many potential landing sites *en route*. The other population normally makes a two-day flight over the western Atlantic, with no possible intermediate stops. I measured how each of these populations behaves prior to and at takeoff on these migratory flights. The comparison between populations may be viewed, up to a point, as the result of an historical "experiment" that occurred as breeding ranges moved northward and migration routes lengthened following the last Pleistocene glaciation. The adaptations of local populations are the "results", and examination of them provides insight into the "experimental procedures" of natural selection.

Inferring past selective pressures by studying current behavior requires the assumption that each population is currently adapted to the contingencies of its flightpath. This seems reasonable in view of the length of time these routes have been followed, and the genetic separation of the populations that can be documented by small morphological differences between them. However, environmental variables other than the difference in flightpath may also differ between the populations, which precludes automatic acceptance of the difference in flightpath as the ultimate cause of any behavioral differences found. For example, systematic differences in the patterns of food availability or in the frequency of favorable migratory weather might also cause differences in the migratory behavior of the populations. In short, the "experiment" to determine the effect of flightpath is imperfectly controlled. Thus, this study addresses the question of how differences in flightpath plus associated environmental differences affect the migratory behavior of birds.

1.2 AUTUMN MIGRATIONS OF SEMIPALMATED SANDPIPERS

Semipalmated Sandpipers (*Calidris pusilla*) breed across arctic North America, and eastern and western populations follow quite different migratory pathways. Populations breeding in Alaska and the western Canadian arctic follow a southeasterly transcontinental course to wintering grounds in coastal Central America and western South America (Harrington and Morrison, 1979; Lank, 1979; Section 3.5.1). These birds may cross the Gulf of Mexico, or fly over portions of the Caribbean, but most of their migration is overland. This contrasts with the migration of populations breeding in the central and eastern Canadian arctic, which follow a southeasterly course that includes a 40-60 hour non-stop flight from the northeast Atlantic coast to the West Indies or northeastern coast of South America (Baird, 1867; Cooke, 1903; McNeil and Burton, 1973, 1977; Richardson, 1979; Stoddard *et al.*, in press; Section 3.4.2).

Prior to this study little was known about Semipalmated Sandpiper migration through the midwest. Information on the timing of seasonal passage was available (e.g. Oring and Davis, 1966; Parmelee *et al.*, 1969; Martinez, unpub data). Concurrent with this study, both

Harrington and Morrison (1979) and Spaans (1979) suggested, with little direct evidence, that midwestern migrants originated in Alaskan breeding populations. Virtually nothing was known of the specific migration routes, the timing of movements by sex and age classes, the amount of fat stores carried, the timing of migration in relation to weather patterns or other environmental variables, or the location of wintering grounds.

Eastern birds have been studied in greater detail. Page (1970) and Page and Middleton (1972) described the migratory timing of age classes, and the fat deposition of Semipalmated Sandpipers staging at Long Point, Ont. A series of papers documented the timing, migration routes, and fat stores carried by *C. pusilla* staging in the Maritimes (McNeil and Burton, 1973, 1977; McNeil and Cadieux, 1972a). Richardson (1976, 1979) correlated radar observations of shorebirds leaving the Maritime coasts with meteorological conditions, but, as with most radar studies, could determine neither the geographical origins nor the species of birds aloft. Morrison (1976-1978, Morrison and Gratto, 1979a) documented the morphometrics and dispersal patterns of the large numbers of Semipalmated Sandpipers staging at James Bay, Ont. Harrington and Morrison (1979, unpublished data) are coordinating ongoing surveys of shorebird staging areas that provide excellent distributional information on the numbers of Semipalmated Sandpipers in eastern North America.

The work presented here differs from previous studies of shorebird migration in its focus on the factors influencing the initiation of migratory flight, and by its comparative approach. Semipalmated Sandpipers were studied at migratory staging areas on both midwestern and eastern routes. Study sites were located between breeding and wintering areas, so that all birds had migrated to, and would migrate from, the areas. The inland site was located in central North Dakota, and the coastal site was just off the New Brunswick coast, where birds were preparing for transoceanic flight. At each location migrants were captured, measured, individually marked, and intensively observed daily to enable description of their behavior at the staging area and determination of the time of departure. Sightings of marked birds provided information on dispersal from staging areas. The staging and takeoff behavior at the two sites was compared and considered with regard to the differences in migratory routes and other environmental factors.

1.3 PROXIMAL REGULATION OF MIGRATORY FLIGHT

Studies of the seasonal regulation of migratory physiology of songbirds have shown the importance of photoperiod (Rowan, 1925, 1929; see Farner and Lewis, 1971, for review) and, more recently, of endogenous circannual rhythms (Gwinner, 1967, 1977; Berthold, 1978a) in the integration of migratory behavior into the annual cycle of birds. The utility of photoperiod as a direct stimulus and/or as a synchronizer of circannual rhythms is clear: it provides a reliable measure of date in the season. Other plausible influences, such as food abundance and temperature, are of only minor importance to arctic and temperate zone passerine migrants (see Berthold, 1975a, for review). Unfortunately, there have been no direct studies of the seasonal regulation of migratory physiology of shorebirds.

In contrast to overall seasonal regulation, the timing of flights _within_ the migratory season is believed to be determined by multiple factors, including date in the season, hour of the day, a variety of meteorological factors, the amount of fat carried, the availability of food at staging areas and along migratory pathways, endogenous rhythms, and the social behavior of other birds. The initiation of migratory flight currently is understood to be a complex function of the factors listed above, and others, combined in a hierarchical or additive fashion (e.g. Hinde, 1951; Lack, 1960; Mueller and Berger, 1966; Dolnik and Blyumental, 1967; Nisbet and Drury, 1968; Able, 1973; Berthold, 1975; Rappole and Warner, 1976; Gwinner, 1977; Baker, 1978:642-644; Alerstam, 1978b). The verbal models and flow diagrams presented in these studies vary in their overall design, emphasis on particular environmental factors, and the postulated degree of internal and external control. Nearly all are presented as general models for migratory birds, rather than as quantitative descriptions of the behavior of particular species.

In contrast, this study attempts to quantify and compare the migratory behavior of two populations of one species. It was designed to measure the behavior of particular individuals and/or daily cohorts, which would enable multivariate estimation of the influences of time of day, date, weather, fat stores, population density and other variables on the probability of emigration, as was done by Rabøl and Hansen (1978). I hoped to use lengths of stay of individuals or estimated daily departure rates derived from censuses of marked birds as dependent variables. Early in the analysis, it became clear that local movements by birds invalidated either measure as an accurate reflection of the migratory behavior of the populations. The primary analyses on the timing of migration used instead direct observations of migratory departures, a variable more difficult to relate quantitatively to the information obtained on individuals. Thus, the treatment of the migratory strategy of Semipalmated Sandpipers as a whole is qualitative, as in all studies except Rabøl and Hansen (1978).

Despite this limitation, the major goals of the study were realized, albeit in a more complex fashion than orginally anticipated. By use of a variety of techniques and analyses involving partial sets of independent variables, I was able to describe the relationships between migratory activity and the variables, uncover significant interactions among them, and quantitatively compare the results from both populations for each analysis.

1.4 PREVIEW

The remainder of the thesis is outlined in this section.

Chapter 2 presents methodology.

Chapter 3 reviews the autumn migrations of Semipalmated Sandpipers. It emphasizes the routes followed by eastern and western breeding populations from breeding to staging areas, and compares the flights faced by birds departing from North Dakota and New Brunswick.

Chapter 4 covers the seasonal timing, population dynamics, foraging behavior, and fattening of birds at the staging areas. Sections deal with 1) local population sizes and competition for foraging space, 2) fat levels of birds caught daily throughout the season, and 3) the length of staging periods relative to initial fat and date in the season.

Chapter 5 deals primarily with migratory departures. Sections cover 1) departure behavior and flight directions, 2) temporal patterning of departures on a daily basis, 3) meteorological correlates of flights, and 4) the relationship of fat and migration.

Chapter 6 summarizes the staging and departure behavior of Semipalmated Sandpipers, and compares it with the behavior of other species. It considers the adaptations of inland and coastal populations to their flightpath and environment. The chapter concludes with speculation on the evolution of transoceanic migration utilizing the findings of this study in conjunction with reconstructions of post-Pleistocene breeding grounds and atmospheric conditions.

Chapter II

METHODS

Studies of the control of bird migration in recent years have been dominated by radar studies, often in conjunction with meteorological analyses (e.g. papers in Gauthreaux, 1974; Richardson, 1978a), and by laboratory studies of patterns of *Zugunruhe*. While these studies have provided much new information, both approaches have limitations. Radar studies, in general, measure the relative numbers of migrants over a given area, but usually cannot determine the size of the potential pool of migrants, the species observed, or the physiological condition of the migrant population (Nisbet and Drury, 1968). They are thus useful in predicting migration volume for planning traffic patterns of aircraft, but less useful in understanding and quantifying the migratory behavior of individual birds (but see Demong and Emlen, 1978). Laboratory studies, while able to quantify individual behavior, suffer from (and gain advantage from) the limitations imposed on a bird's movements. Birds cannot migrate in the laboratory, and interpretation of their behavior under laboratory conditions is complex (see Gwinner, 1977, for discussion). In contrast to both these approaches, this was a field study. It stressed data collection on the morphology and behavior of individuals in conjunction with local environmental conditions. I hoped in this way to reach an increased understanding of the processes that cause a bird to launch itself on a 3000 km. migratory flight.

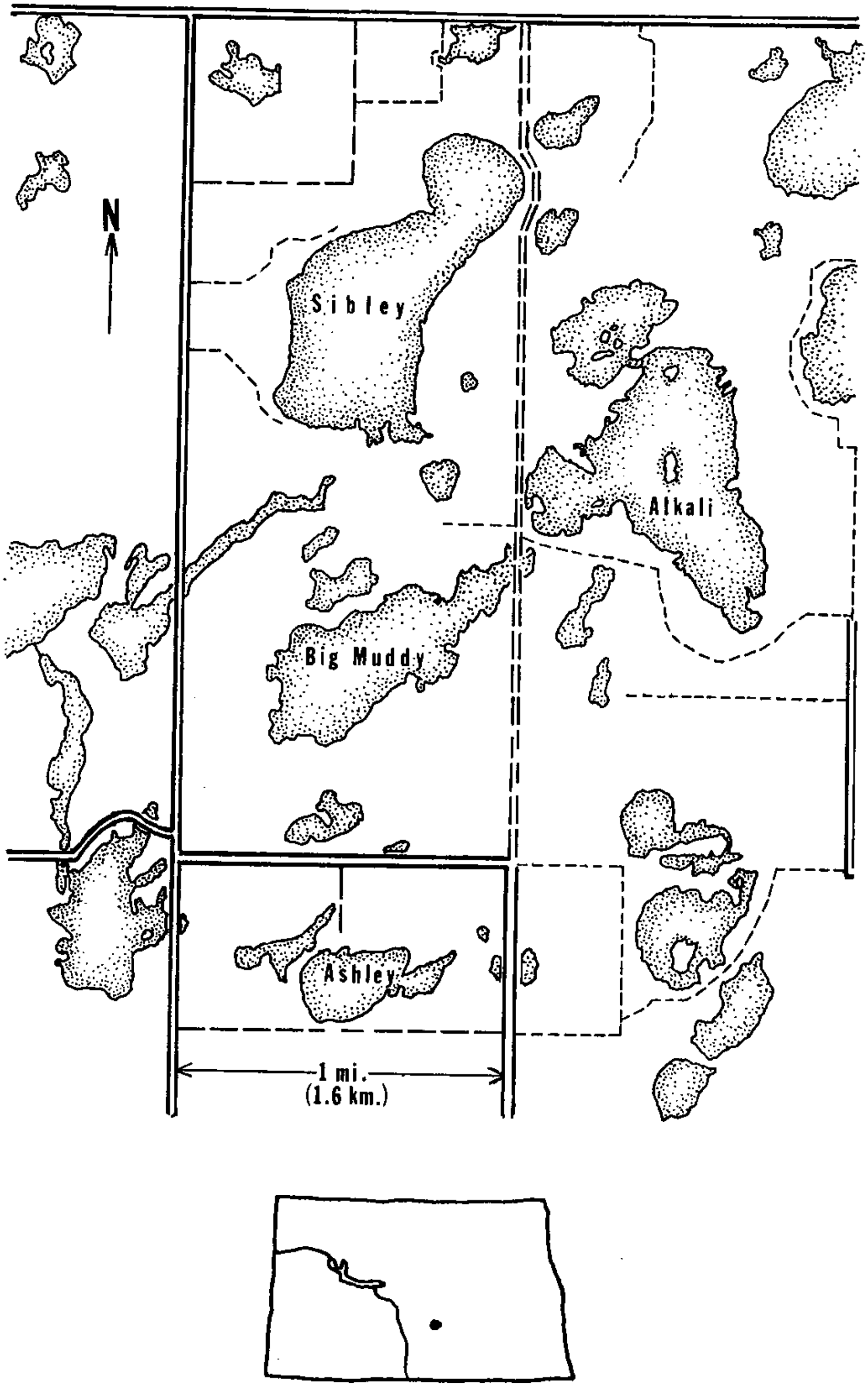
2.1 STUDY SITES

Semipalmated Sandpipers were studied at two locations: the area around Sibley Lake, North Dakota (46°57'N,99°43'W), between 13 July and 27 September, 1978, and on Kent Island, New Brunswick, (44°35'N, 60°27'W) from 11 July to 23 September, 1977. Both locations are intermediate staging areas for autumn migrants, being well south of the breeding grounds and north of wintering areas. At the height of the season, each area hosted up to 5,000 Semipalmated Sandpipers, but in general the local population size ranged between 300-1,000 birds.

2.1.1 Sibley Lake

Sibley Lake is a permanent saline lake covering approximately 322 ha. in the rolling Missouri Coteaux area of south-central North Dakota (Figure 1), near the western edge of the migratory range of Semipalmated Sandpipers at this latitude. This area of glacial deposit contains numerous small ponds and lakes of varying depth and degrees of permanence, and is highly attractive to spring and fall migrant shorebirds. Sibley Lake itself is surrounded by other wetlands that varied greatly in their attractiveness to shorebirds as water levels dropped during the summer. Four areas attracted Semipalmated Sandpipers at some time during the season: Sibley, Big Muddy, Alkali, and Ashley (Figure 1). Sibley, in particular, attracted significant numbers of migrants throughout the season, and was the focus of the study. The unlabeled wetlands shown in Figure 1 were either too deep, too vegetated, or too dry to be utilized by Semipalmated Sandpipers. I will refer to the

Figure 1. The North Dakota study site around Sibley Lake. Birds were captured on the south and east shores of Sibley Lake. Sibley and the other labeled lakes provided suitable habitat for foraging sandpipers at some time during the season, and were censused at these times. The dot on the inset map shows the location of the study site in North Dakota.


N
Sibley
Alkali
Big Muddy
Ashley
1 mi.
(1.6 km.)

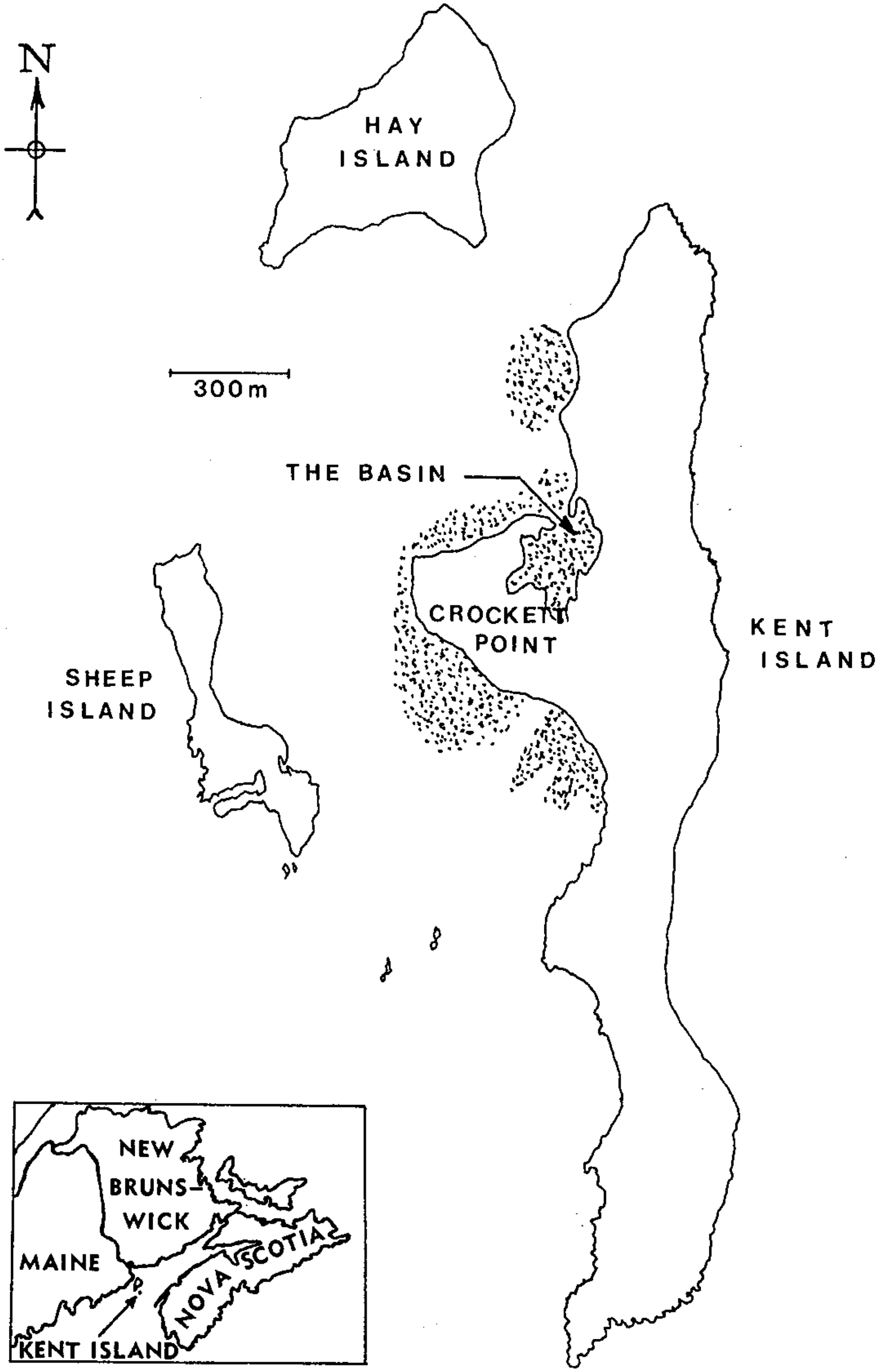
North Dakota study site as "Sibley Lake", which includes Sibley Lake proper and the surrounding areas.

2.1.2 Kent Island

Kent Island is the southernmost part of the Grand Manan archipelago, 10-15 km. from the Maine-New Brunwick border, in the mouth of the Bay of Fundy (Figure 2). Although its coast is mostly rocky, several areas of tidal flats regularly attract Semipalmated Sandpipers during fall migration.

Kent Island is not subject to gross changes in habitat availability, as occurred when water levels changed in the midwest, but the area available to foraging Semipalmated Sandpipers varied systematically with the strong tides. The 24.2 hour "daily" cycle involved two nearly equal amplitude cycles, and the height of the tides varied between 4.1 and 5.3 m. during the study. In general, birds foraged on falling, low, and rising tides, and roosted at high tide. The foraging areas shown in Figure 2 varied in height above the tide, and were therefore covered and exposed by the tide at different times. Foraging birds took advantage of this and shifted areas as the tide rose and fell. The flats south and southwest of Crockett Point flooded 3-4 hours before high tide, as did the northern flats. The Basin flooded 1-2 hours before high tide, and birds often moved there when forced off other areas.

Figure 2. The Kent Island study site. Birds were captured near the mouth of the Basin, and censused in the stippled foraging areas at low tide. The inset map show the location of the study site in the Bay of Fundy, relative to Maine and the Maritime provinces.


N
HAY ISLAND
300m
THE BASIN
CROCKETT POINT
KENT ISLAND
SHEEP ISLAND
NEW BRUNSWICK
MAINE
NOVA SCOTIA
KENT ISLAND

2.2 FIELD METHODS

2.2.1 Capture, Measurement, and Marking of Birds

At both locations birds were captured, measured, and marked each day. This procedure created a series of daily cohorts that could be analyzed for seasonal changes in morphometrics, length of stay, and fat stores. Bill measurements provided information on the sex and/or geographical origin of migrants (Harrington and Morrison, 1979). Fresh weight and wing measurements were used to estimate fat stores, and individual marking allowed determination of the lengths of stay, use of space, and estimation of daily emigration rates (Section 2.5).

In North Dakota birds were caught with mist nets and walk-in traps. Nets were placed along the south and east shores of Sibley Lake, and birds were captured primarily in the morning. The walk-in traps, placed along the eastern shore, were generally opened just after sunset and emptied just prior to dawn. Walk-in traps were not used effectively until 4 August, after which they were the principle capture method. At Kent Island only mist nets were used, as the tides made walk-in traps impractical. Most netting was done as birds shifted foraging areas on rising tides during the day. Thus the timing of captures varied with the progression of tidal cycles.

The capture methods used were biased towards capture of individuals unfamiliar with the area, especially on the coast, where only nets were used. Birds quickly become familiar with nets, and flocks routinely avoided them. Only eight of the first 1000 birds caught at Kent Island were recaptures. Twice during the season I netted at night specifically to obtain reweighings. Walk-in traps were much more effective at recapturing individuals. This may have resulted from placing a trap within a particular bird's feeding area. However, here too individuals were seen avoiding the traps, and trap-samples were probably also biased towards the capture of new arrivals. At one time of year when new arrivals could clearly be identified - when the first juveniles came - both trapping methods caught them in far greater numbers than would have been expected from their overall abundance. This bias could have been a function of age and inexperience as well as local unfamiliarity, however.

The degree to which daily samples of birds represented random cross-sections of the birds present that day varied with the proportion of new birds present. In general, I attempted to capture a fixed number of birds per day, and stopped trapping if that number was reached. Thus, on days when many new birds arrived, and were quickly caught, my samples were probably quite skewed towards new arrivals. On days when few birds arrived, trapping continued for a longer period, and the samples were probably more representative. This variation, which I cannot quantify, complicated the interpretation of some analyses, and precluded certain uses of the data.

Following capture, birds were processed as follows: Each was given a numbered U. S. Fish and Wildlife Service aluminum band. Birds were weighed to the nearest 0.5 g. on a Pesola spring scale. Exposed culmen was measured with a verner calipers to the nearest 0.1 mm. at Sibley Lake, and with a dividers to the nearest 0.5 mm. at Kent Island. Wing length was measured to the nearest 0.5 mm. by holding the wing perpendicular at the wrist, and flattening and straightening the longest primary. Finally, most birds received individually identifying wing tags, as described fully elsewhere (Lank, 1979). At Sibley Lake, but not at Kent Island, most birds were breast-dyed with Feibing's Green Leather Dye. The dye did not fix, and faded within a few weeks.

Mist-netted birds were generally processed within an hour of capture. Since the walk-in traps often held 50-100 birds at dawn, some individuals were held several hours before release. In general, processing time was shorter at Kent Island than at Sibley Lake.

Semipalmated Sandpipers could be readily aged on the basis of plumage (E. Martinez, personal communication; Prater et al., 1978). Juveniles were distinquished from adults by their new, light-edged wing coverts and new primaries. No direct attempt was made to sex individuals. Inferences about the sex ratio were drawn from statistical treatment of bill-length data (Harrington and Morrison, 1979; Harrington and Taylor, 1982).

I attempted to capture and mark at least 25 birds per day; Figures 3 and 4 show the numbers of birds captured and marked throughout the season. When population size was low, or weather unfavorable, fewer birds were caught, while on other days so many were captured that only a sample of those measured were individually marked. Only data from marked birds were used in the analyses. A total of 1472 and 1456 Semipalmated Sandpipers were individually marked at Sibley Lake and Kent Island, respectively.

Figure 3. Numbers of adult and juvenile Semipalmated Sandpipers individually marked each day of the season at Sibley Lake.

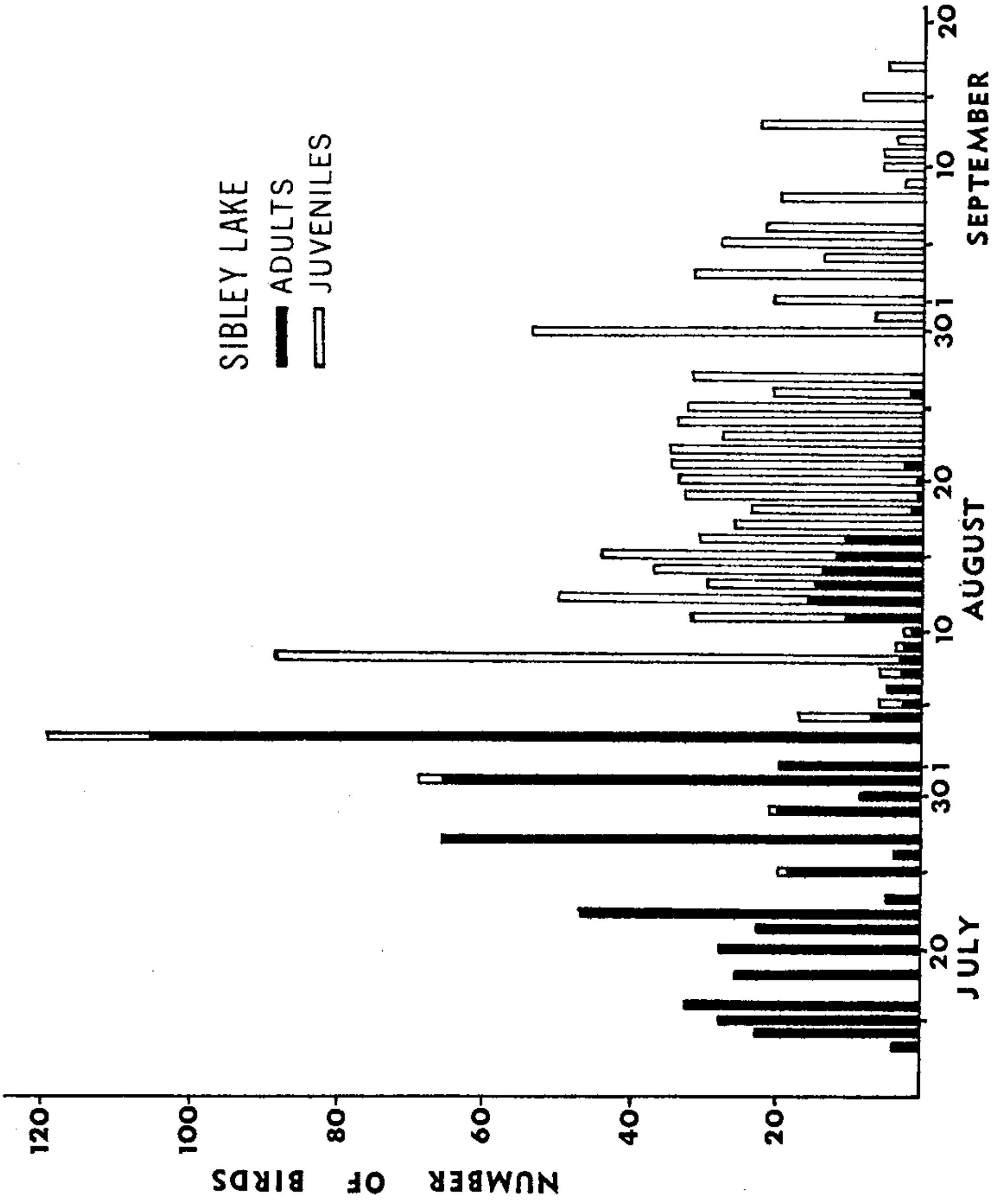
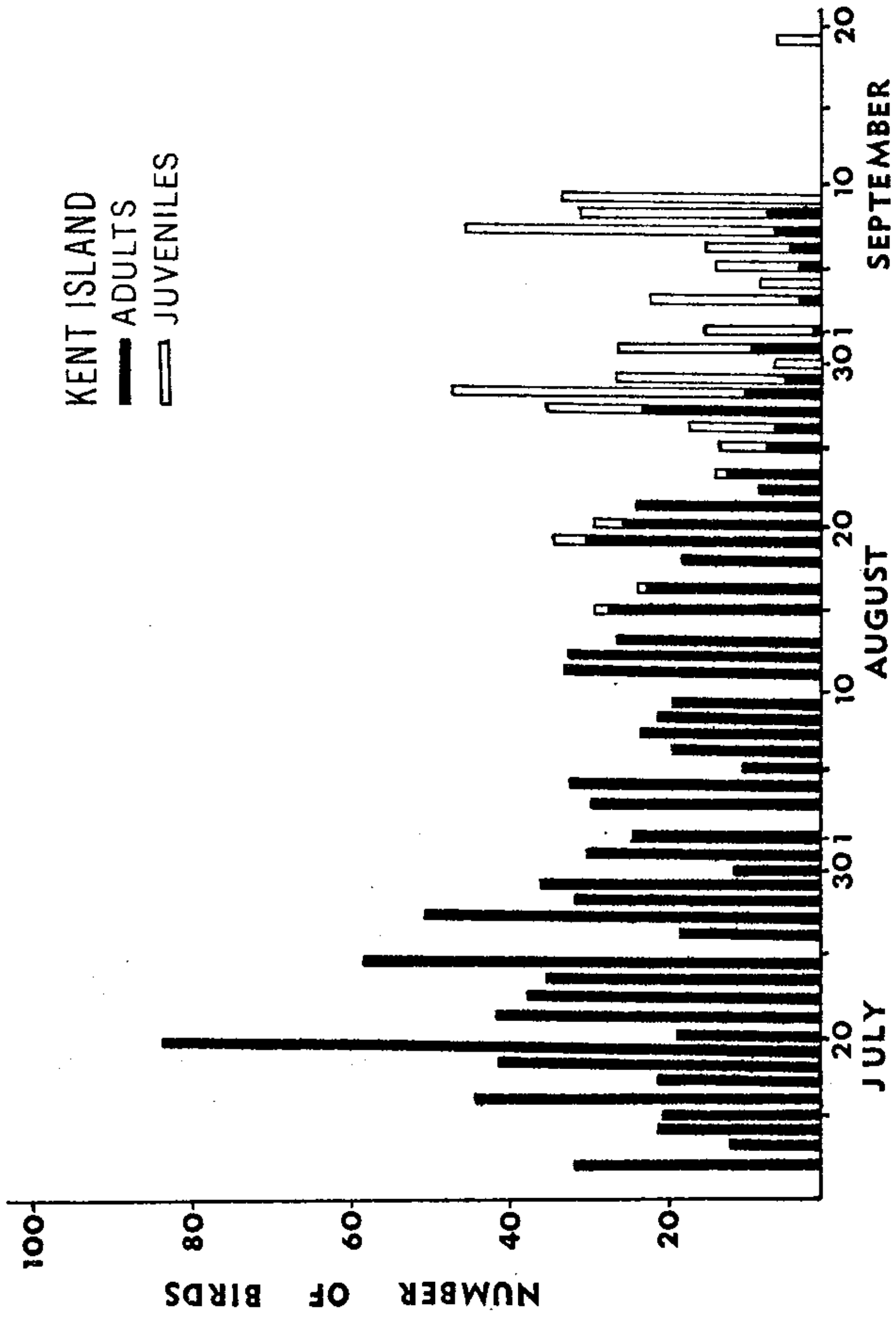

SIBLEY LAKE
ADULTS
JUVENILES
NUMBER OF BIRDS
120
100
80
60
40
20
JULY
AUGUST
SEPTEMBER
20
30 1
10
20
30 1
10
20

Figure 4. Numbers of adult and juvenile Semipalmated Sandpipers individually marked each day of the season at Kent Island.


KENT ISLAND
ADULTS
JUVENILES
NUMBER OF BIRDS
100
80
60
40
20
JULY
20
30
1
10
AUGUST
20
30
1
10
SEPTEMBER
20

2.2.2 Censusing

The study sites were censused daily, both for total numbers of Semipalmated Sandpipers and for the presence of marked individuals. Each study site was divided into five to ten census areas that were tallied separately. At each location a small area was subdivided with markers at 5-meter intervals to help quantify territoriality. Sightings of marked individuals provided information on staging periods, flock cohesion, and use of space by individuals, and enabled estimation of emigration rates. "Staging periods" were defined as the number of days from a bird's capture and marking until its last sighting. They accurately measure a bird's real time in the local area insofar as birds were caught early after their arrival and seen the last day they were present. They are minimum measures. Despite this limitation, they provide much more accurate data than methods based on recapture distributions, which prevail in current literature.

At Sibley Lake, the areas censused varied as dropping water levels changed the location of suitable feeding habitat throughout the season. The southern and eastern shores of Sibley Lake were always utilized and censused; the north and western shores did not attract Semipalmated Sandpipers. Alkali, Ashley, and Big Muddy attracted birds for about five, five, and one weeks, respectively. During two weeks when Alkali attracted several thousand birds, estimates of total numbers and complete searches for marked birds were difficult, since large flocks could move across the mud far more rapidly than the observer. Censuses were made primarily in the late morning, afternoon, and evening.

Census areas on Kent Island are shown in Figure 2. Most censuses were made at low or on falling tides, and all significant low-tide feeding areas were examined. High tide roosts were occasionally scanned for marked birds. The rising tides at times caused movements of flocks from one census area to another, making estimates of total numbers difficult. When large movements were noted, either in the field or through detection of marked birds in several census areas, the estimates of total numbers for that day were adjusted or excluded.

In addition to regular censuses, a limited amount of information was obtained on local movements outside of the study site. At Sibley Lake, surrounding areas were surveyed on an *ad hoc* basis. At Kent Island, reports of marked birds were received from adjacent islands in response to requests for sightings.

2.2.3 Migratory Departures

I was able to make direct observations of presumed migratory departures. On about 50 occasions at each study site, flocks of birds flew upwards away from the study site, calling while ascending, and continued flying until they vanished against the sky while being followed with binoculars or spotting scope. Cases where flocks descended while still in sight, or flew too low to disappear against the sky were not considered departures. Birds were often less vocal during low flights. The time of the departure, the number of birds in the flock, and the direction taken were recorded. At Sibley Lake directions were measured to the nearest degree with a sighting compass. At Kent Island vanishing bearings were recorded only to the nearest 1/16th of a circle (N, NNE, NE, etc.). At both locations a clear view of the horizon was available in all directions. local movements to other feeding or roosting areas.

Data were taken on departing flocks at all times while in the field. Since departures were analyzed as a function of time of day, the temporal distributions obtained may be biased due to differential sampling effort throughout the day. Figure 5 shows the percent time that departures might have been observed at each site during each daylight hour. These distributions of sampling time should be kept in mind when examining the temporal frequencies of departures presented below.

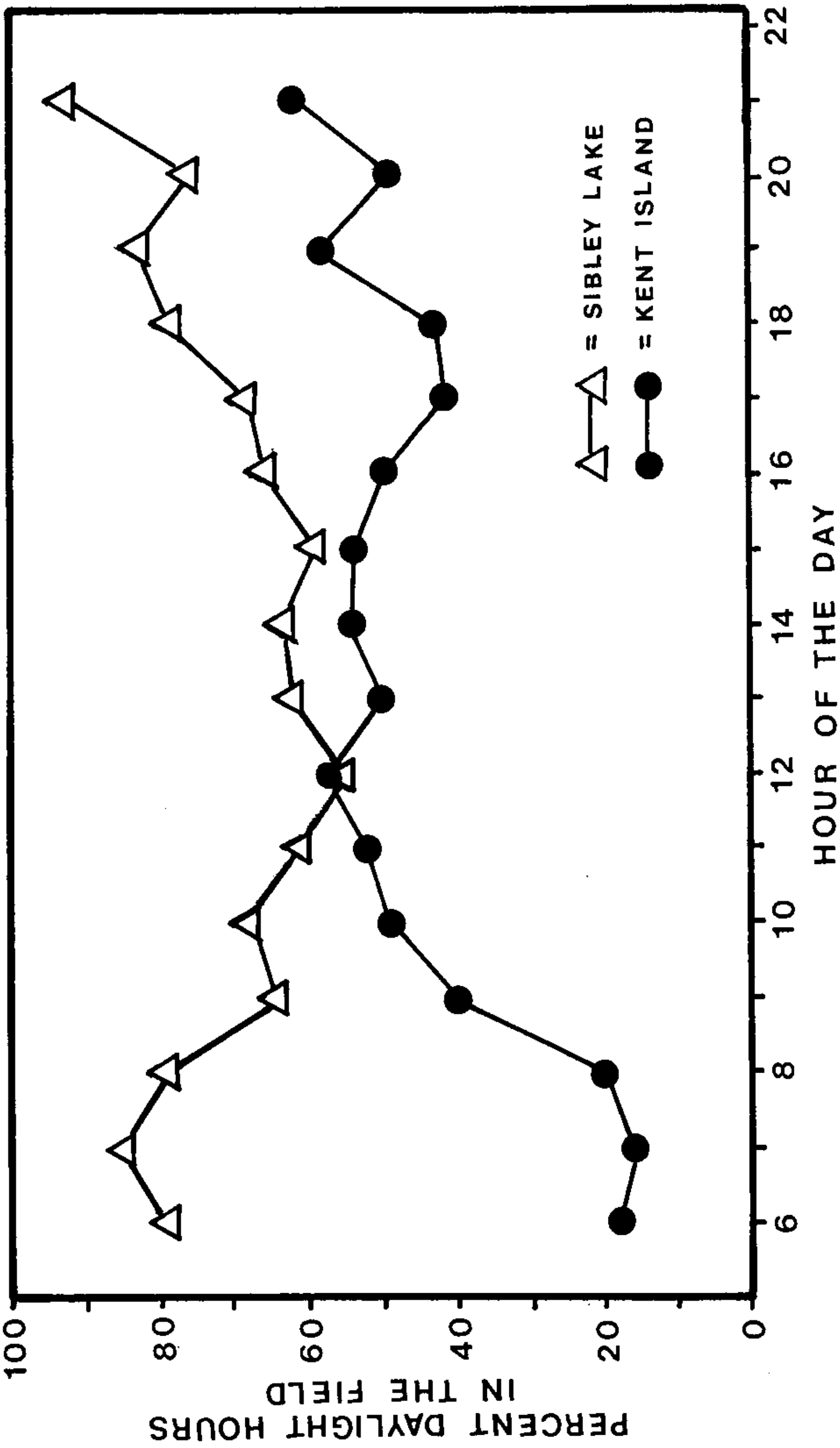
2.3 METEOROLOGICAL ANALYSES

Meteorological analyses were done in two complementary ways:

1. a graphic method plotted information on a generalized synoptic weather map, and
2. both univariate and multivariate methods compared specific local weather variables with the occurrence and non-occurrence of migratory departures.

The first analysis provides a clear view of the general weather conditions under which birds initiated flights, and shows how large-scale weather systems ("high and low pressure systems") relate to the timing of migration. The second analysis suggests possible specific physical stimuli for meteorological responses.

Figure 5. Percentage of daylight hours spent in the field at Sibley Lake and Kent Island.

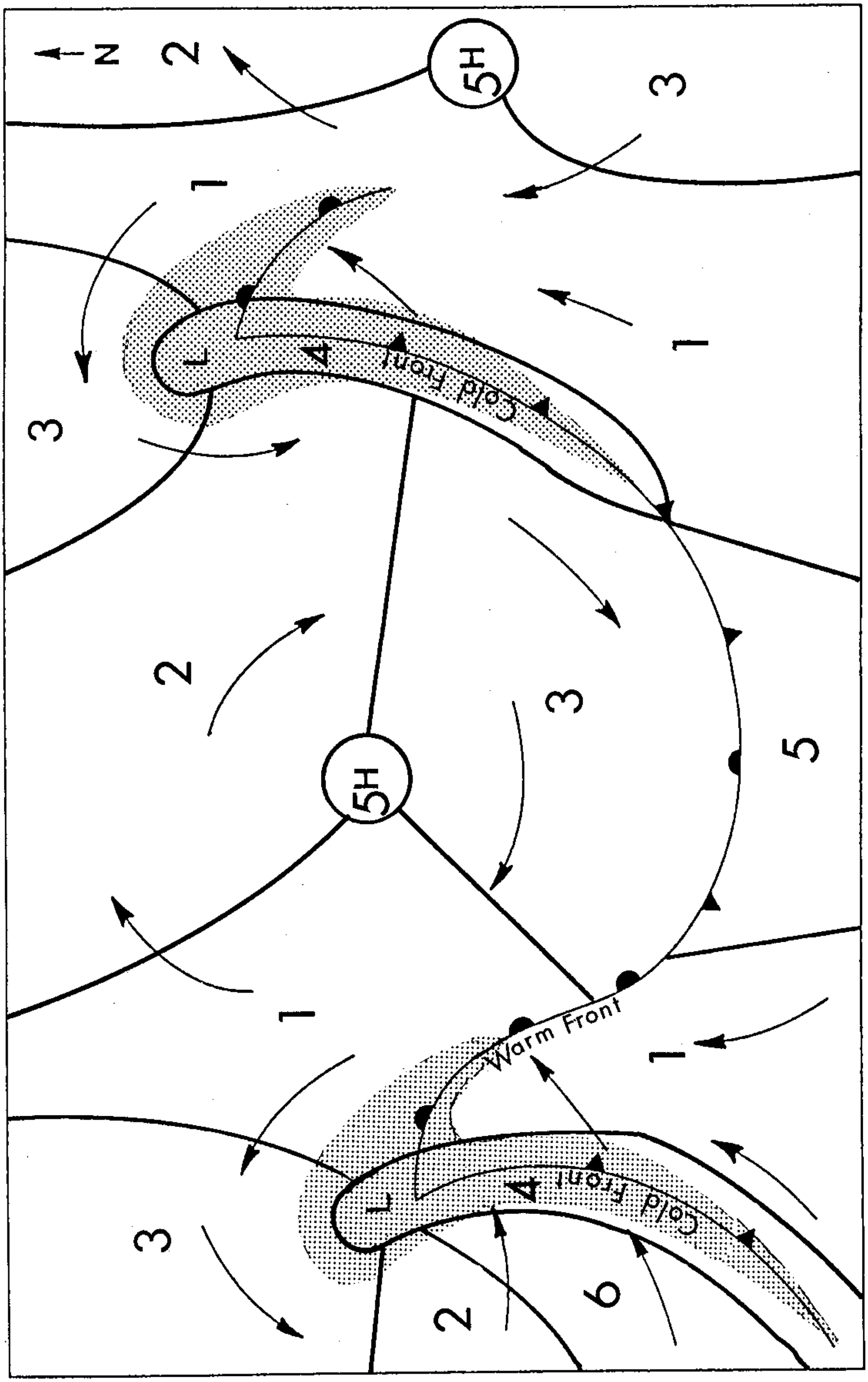

PERCENT DAYLIGHT HOURS IN THE FIELD
0
20
40
60
80
100
HOUR OF THE DAY
6
8
10
12
14
16
18
20
22
= SIBLEY LAKE
= KENT ISLAND

2.3.1 Synoptic Analysis

Examination of migratory events with reference to synoptic weather maps was fully developed by Bagg et al. (1950), who correlated bird movements with weather maps from specific dates. Richardson (1970; Richardson and Haight, 1970) introduced a generalized representation of synoptic conditions, a kind of meteorological space, on which events from a number of days could be located with respect to the weather. Similar maps have been used by a number of authors (Muller, 1976; Demong and Emlen, 1978; Williams and Williams, 1978; Larkin and Thompson, 1980). The generalized map used in this study was taken directly from Richardson (1976a), and is shown in Figure 6. This map had been used previously to summarize weather data from both the midwest and the northeast coast (Richardson, 1970, 1972), and accurately depicted nearly all weather conditions encountered during this study. The map shows the relative positions of three pressure systems, including warm, stationary and cold fronts, and the prevailing direction of the geostrophic winds (arrows) that will be encountered at the altitudes at which many birds migrate.

To use the generalized map, I determined the location of the study site relative to pressure systems on U.S. surface weather maps. A dot was then placed on the generalized map at the location that most nearly fit conditions surrounding the study site. While on conventional weather maps pressure patterns are plotted relative to geography, on these maps the weather patterns remain fixed and the study site "moves" in this idealized meteorological space. Barometric pressure and pressure trend, wind direction, location of pressure centers and fronts,

Figure 6. The generalized synoptic weather map, and the six synoptic categories used in analyses. The thin lines represent cold, warm, and stationary fronts around high and low pressure systems. Arrows represent the prevailing wind direction around pressure systems and at fronts. The heavy lines separate the six synoptic weather categories (see text). Stippled areas represent regions where rainfall is likely.


N
2
5H
3
1
L
4
Cold Front
1
3
2
3
5H
5
1
Warm Front
1
3
L
4
Cold Front
2
6

temperature and temperature trend, precipitation, and cloud cover were all considered in the placement of a dot. No absolute distance relationship between study site and pressure systems was considered; the generalized map was scaled relative to the size of local systems.

In the results section, I present three kinds of maps:

1) I plot the prevailing weather at the time of specific events, such as migratory departures. This allows a quick visual summary of departure conditions. A novel application of this procedure is the presentation of "path diagrams", which trace the movement of the weather for 3-day periods prior to, at the time of, and after migratory takeoffs.

2) I plot one point per day, showing weather conditions prevailing at the median departure hour for each location (a half hour before sunset at Sibley Lake, two and a half hours before sunset at Kent Island). On some maps, the daily point is a circle that shows the value of a variable for that day, such as the emigration rate or change in mean fat level of captured birds. Given a strong relationship between weather and migration, these maps enable visualization of the relationships between weather, migration, and the third variable plotted.

3) For statistical purposes, I defined six synoptic regions on the map, based on geostrophic wind directions (see Figure 6), and each data point was assigned to one category. The categories were:

1. southerly winds, from SE to W, except immediately following a cold front;
2. northwesterly winds, from W to N;
3. northeasterly winds, from N to SE;
4. the center of a low and the area around a cold front;

5. calm weather at the center of a high or in poorly organized areas south of a stationary front;
6. W to SW winds following a cold front.

This categorization allowed statistical testing of the relationships between events or levels of variables in different areas of the map.

Data on the synoptic conditions occurring during the field season were taken from U.S. surface weather maps, prepared at 3-hour intervals, obtained on microfilm from the U. S Environmental Data Service, National Climatic Center, Asheville, N.C., covering both field seasons. I examined 1208 maps (8 points/day at 3-hour intervals for 151 days), and in only 22 cases (2%) was I unable to relate the prevailing weather to a spot on the generalized map. These cases were omitted. Determination of prevailing weather at times between the 3-hourly fixes was done by drawing a straight line between successive points. I assumed that the weather moved at a constant rate between fixes, and extrapolated a location along the line. Compilation of daily maps, with fixes every three hours, was done before examination of the rest of the data.

In addition to examining the weather prevailing during my study seasons, I measured the frequencies of the six weather categories during the five fall migratory seasons prior to the study (1972-1976). These data were determined by examination of the "Daily Weather Maps", issued weekly by the Environmental Data Service in printed form. Of the 720 synoptic categorizations in this analysis (one for each study site for a 72 day season for five years), 58 (8%) could not be placed on the generalized map. The higher proportion of non-placements of the 1972-76 data than of the 1977-78 data (8% vs 2%) is due to the coarser resolution of the Daily Weather Maps.

2.3.2 Quantitative Analysis of Specific Variables

While the synoptic analysis provides an overview of the conditions under which birds did and did not migrate, determination of particular physical factors that might stimulate the birds requires a quantitative analysis of particular local variables. This analysis also might clarify the ultimate selective pressures involved. The data base was hourly surface readings taken at Bismark, N.D., 80 km. due west of Sibley Lake, and at St. Johns, N.B., 98 km. northeast of Kent Island. Bismark data were obtained on computer tape (TD-1440) from the U. S. Environmental Data Service, and the St. Johns data were photocopies of daily record sheets, obtained from the Canadian Climate Centre, 4905 Dufferin St., Downsville, Ont.

Three data sets were formed from these sources. 1) The first data set consisted of daily observations at the median time that flocks were seen departing throught the season at each location: a half hour prior to sunset at Sibley Lake, and two hours prior to sunset at Kent Island. 2) The second data set was daily observations eight hours prior to the first set. Together, these daily obrvations formed a "background distribution" of the weather, a sampling of conditions prevailing at each site. 3) The third data set consisted of observations at the hour closest to each observed flock departure, labeled "GO" hours. Hours in the background distribution were considered "NOGO" hours, unless they coincided with a GO hour from the third data set. Some NOGO hours may have been misclassified, since departures may have occurred but not been observed.

This sampling scheme enabled comparison of conditions under which birds were observed to depart (GO hours) with either those in which they were not (NOGO hours), or a systematic sampling of the existing weather conditions (the background distributions). I could thus examine differences between the prevailing weather at the two locations, differences in the weather in which birds left or did not leave the areas, and the degree of selectivity in departure weather shown by each population relative to the conditions in each area.

For each hour sampled, the following variables were recorded or calculated:

1. Wind direction (WD): defined as the direction from which the wind was blowing, measured in degrees.
2. Wind speed (WS): measured in knots.
3. Tailwind-Headwind component (THC): the wind vector along an axis parallel to the general direction of migration (NW-SE). THC was calculated as: $THC = WS * \cos(WD-45^{o})$, thus tailwinds had positive values while headwinds were negative.
4. Sidewind component (SWC): the wind vector along an axis perpendicular to the migratory direction (thus SW-NE). SWC was calculated as: $SWC = WS * \cos(WD + 135^{o})$, thus positive values were winds blowing from the southwest, while negative values were winds from the northeast.
5. The absolute value of the sidewind component: this value sums up the potential displacement relative to the ground that would be experienced by a bird flying on a fixed aerial heading in the migratory direction, whether to the right or the left.

6. Tailwind-Headwind 9-hour trend: the change in the THC vector length over the previous nine hours. Positive values indicate winds becoming more northwesterly, and negative values indicate more southeasterly.
7. Sidewind 9-hour trend: the change in the SWC vector length over the previous nine hours. Positive values indicate winds becoming more southwesterly, and negative values mean more northeasterly winds.
8. Tailwind-Headwind 24-hour trend: as variable 6, but over the previous 24 hours.
9. Sidewind 24-hour trend: as variable 7, but over the previous 24 hours.
10. Barometric pressure: atmospheric pressure, measured in millibars, minus 1000.
11. Pressure 6-hour trend: the change in pressure over the previous six hours, in millibars.
12. Temperature: the temperature in degrees Celsius.
13. Temperature 24-hour trend: the change in temperature over the previous 24 hours, in degrees Celsius.
14. Relative Humidity: the relative humidity.
15. Humidity 12-hour trend: the change in humidity over the previous 12 hours.
16. Precipitation: the amount of rain that hour, measured on a 4-point ordinal scale.
17. Opacity: cloud cover and/or fog, measured in 1/10s of sky covered by clouds.

18. Horizontal visibility: the horizontal visibility, measured on a 4-point ordinal scale.

All variables were examined for seasonal trends, to deal with the potential problem of non-stationarity (Richardson, 1974). Temperature showed seasonal trends at both locations; barometric pressure increased and relative humidity decreased at Kent Island. If the assumption is made that birds respond not to absolute values of variables, but rather to their variation around seasonally normal values, it is appropriate to use the departure from normal values on that date as predictors. This was done for the variables mentioned above. However, the adjusted variables performed little better (or worse) than the originals, and the final analyses presented used the absolute values of the variables. There was no seasonal trend in the occurrence of departure hours, which represented the dependent variable in these analyses.

These variables covered the spectrum used in other studies of meteorology-migration correlations (see Richardson, 1978a). Sample sizes limited the number of variables I could reasonably include in multivariate models (Richardson, 1978a). Features that Richardson (1979) found significant in univariate and multivariate correlations with shorebird migration density in the Maritimes were included, except for ceiling. I have examined wind more carefully than other features due to its obvious energetic consequences and its demonstrated importance in other studies.

2.4 ESTIMATION OF FAT STORES

Fat is the primary source of energy for migratory flight in birds, thus an assessment of the amount of fat stores carried by individuals is an important element in understanding staging and migratory behavior. Migration studies have used a variety of techniques to assess the relative or absolute fat content of live birds: weight at capture (Odum, 1949; Helms, 1959; Middlemiss, 1961; Mascher, 1966; Mueller and Berger, 1966; Rappole and Warner, 1976), visual fat class (Wolfson, 1954; Helms and Drury, 1960; Dolnik and Blyumental, 1967; Mueller and Berger, 1966; West _et al._, 1968), and, especially in shorebirds, estimates of fat content from fresh weight with a correction for body size based on wing length (Mascher, 1966, Mascher and Markstrom, 1976; Page and Middleton, 1972; McNeil and Cadieux, 1972b). The last method provides the most quantitative estimates available from live birds, and was used in this study.

Fat stores carried by individuals were estimated by the following general equation:

$$\text{Fat} = \text{Fresh Weight} - \text{Fat-free Weight} \quad (1)$$

Fresh weight was measured in the field. Significant regressions of fat-free weight on wing length have been presented for Semipalmated Sandpipers by two separate investigators (Page and Middleton, 1972; McNeal and Cadieux, 1972b). Neither of the regressions presented in these papers could be applied directly to data from this study, due to differences in the methodology of wing measurement. Page and Middleton (1972) measured natural wing chord, McNeil and Cadieux (1972b) measured the flattened and straightened primary of a folded wing, while measurements from this study were of flattened and straightened primaries of wings held perpendicular at the wrist. The relationship between the latter two systems was determined by measuring a sample of birds both ways. Semipalmated Sandpipers were captured on 31 August, 1979, at Sylvan Beach, N.Y. (43°10'N, 75°40'W), and the flattened and straightened primaries were measured with wings perpendicular and folded. The resulting regression (2) was combined with that given by McNeil and Cadieux (1972b) (3), to produce the equation used to estimate the fat content of all birds in this study (4), as shown below:

(2) $WL_f = 18.8 + (0.767 \times WL_p)$ $(r^2 = .42, n=11, p<.02)$

(3) $FFW = -7.01 + (0.334 \times WL_f)$ $(r^2 = .41, n=167, p<.05)$

(4) $FAT = FW + 0.731 - (.2652 \times WL_p)$

where FAT = fat, FW = fresh weight, and FFW = fat free weight, measured in grams; and WL_f = wing length, folded, and WL_p = wing length, perpendicular, measured in millimeters.

Estimates of fat content ranged from just under -6 g. to over 25 g. The impossible negative fats suggest that the linear regression may not have been accurate at the extreme low end, and/or that estimates were systematically low throughout the range. The maximum estimate of just over 25 g. is reasonable for birds with fat-free weights ranging from 17.4 to 24.8 g. (Page, 1970). Fat stores equal to fat-free weights have been found in lipid extractions from several species of long-distance migrants, including Semipalmated Sandpipers (Odum et al., 1961; Dolnik, 1970; McNeil, 1970, McNeil and Cadieux, 1972).

2.5 ESTIMATION OF DAILY EMIGRATION RATES

Data from marking and resightings obtained on daily censuses were used to estimate daily emigration rates. A total of 5120 and 3431 resightings of marked birds were obtained at Sibley Lake and Kent Island, respectively. The method used was a modified Jolly-Seber mark-recapture method (Jolly, 1965; Seber, 1965) developed by Dr. Cavelle Brownie, of the Cornell University Biometrics Unit (see Brownie and Robson, 1980). This method excluded birds which were never seen following the day of marking from the emigration estimates, reducing the effect of movements caused by the trauma of capture and tagging, and the influence of transient birds. Rates presented in this study were based on a minimum of ten individuals resighted/day. Emigration rates reflect birds leaving the census areas for any reason: migration, local movements, or death. I selected study sites that were fairly well isolated from other feeding habitat to minimize the effects of local movements, and it was hoped that sources of disappearance other than migration would be small enough to permit the use of emigration rates as a daily, quantitative measure of migratory activity. The validity of such usage will be examined in the analysis.

2.6 DATA PROCESSING AND STATISTICAL METHODS

Data were handled in a series of computer files on IBM 370-series computers at Cornell University and at the University of North Dakota. An original program organized the capture and census data by individual bird and daily cohorts for further processing. Standard statistical computer packages were used for further analyses (SAS Institute, 1979;

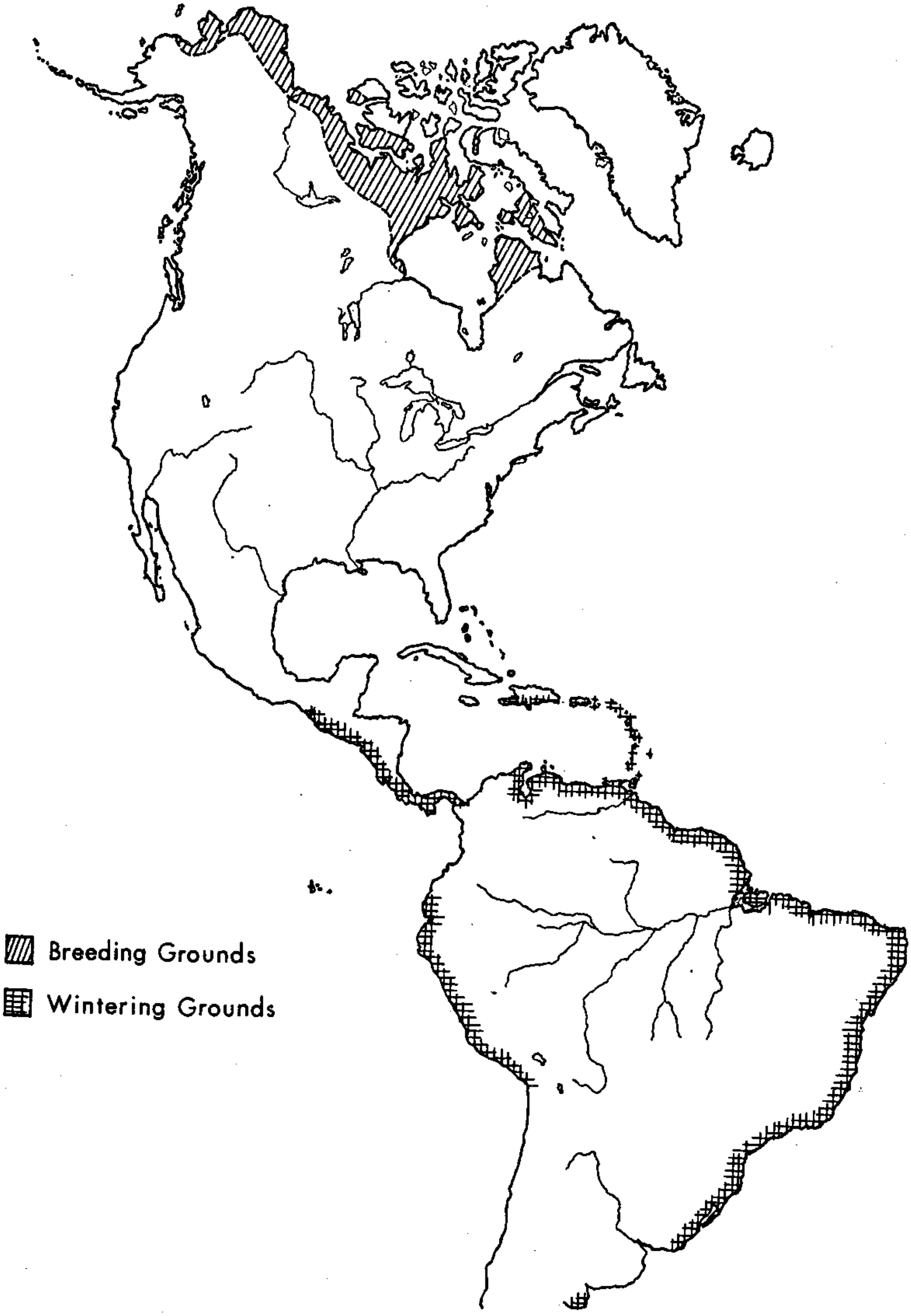
Nie *et al.*, 1975; Ryan *et al.*, 1976). Some analyses of fat levels and lengths of stay involve computations based on the means of daily cohorts. Only means based on seven or more points are used in these analyses. The SPSS procedure "Discriminant" (version H, release 8.0; Hull and Nie, 1979) was used for the discriminant function analyses of meteorological variables, with the prior probabilities proportional to the original sample sizes, and all variables entered into the model at the same level. Circular statistics were calculated using programs written by Tim Larken, Cornell University, following procedures outlined in Batschelet, 1965 and 1972. Band return data were analyzed with a program written for such data by Zar and Southern (1977).

Chapter III

AUTUMN MIGRATION OF SEMIPALMATED SANDPIPERS

Semipalmated Sandpipers breed in a low arctic tundra zone extending across North America, and spend the boreal winter along the coasts of South and Central America, and in the Caribbean (Figure 7). Their autumn migrations are multistage journeys between these areas. From arctic breeding grounds, birds fly over inhospitable boreal forest to temperate zone staging areas. They continue on, in one or more flights, to Central America, the West Indies, or the northern coast of South America. Little is known of migratory routes beyond this point, but the wintering grounds cover a tremendous range, with some individuals found as far south as Argentina or northern Chile, while a few may be found at the tip of Florida (Phillips, 1975). Hypothetically, one-way migration distances might range from a minimum value of about 3400 km., for a migrant flying from Churchill, Manitoba, to the Florida Everglades, to a maximum on the order of 14,400 km. for a bird moving from Barrow, Alaska, to Buenos Aires, Argentina. Clearly, <u>Calidris pusilla</u> is a long-distance migrant.

Figure 7. Breeding and wintering grounds of the Semipalmated Sandpiper. Shaded areas represent breeding grounds, cross-hatched areas represent wintering grounds.


▨ Breeding Grounds
▦ Wintering Grounds

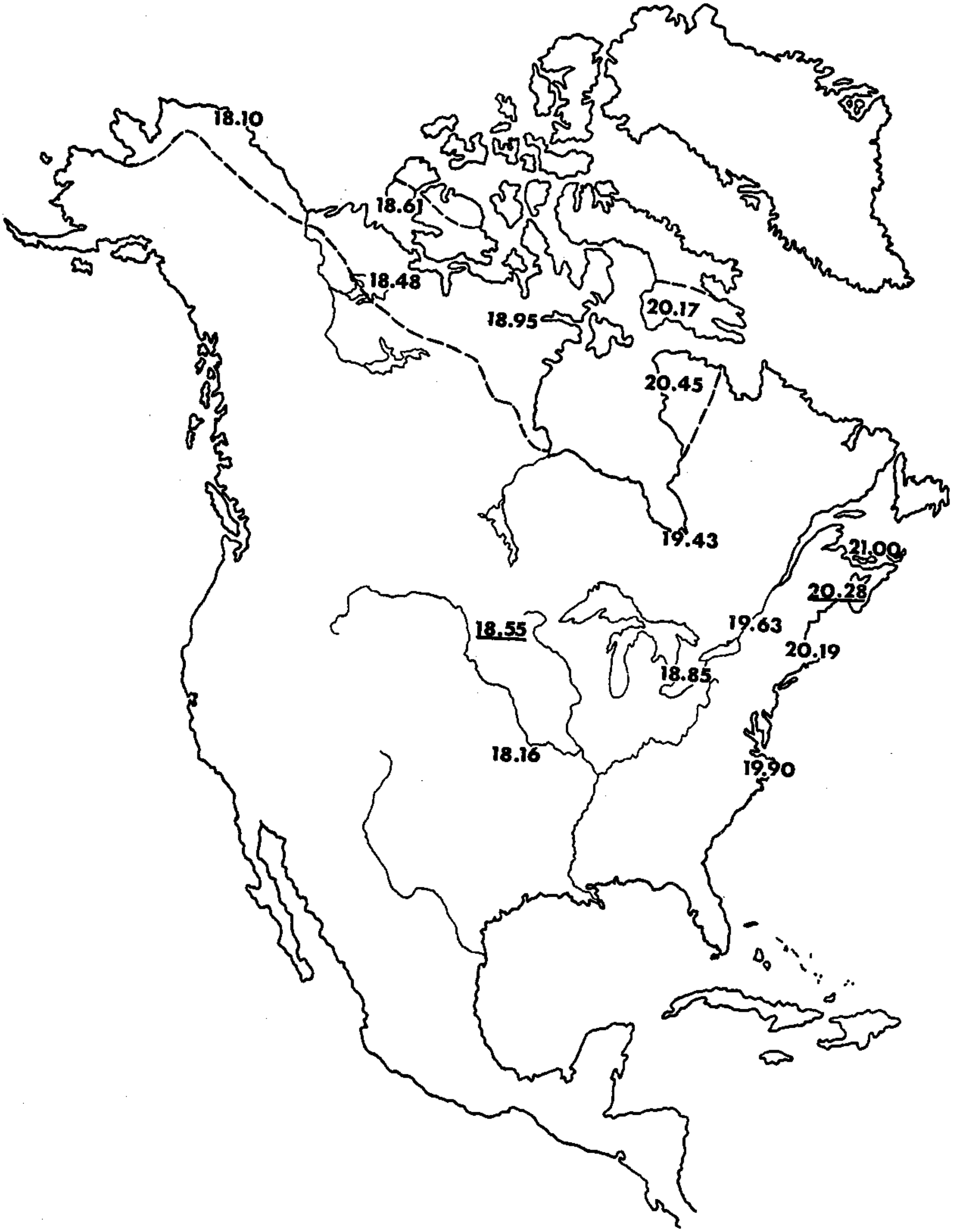
3.1 BREEDING SYSTEM AND MIGRATION TIMING

Semipalmated Sandpipers have a monogamous breeding system (Pitelka *et al*., 1974). They are site-faithful from year to year, and commonly mate-faithful as well (Safriel, 1971; Hanson and Eberhardt, 1978). Both sexes incubate in roughly equal proportions, but the male provides most of the parental care, with females leaving the breeding territory one to eight days after hatching (Brooks, 1915; Ashkenazie and Safriel, 1979a, b). Females and failed breeders form feeding flocks, and become the earliest migrants. Males abandon the chicks around the time of fledging, join the feeding flocks, and form a second wave of migrants. Late-season flocks are composed almost entirely of juveniles, which migrate last (Parmelee *et al*., 1967; Ashkenazie and Safriel, 1979a).

3.2 MORPHOLOGICAL DIFFERENTIATION OF BREEDING POPULATIONS

Calidris pusilla has been divided into two intergrading forms: a short-billed, slightly smaller western race, and a long-billed, slightly larger eastern race (Manning *et al*., 1956; Harrington and Morrison, 1979; H. Ouellet, personal communication). Data compiled by Harrington and Morrison (1979) show a slight cline in adult bill lengths from Alaska across arctic Canada to the central Northwest Territories, an intergradation zone west of Hudson's Bay, and clearly longer-billed populations east of the Bay (Figure 8). These morphometric differences allow analysis of the geographical origins of migrant populations and determination of their migratory routes. These analyses are complicated by a slight sexual size dimorphism combined with plumage monomorphism of the sexes. Within each population, bills of females average 8.9% longer

Figure 8. Measurements of bill lengths of Semipalmated Sandpipers from breeding and migratory staging areas. The measurements from the breeding grounds were of museum specimens, and are an average of the means for males and females from those areas. Measurements from staging areas were taken from unsexed samples of live birds caught during autumn migration. All data are from Harrington and Morrison (1979), except for the Sibley Lake and Kent Island values from this study, which are underlined.


18.10
18.61
18.48
18.95
20.17
20.45
19.43
21.00
20.28
19.63
18.55
20.19
18.85
18.16
19.90

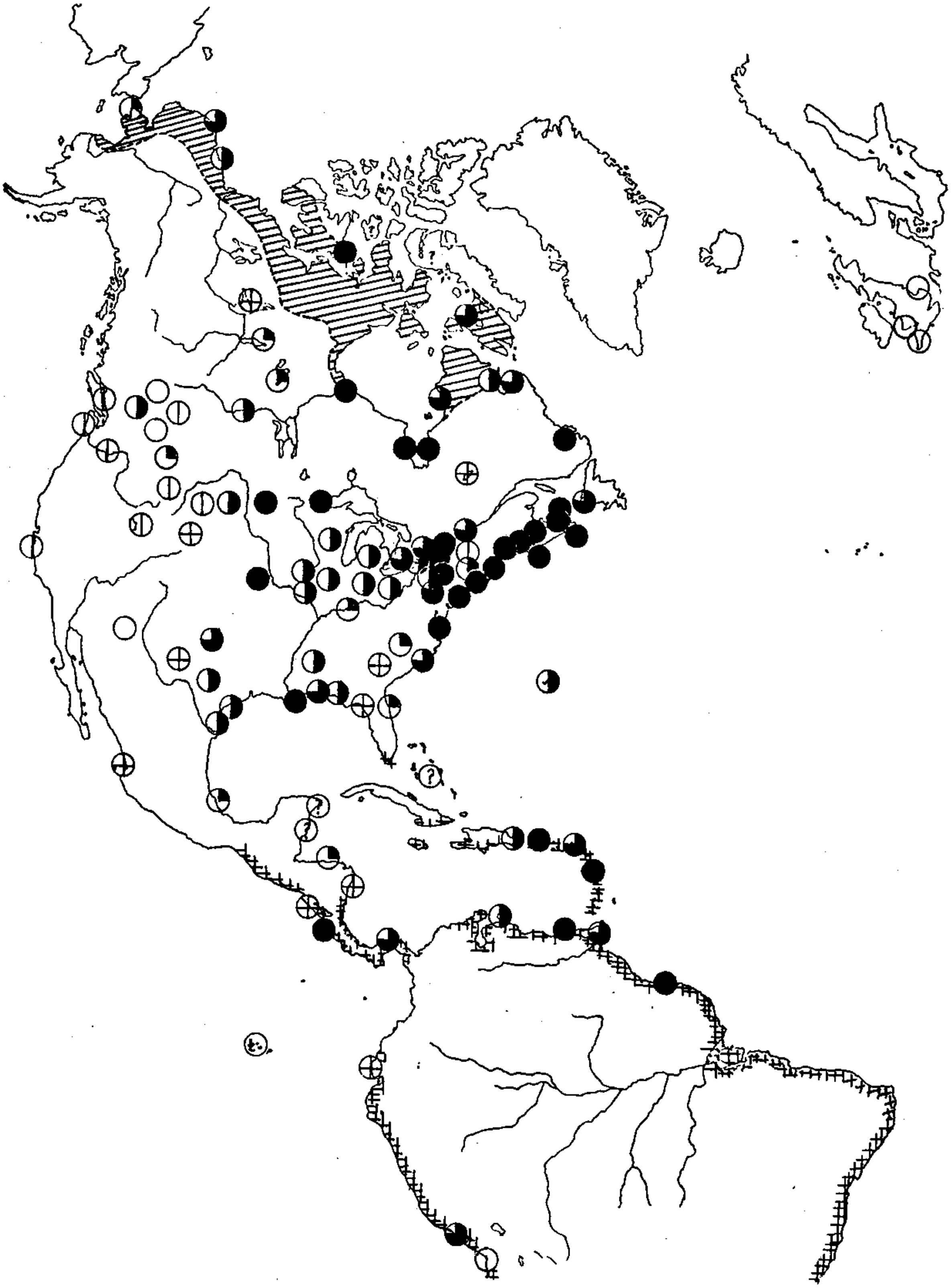
than those of males (Harrington and Morrison, 1979; Harrington and Taylor, 1982). Since populations differ in bill length by no more than 13%, samples of western females overlap extensively with those of eastern males. Unless either sex or originating population is known, determination of the status of a sample of birds is equivocal. Thus data from live, unsexed samples must be interpreted carefully.

3.3 GEOGRAPHICAL DISTRIBUTION AND ABUNDANCE ON MIGRATION

Between early July and early October, migrant Semipalmated Sandpipers may be found in suitable habitat throughout most of North America south of the boreal forest and east of the Rocky Mountains. Figure 9 shows the maximum abundances of Semipalmated Sandpipers between 1 July and 30 October in North and South America. Migrants are most numerous along the northeast Atlantic coast, especially at the head of the Bay of Fundy, where over 200,000 have been censused at one location on a single day in several different years (Harrington and Morrison, 1979; Morrison and Gratto, 1979b). Caldris pusilla is the most common small shorebird along the coast as far south as northern Virginia. While still common, Semipalmated Sandpipers are less abundant at inland locations, with the exception of the shores of James Bay, and isolated areas in eastern and central North and South Dakota, and Kansas. Thus, in the northern U.S. and southern Canada, there is a bimodal longitudinal distribution of Semipalmated Sandpipers, with a peak in the Great Plains and a much larger one along the northeast coast. These data provide a partial basis for speaking of eastern and midwestern migration routes. Evidence that different breeding populations use these routes is available from the morphological analyses presented below.

Figure 9. Relative abundance of Semipalmated Sandpipers in North and South America during autumn migration. Each circle plots the maximum abundance at a single location between 1 July and 30 October. Increasing darkness reflects greater abundance, according to the scale shown below. The sources consulted and methods followed are given in the appendix.

○ = incidental
⦶ = rare or scarce
⊕ = occasional or uncommon
◔ = regular or fairly common
◑ = common
◕ = very common or numerous
● = abundant
(?) = present, but abundance unknown
▨ = breeding range
▦ = wintering range



3.4 MORPHOLOGICAL ANALYSES OF MIGRANT POPULATIONS

Analysis of bill lengths in different parts of the migratory range, and throughout the season, show that western and eastern breeding populations follow different migratory routes.

3.4.1 Geographical Patterns

Harrington and Morrison (1979) outlined the movements of *Calidris pusilla* from specific breeding grounds to staging areas by comparing bill lengths of sexed museum specimens from the breeding grounds with bills of both museum specimens and live populations at staging areas. A summary of their data, plus measurements made at Kent Island and Sibley Lake during this study, is shown in Figure 8. The numbers shown for breeding populations are combined values from museum specimens of males and females, equally weighting the sexes, while the figures shown for staging areas are from unsexed samples of live adult birds.

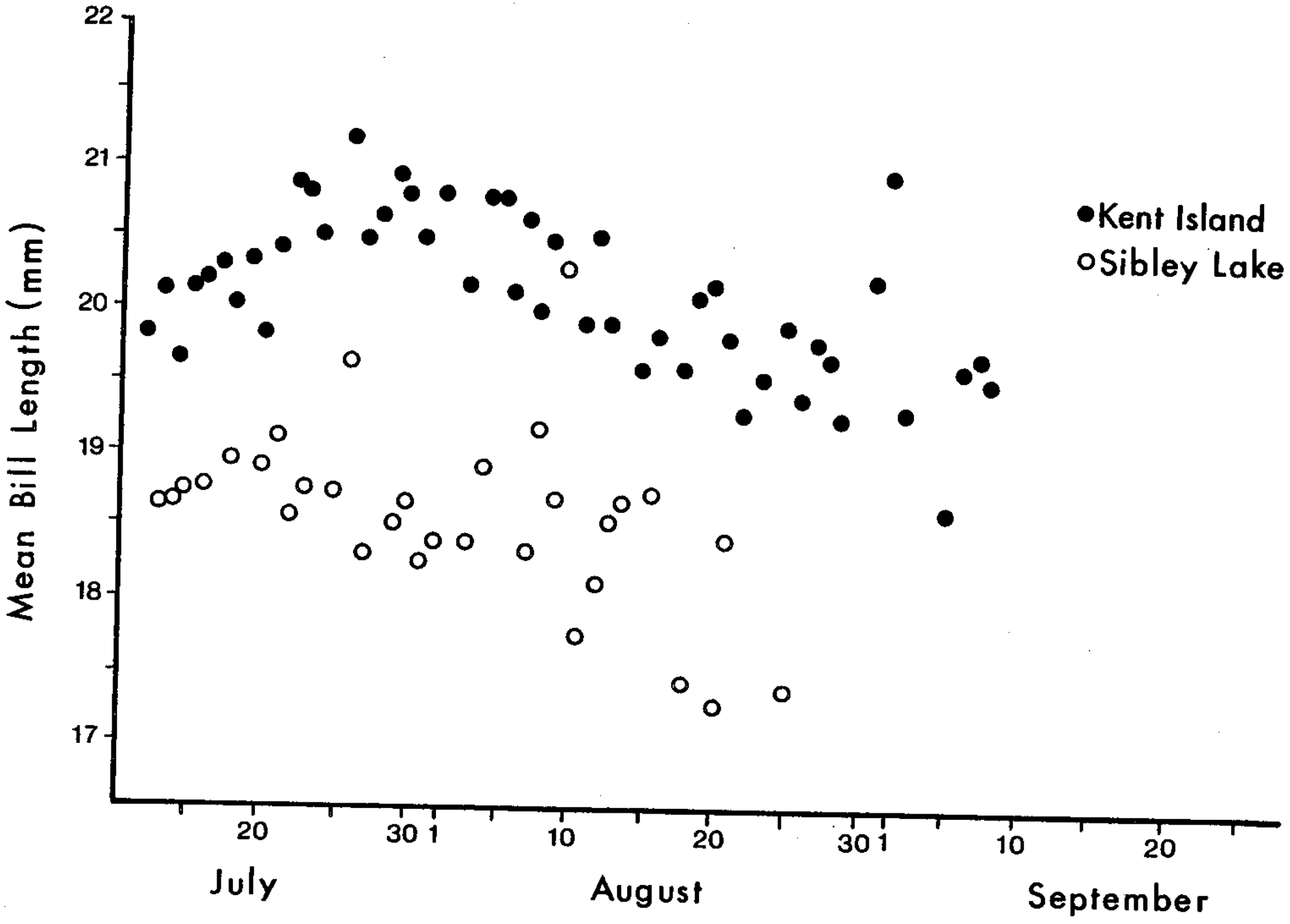
There are two potential problems in comparing values of bill lengths among populations shown on the map. First, bill lengths of museum specimens will be slightly smaller than those of live birds, due to shrinkage. However, Prater *et al*. (1977) found no significant differences in the bill lengths of live and museum specimens of a variety of species of shorebirds, so this is probably a negligible, and systematic, difference. Secondly, mean bill lengths for the samples of live birds will vary with the sex ratio, which changes throughout the season. The values from this study, and those from James Bay and Plymouth, should not be affected by this, since they are grand means from populations sampled throughout the season, and will not be biased unless geographical migration patterns differ by sex. The sampling schemes from the other locations are unpublished.

Despite these potential problems, the pattern shown in Figure 8 seems clear: the east-west cline in bill lengths seen on the breeding grounds is maintained at staging areas. This implies more or less parallel, southeasterly movements by all populations. The mean bill length at Sibley Lake was 18.5±1.2 mm. (n=617), while at Kent Island it was 20.3± 1.5 mm. (n=1161). The means are significantly different (t-test, $p < .001$). The Sibley Lake and Kent Island samples are also statistically different from those at all other staging areas on the map (variances taken from Harrington and Morrison, 1979; t-tests, 1-tailed, since the direction of the differences were predicted, $p < .05$). Thus, the apparent cline in Figure 8 is real, and bill lengths from migratory stopover sites may be associated with corresponding values from the breeding grounds. The center of origin of birds moving through Sibley Lake is in the western Canadian arctic, while birds moving through Kent Island originate primarily from east of Hudson's Bay.

3.4.2 Seasonal Patterns

The mean bill lengths of adults caught daily at Sibley Lake and Kent Island are plotted in Figure 10. The difference between sites is clear, and there also are consistent seasonal trends within each area. Mean bill lengths rise slightly at the start of the season, level out early, and slowly decline. This pattern reflects changing sex ratios of migrants, in accordance with the breeding biology (Section 3.1). The earliest migrants are probably a mixed-sex sample of failed breeders.

Figure 10. Mean bill lengths of adult Semipalmated Sandpipers caught each day of the season at Sibley Lake and Kent Island.



ADULT BILL LENGTHS

The arrival of longer-billed females cause the mean to rise, and it gradually falls as males arrive later in the season.

Harrington and Morrison (1979) interpreted similar seasonal patterns of adult bill lengths found at James Bay and Plymouth as reflecting not only changes in sex ratios, but also as the movement of shorter-billed western forms through central and eastern staging areas later in the season. This hypothesis was supported by an elegant analysis of the amount of variability to be expected from mixed-sex samples of migrants from western, central, or eastern breeding areas, and from combinations of areas. They found that while the variability of birds moving through in July was consistent with origin in a single region, the values in August rose to levels expected in mixed samples from both eastern and central areas.

Data from this study only partially support this interpretation. While the population moving through Kent Island was more variable than that at Sibley Lake, I did not find similar monthly differences. At Sibley Lake, the coefficients of variation in bill lengths were 6.49% and 6.79%, in July and August, respectively. These values are in the ranges given by Harrington and Morrison for a mixed-sex sample of birds from a single breeding area, as expected. The values from Kent Island in July and August were 7.47 and 7.15, both in the range expected from mixed sex populations from eastern and central areas. Thus, while the data support the idea that eastern migrants originate from a wider area of the breeding grounds than midwestern migrants, there is no seasonal difference of the sort reported elsewhere.

The analysis of variability supports the previous conclusion, based on comparisons of means, that adults moving through the study areas originated in separate breeding populations. Although bill lengths of juveniles do not separate populations as reliably as those of adults (Harrington and Morrison, personal communication), Sibley Lake juveniles had significantly shorter bills than those at Kent Island ($\bar{x} = 18.5 \pm 1.2$ vs. 19.7 ± 1.3, t-test, $p < .01$). This suggests that juveniles follow the same routes as their parents. Thus, when comparing the migratory behavior of birds moving through the two sites, there is justification for expecting specific adaptation by each population to its migratory route.

3.5 WESTERN AND EASTERN MIGRATION ROUTES

These sections summarize the migration routes used by birds staging at Sibley Lake and Kent Island.

3.5.1 Western Routes

As shown above, morphometric evidence shows that Semipalmated Sandpipers migrating through Sibley Lake originate in western breeding areas. Direct evidence of a movement from Alaska to Sibley Lake was obtained. A juvenile bird, color-banded near Beechy Point, AL (near Prudhoe Bay) on 9 July, 1978, was trapped at Sibley Lake on 23 August. The bird left its nesting area during the first or second week of August (W. Hanson, personal communication). There were no other records in the U. S. Bird-banding Laboratory files (1979) of Alaska-marked Semipalmated Sandpipers recaptured the same autumn at temperate latitudes.

A flight from the tundra of western Canada, or from Alaska, to staging areas in the northern Great Plains passes over habitat that is basically inhospitable to Semipalmated Sandpipers. Figure 9 shows that C. pusilla is not abundant at locations in the boreal forest. Crossing the forest in a single flight would mean traveling 2000 km. or more, and if they make such a flight, birds would have little stored fat on arrival in the plains.

As expected from the breeding biology, adults precede juveniles on migration. Figure 11 shows the proportions of birds caught each day that were adults. Juveniles were first seen at Sibley Lake in late July, but did not show up in large numbers until early August. Figure 11 is somewhat misleading with respect to proportions of adults present; significant numbers stayed through August but these "residents" avoided traps and nets.

The destinations of autumn migrants staging in the midwest have not been documented previously. Files from the U. S. Bird-banding Laboratory (1979) showed a single autumn same-season recapture, a movement from Kansas to Guyana. Eleven birds marked at Sibley Lake were reported that fall more than 50 km. from the study site (Figure 12 and Table 1). Sibley Lake migrants dispersed in a clear southeasterly pattern (mean direction = 139°, r statistic = 0.94, $p < .001$). Some birds made fairly short flights, such as those sighted in Minnesota and Wisconsin, showing that at least some overland migrants exercised their option for multiple-stage journeys. However, the average distances flown by birds leaving the upper midwest remain unknown.

Figure 11. Percent of birds caught each day that were adults at Sibley Lake and Kent Island. A dashed line means that no birds were captured on that day.

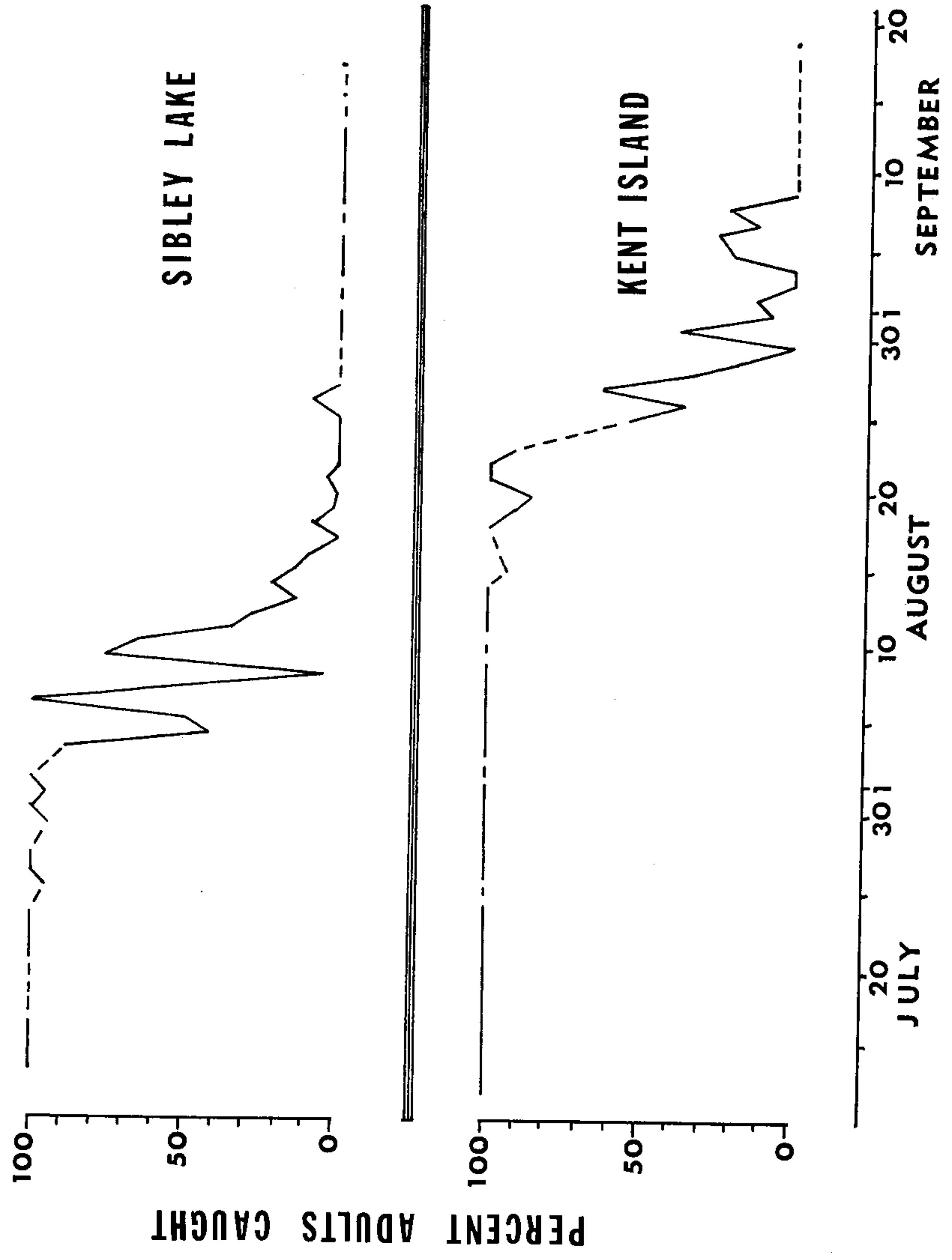

SIBLEY LAKE
KENT ISLAND
PERCENT ADULTS CAUGHT
100
50
0
100
50
0
20
JULY
30 1
10
AUGUST
20
30 1
10
SEPTEMBER
20

Figure 12. Sightings and recoveries of individually marked Semipalmated Sandpipers from this study. Closed symbols indicate birds marked or seen at Sibley Lake. Open symbols indicate birds marked or seen at Kent Island. Lines connect same-season movements.

☆ ★ = Sibley Lake, Kent Island

⦿ = birds reported fall, 1977

□ = birds reported spring, 1978

○ ● = birds reported fall, 1978

△ ▲ = foreign location of marked birds seen or captured at Sibley Lake or Kent Island.

Table 1. Foreign recoveries and sightings of birds marked at Kent Island and Sibley Lake.

Recovery Data			Marking Data			
Location	Date	ID Method	Date Marked	Last Seen	Age[a]	Band Number
			Birds marked at Kent Island, 1977			
Salisbury Beach, MA	08-23-77	tag	07-16-77	08-22-77	A	1211-15129
Alness Village Berbice, Guyana	09-03-77	band	08-16-77	----	A	1211-15104
Kitty Hawk, NC	09-05-77	tag	08-01-77	08-16-77	A	1211-02362
Nigg, Berbice Guyana	09-10-77	band	08-09-77	08-25-77	A	1211-02607
Stone Harbor, NJ	06-16-78	tag	07-21-77	07-24-77	A	1211-15323
Pt. Louis, Guadeloupe	08-06-78	band	08-08-77	08-23-77	A	1211-02799
Lubec, ME	08-18-78	tag	08-01-77	08-21-77	A	1211-02374
Assateague Is, MD	09-18-78	tag	08-07-77	08-07-77	A	1211-02745
			Birds marked at Sibley Lake, 1978			
Breckenridge, MN	08-19-78	tag	07-21-78	08-12-78	A	1241-30955
Gallatin, TN	08-19-78	tag[b]	07-15-78	07-27-78	A	1241-30856
Madison, WI	08-20-78	tag	08-05-78	08-14-78	I	1241-31363
Crystal Springs, ND	08-29-78	tag	----78	----	-	----
Johnsons Bayou, LA	09-04-78	tag	08-06-78	08-19-78	A	1241-31276
Bubali, Aruba Neth. Antilles	09-06-78	tag	07-27-78	08-03-78	A	1241-31050
Lake Williams, ND	09-19-78	tag	----78	----	-	----
Chichiriviche, Venezuala	09-23-78	tag	07-31-78	08-15-78	A	1241-31200
Coco Solo, Canal Zone	10-13-78	tag	07-27-78	07-27-78	A	1241-31075
Cheyenne Bottoms, KS	10-20-78	tag	----78	----	-	----
Okeechobee, FL	10-27-78	tag	08-11-78	08-17-78	A	1241-31495

a) A for adult; I for immature.

b) Tag reported to be bothering this bird.

Three birds were sighted on the wintering grounds, two on or off the coast of Venezuela, and one in Panama. This is the first direct evidence showing that midwestern migrants move to the western part of the winter range. Stiles and Smith (personal communication) confirm that Semipalmated Sandpipers moving through, and wintering in, Costa Rica have short bills (18.3-18.8 mm.).

The basic migratory route of western migrants is now clear. Breeders fly from the tundra to the northern plains, make one or more stops along an overland, southeasterly route, cross over the Gulf of Mexico and/or Caribbean, and winter in the western part of the non-breeding range.

3.5.2 Eastern Routes

Migrants moving through eastern areas have been much more thoroughly studied than western populations. Information is available on their abundance and fat stores at staging sites, and a good deal of attention has focused on their overwater flight.

3.5.2.1 Staging Areas

The bill length data reviewed above suggested that both central and eastern breeders stage in New England and the Maritimes. Movements from James Bay to the coast have been documented by a massive color-marking program carried out by the Canadian Wildlife Service at North Point, James Bay, Ontario (Morrison, 1976-1978; Morrison and Gratto, 1979a). James Bay provides excellent feeding habitat for Semipalmated Sandpipers, and migrants staging there face shorter flights over boreal forest than those made by western migrants. The Canadian Wildlife Service color-marked over 30,000 Semipalmated Sandpipers between 1974-1978, producing over 1500 "bird-days" of sightings. Birds from James Bay dispersed in a broad fan extending to the southeast, and nearly all sightings were coastal. In 1978, only four reports were received from locations west of James Bay, while 415 were sighted along the Atlantic coast between Virginia and Prince Edward Island (Morrison and Gratto, 1979b). Twenty-seven sightings of James Bay birds, probably representing 22 individuals, were made at Kent Island in 1977. No James Bay birds were seen at Sibley Lake in 1978.

Figure 11 shows that eastern adults preceded juveniles. At Kent Island in 1977 juveniles did not show up until well after the middle of August, and never came through in large numbers. This pattern contrasts with Sibley Lake, where juveniles appeared by late July, were abundant in early August, and eventually came through in numbers nearly equal to the adults. It is tempting to conclude from these data that Semipalmated Sandpipers might behave like Golden Plovers, with juveniles from eastern or central populations migrate through inland routes, while the adults fly over the Atlantic (MacKay, 1891; Rowan, 1923, 1926). However, it was shown above that juvenile bill lengths were significantly shorter in the midwest, suggesting that juveniles segregate as do the adults. Longer-term studies have found large yearly variations in the numbers of juvenile Semipalmated Sandpipers moving through particular areas (Morrison, 1976-1978; Morrison and Gratto, 1979a; Page _et al._, 1977; Harrington, personal communication). The difference in the timing and abundance of juveniles at Sibley Lake and Kent Island is probably related to the seasonal phenologies and productivities of different parts of the breeding grounds in the two years. I conclude that juveniles follow routes similar to those of their parents.

3.5.2.2 Transoceanic Flights

From coastal staging areas, and probably from inland locations in the northeast also, most Semipalmated Sandpipers make a non-stop, transoceanic flight to the West Indies or northern coast of South America. The notion that shorebirds migrate far out to sea dates back to 19th-century ornithologists and hunters. In his 1866 paper on the distribution and migration of North American birds, S. F. Baird wrote of the Golden Plover:

> Generally, large flights would seem to start directly from Newfoundland and Nova Scotia for the West Indies, where they are met with every autumn passing still southward into South America. . . . but it is well known to the sportsman of New England that, should a violent north-east storm occur off the coast toward the end of August unusual flights of Plover and Curlew may be looked for. (p. 292).

Modern documentation of this flight comes from marking and radar studies. Color-marking of Semipalmated Sandpipers staging in the Maritimes produced returns from two areas: the Atlantic coast north of Virginia, and a greater number of reports from the Lesser Antilles and northern coast of South America between Brazil and western Venezuela (McNeil and Burton, 1973). Of the 1456 birds wing-tagged at Kent Island, two reports were received the first fall from the Atlantic coast, and two were received from Guyana (Figure 12, Table 1). Considering the probabilities of obtaining returns from the two areas, it seems likely that relatively few marked birds from either this study or McNeil and Burton's moved southwest along the coast; thus most flew directly out over the ocean. Radar studies have confirmed large-scale departures of shorebird flocks to the southeast of the Maritime and New England coasts (Drury and Keith, 1962; Nisbet, 1963; Richardson, 1972; Williams, et al., 1977; Richardson, 1979). They occur in weather conditions with following winds, rising pressure, and clearing conditions (Richardson, 1979). Unfortunately, southwesterly movements of shorebirds are swamped on radar screens by concurrent passerine movements, so that a radar assessment of the relative proportions of coastal versus overwater flights is not available.

The winter-range recoveries of sandpipers marked in the northeast are east of the areas where the Sibley Lake birds were seen. Combining the results of McNeil and Burton (1973, 1977), Morrison and Gratto (1979a), the Bird-banding Laboratory files (1979), and the first-fall returns from Kent Island, it is clear that eastern migrants end up no further west than eastern Venezuela.

Semipalmated Sandpipers at coastal staging areas put on large amounts of fat prior to departure. McNeil and Cadieux (1972a) found that some individuals on Sable and the Magdalen Islands carried fat reserves equal to their fat-free body weight. Using the equation for flight metabolism presented by Raveling and Lefebvre (1967), flight times of about 50 hours were estimated for the fattest individuals sampled. The accuracy of this and other procedures for estimating flight metabolism of migrating birds has recently been brought into question (see Larken et al. 1979). There is direct evidence that the birds are stressed by the flight. Semipalmated Sandpipers collected in Venezuela in August and September had lower fat levels and smaller dry weights than birds caught at any other time of year (McNeil, 1970).

Baird (1867) believed that "many of these species take their flight southward from Nova Scotia and Newfoundland straight for the West Indies, and pass directly over Bermuda" (Baird, 1867:288). Cooke (1903) stated, and modern studies have confirmed, that the flight is not straight, but rather is a eastward arc over the ocean. Although the Lesser Antilles are on a great circle course of about 175° from Nova Scota, radar tracks of shorebird flocks leaving the coast have a mean direction of 134° (Richardson, 1979). Over Bermuda, shorebirds are still flying a southeasterly course (Ireland and Williams, 1974). They commonly arrive over the Lesser Antilles or Puerto Rico with tracks from the north or northeast (Hilditch et al. 1973; Richardson, 1976b). Although species cannot be distinguished on radar, Semipalmated Sandpipers were found to be the most abundant North American migrant in Antigua when radar data were gathered in 1970 (Hilditch et al. 1973).

Current interpretation of this curved course relates it to prevailing wind patterns over the western Atlantic, a factor first recognized by Clarke (1905). During this flight, birds pass from a temperate region of westerly air flow, with strong cyclonic and anticyclonic organization, through, or to the east of, a region of light winds with basically anticyclonic flow known as the Bermuda high, and into the strong northeasterly trade winds. If birds leave the coast when alternating highs and lows provide following winds (e.g. MacKay, 1892; Richardson, 1979), the flight can be made with following winds for nearly its entire length (Drury and Keith, 1962). Williams et al. (1977), examining primarily non-shorebird data, proposed that the curved flight could result entirely from a combination of prevailing wind directions and maintenance by the birds of a fixed flight direction relative to the air. This fixed heading hypothesis would require no change in the direction of flight by the bird. Consideration of the known departure directions, flight speeds, and wind conditions over the western Atlantic make this flight strategy improbable for shorebirds leaving Nova Scotia, and a change in heading seems necessary to achieve a landfall in the Western hemisphere (Richardson, 1979; Stoddard et al., in press).

The transoceanic flight from Nova Scotia to the northernmost Antillies covers a great circle distance of 3000 km. A curved flightpath would be longer, and shorebirds may continue on to destinations further south, including the coasts of Venezuela and the Guyanas. From simultaneous radar observations of departures on the northeast coast, and/or correlation of migrant density in the Caribbean with departure conditions in the northeast, both Richardson (1976b) and Williams et al., (1978) estimated flight times of around 60 hours from the coast to the West Indies. These estimates are based primarily on passerine data, and even small shorebirds, with their faster air speeds, might make the trip more quickly. Shorebirds departing Nova Scotia have ground speeds averaging 75 km./hr. (Richardson, 1979). Their air speeds are probably averaging 45-50 km./hr., since they gain additional ground speed from the following winds in which they fly. If they maintained these ground speeds, they would cover nearly 4000 km. in the 50 hours of flight time estimated for the heaviest individuals by McNeil and Cadieux (1972a). Pennycuick (1969) theorized that if birds fly at their optimal speed, in terms of distance covered per gram of fuel used, they will slow down as they become lighter, but radar observations have not been able to provide data on this possibility. If shorebirds follow Pennycuick's model, their total flight ranges will be considerably shorter than those estimated above (Summers and Waltner, 1979).

Finally, what are the en route options for birds initiating transoceanic flight? The quote from Baird that began this section stated that under "violent north-east storm" conditions unusual numbers of "Plover and Curlew" occurred on New England shores. MacKay (1891, 1892), who observed and hunted on Nantucket for over 20 years, wrote of Golden Plover:

> Their presence here, therefore, is purely the result of tempestuous weather as the occurrence of south-easterly or north-easterly storms, thunder and lightning with rain, or thick fog with a south-west wind, while they are on their passage, by which they are driven from their course, confused, and deflected to the westward; in which event they pass along the New England coast, and over the outlying islands and promintories. They are then eargerly (sic) pursued and many killed. (MacKay, 1891, p.18).

Writing of the probably extinct Eskimo Curlew (Numenius borialis), he states:

> When I take a retrospective view for a series of years I am more than ever impressed with the few birds killed except in some very exceptional year. In most years thay are far from being abundant, in fact are the reverse. I am inclined to the opinion that these birds generally pass our coast much further from land than has been usually supposed, for it rarely happens that any large numbers of them are deflected over the land by ordinary storms, very severe thunder and lightning with heavy rain, or dense fogs, apparently being required to drive them from their customary line of flight and force them to seek land until more favorable conditions for migrating take place, for they are unusually strong and and high fliers of great endurance. (MacKay, 1892, pp.16-17).

There is little modern evidence with regard to the behavior of transoceanic migrants as they encounter strongly unfavorable weather. Their tendency to depart in favorable weather following cold fronts (Richardson, 1979; see section 5.3) ironically almost assures that they will catch up with the fronts as they follow them out to sea. Richardson (1979) describes radar observations of shorebird flocks moving "through (or over?)" such fronts, and this is apparently a normal part of their flight. However, birds encountering weather that was not generated on land, such as tropical storms moving northward, are in a different situation. Richardson (1972, 1976a) describes downwind movements of birds in the counter-clockwise circulation on the northern side of advancing tropical storms. Williams and Williams (1978) show birds, probably passerines, with unusual northerly or westerly flight directions over the ocean north of advancing tropical storms. Thus, there is evidence that if strong southeasterly winds are encountered, transoceanic migrants will change course, fly downwind, and reach the coast south of their starting point. Such a flight strategy would account for the observations of plovers and curlews quoted above. The recoveries along the Atlantic coast of shorebirds marked in the Maritimes (see above) may have been a result of such flights. However, for both passerines and shorebirds, the existing evidence suggests that birds persist with southeasterly flights in the face of moderately unfavorable weather (e.g. Williams and Williams, 1978; Richardson, 1979).

A little is known of the movements of sandpipers following their arrival in South America. The influx of migrants is clearly visible in eastern Venezuela by the end of July (McNeil, 1970), but large increases are not seen in Suriname until late August or early September (Spaans, 1978). It seems likely that eastward coastal movements follow transoceanic flight.

In summary, birds from central and eastern breeding populations move, in one or more flights, to coastal staging areas. Here they deposit up to their own basic weight in fat, and, under appropriate weather conditions, initiate transoceanic flights to the West Indies or beyond. They winter in the eastern portion of the species' range.

3.6 CONCLUSION

Semipalmated Sandpipers breeding in western and eastern parts of the breeding range are morphologically distinct, and the breeding populations follow different migration routes. It is reasonable to expect specific behavioral adaptations to the contingencies each population faces on migration. A comparison of the behavior of the two populations will allow a greater understanding of what these contingencies are.

Chapter IV

BEHAVIOR AT STAGING AREAS

Semipalmated Sandpipers arriving at staging areas at the end of migratory flights must procure food to replenish fat depleted *en route* and to provide for the next flight. They may cue in on habitat and/or on the presence of conspecifics in determining where to end a flight, and adults may return to previously utilized areas (Morrison and Gratto, 1979a). Once a bird arrives, it encounters conspecifics as competitors for resources, the most important of which, for Semipalmated Sandpipers, is foraging space. If birds establish themselves as local feeders, we expect them to fatten and depart. This chapter covers the behavior of birds from first arrival in an area through, but not including, departure on migration. The major question asked is: what determines how long a bird will stay at the staging area?

4.1 POPULATION DYNAMICS AND SOCIAL BEHAVIOR

This section examines how changes in habitat and intraspecific interactions affect a bird's behavior at the study site.

4.1.1 Local Population Dynamics

The total numbers of Semipalmated Sandpipers censused daily at Sibley Lake and Kent Island are shown in Figures 13 and 14. The North Dakota data are broken down by lake. While the shores of Sibley Lake provided

Figure 13. Total number of birds seen on daily censues at Sibley Lake.

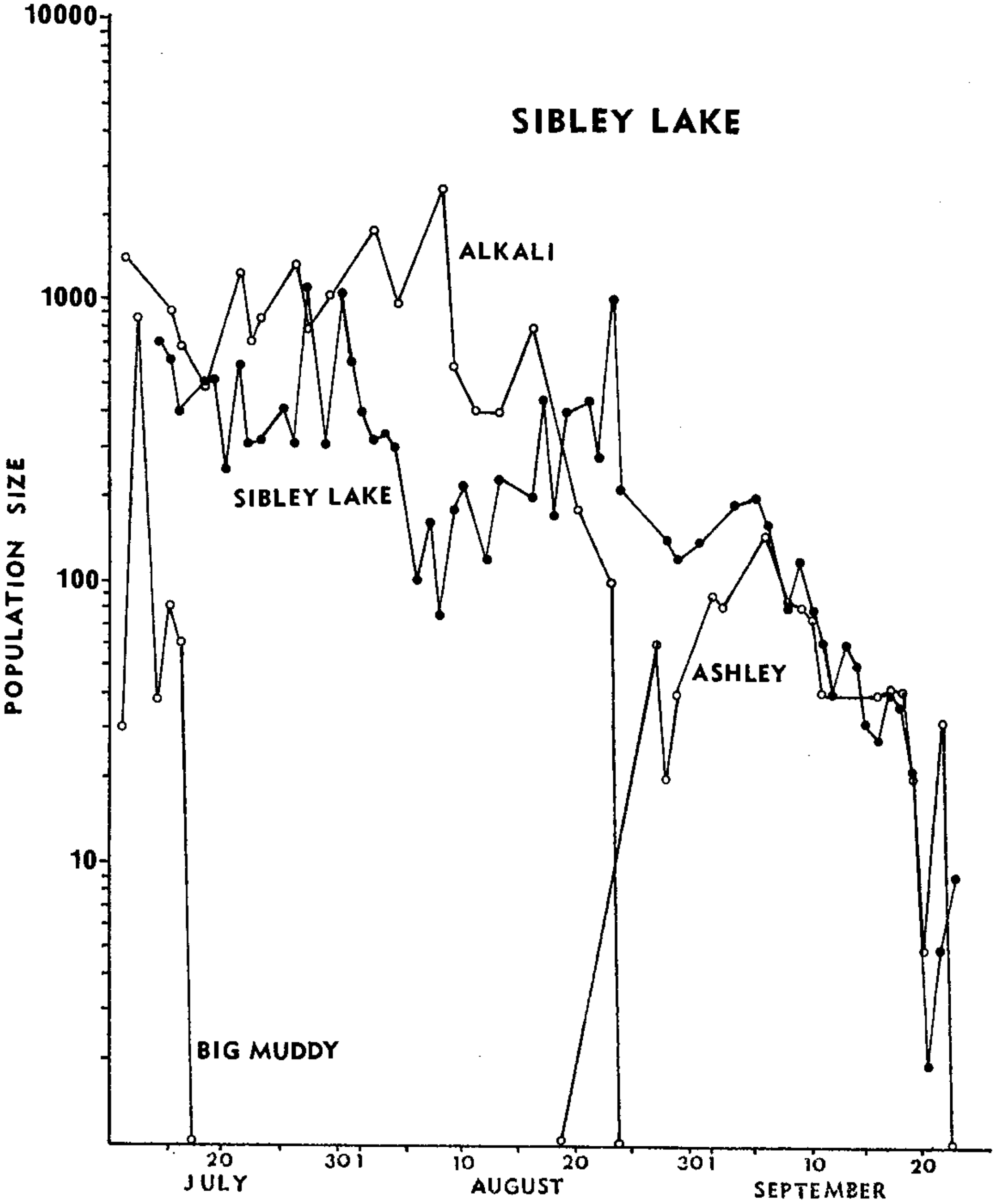
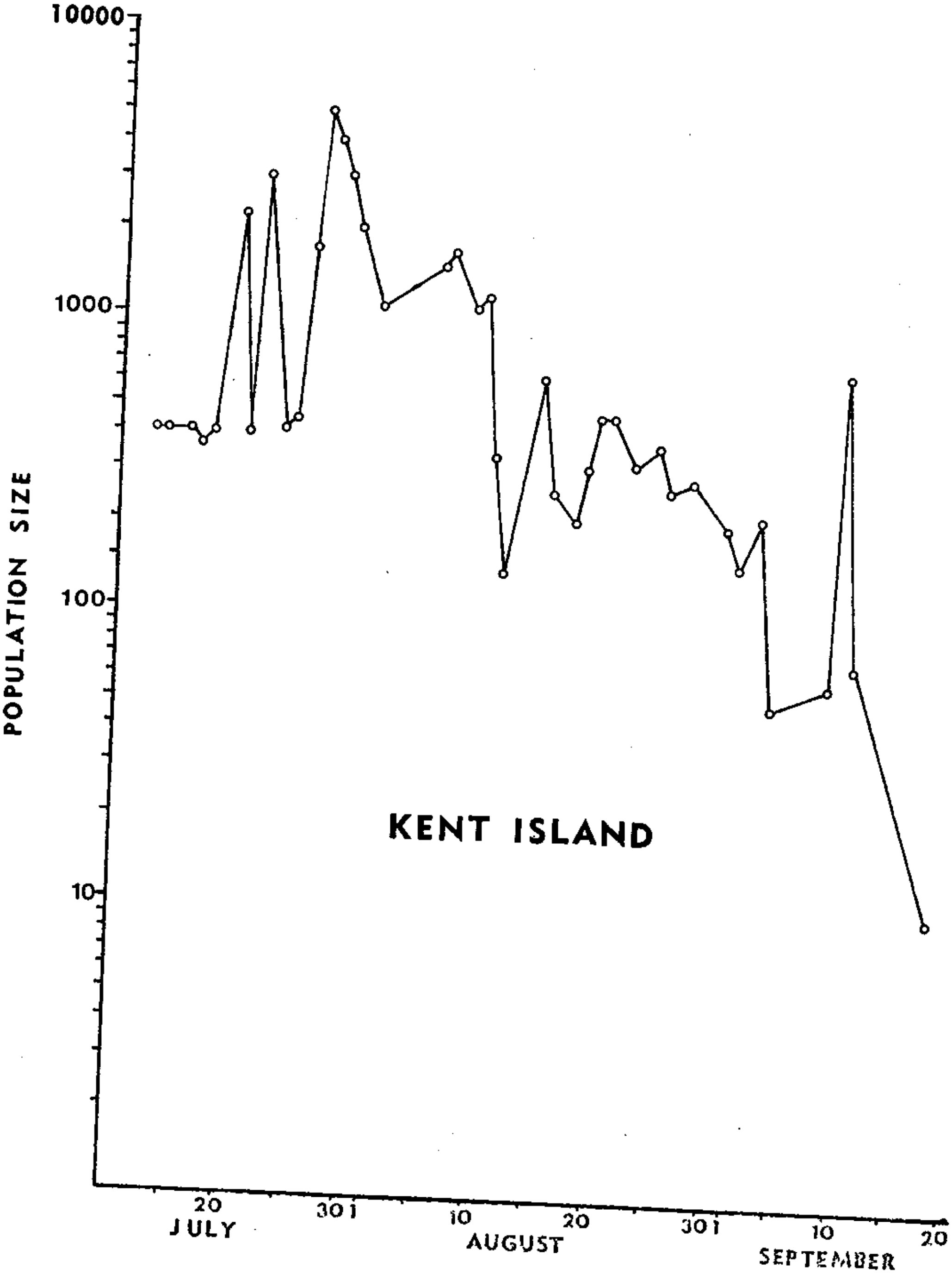

SIBLEY LAKE
POPULATION SIZE
10000
1000
100
10
ALKALI
SIBLEY LAKE
ASHLEY
BIG MUDDY
20
30 1
10
20
30 1
10
20
JULY
AUGUST
SEPTEMBER

Figure 14. Total number of birds seen on daily censuses at Kent Island.


10000
1000
100
10
POPULATION SIZE
KENT ISLAND
20
JULY
30
1
10
AUGUST
20
30
1
10
SEPTEMBER
20

feeding habitat throughout the season, the other three lakes experienced drastic changes in their attractiveness to shorebirds. Ashley was a cattail-surrounded pond with little shallow water until late in the season. Alkali and Big Muddy were essentially huge, nearly flat-bottomed puddles. As they dried up, strong winds exposed areas of virgin mudflat, which attracted hundreds of shorebirds. When the wind died, often towards evening, birds congregated along the advancing edge of the water as it reflooded exposed areas, just as they do when ocean tides begin to cover feeding areas (Recher and Recher, 1969). During the first two weeks in August, Alkali drew large numbers of birds away from Sibley. The variability in the location and amount of feeding area available resulted in opportunistic exploitation of these areas by birds, producing wide fluctuations in the numbers of birds present from day to day.

Local population size was more stable at Kent Island (Figure 14). Waves of immigration were visible, but populations greater than 1500 did not persist. Since the area available for foraging was fairly constant at Kent Island, the short duration of the peaks implies that density-dependent mechanisms limited the number of residents in the area.

4.1.2 Competition for Foraging Space

Competition for foraging space was observed directly as aggressive and territorial behavior, and inferred from certain aspects of population dynamics and the difficulty birds had in establishing themselves as local feeders.

4.1.2.1 Aggressive and Territorial Behavior

At both study sites, individuals were intraspecifically aggressive. Their behavior was similar to that described by Recher and Recher (1969), who showed that rates of aggressive encounters were positively correlated with sandpiper density. Recher and Recher observed unmarked birds; by watching marked birds I was able to confirm their speculation that many migrant Semipalmated Sandpipers are territorial. At both study sites certain individuals consistently defended specific foraging areas. At Kent Island, these territories were sections tidal mudflat about 3-15 $m.^2$ in size. At Sibley Lake, individual birds defended portions of the shoreline about 3-5 m. long. The longest record of continual occupation was nine days for an individual at Sibley Lake. Birds did not defend territories on the unstable Alkali and Big Muddy Lakes. At both study sites, both territorial and non-territorial birds were present, as was the situation in migrant Pectoral Sandpipers (*Calidris melantos*) (Hamilton, 1959) and for wintering Sanderlings (*C. alba*) (Myers *et al*. 1979).

At Kent Island, where feeding grounds were regularly covered by the tide, territorial birds returned to the same feeding location after each cycle. Some individuals held territories in two areas: one used at dead low tide in the feeding areas around Crockett Point or north of the Basin, and a second territory in the Basin proper, which flooded about two hours later in the tidal cycle and was also exposed earlier on the ebb tide (see Figure 2).

Semipalmated Sandpipers were the numerically dominant foraging species at both locations, but interactions with other shorebirds may have influenced their foraging behavior. Burger *et al.* (1979) showed that *C. pusilla*, as nearly the smallest member of the New Jersey shorebird community, was infrequently involved in (avoided?) interspecific aggressive interactions. Recher and Recher (1969), observing *C. pusilla* at numerous coastal locations, concluded that intraspecific interactions were of far greater significance (at least in "ecological time") than interspecific encounters. Although there is considerable overlap in prey items taken and foraging behavior among small calidrids at staging and wintering areas (Brooks, 1967; Baker and Baker, 1973), I have not considered the density of other species in the following analysis since *C. pusilla* outnumbered congenerics at both study sites by a factor of ten or more.

4.1.2.2 Population Density and Transience

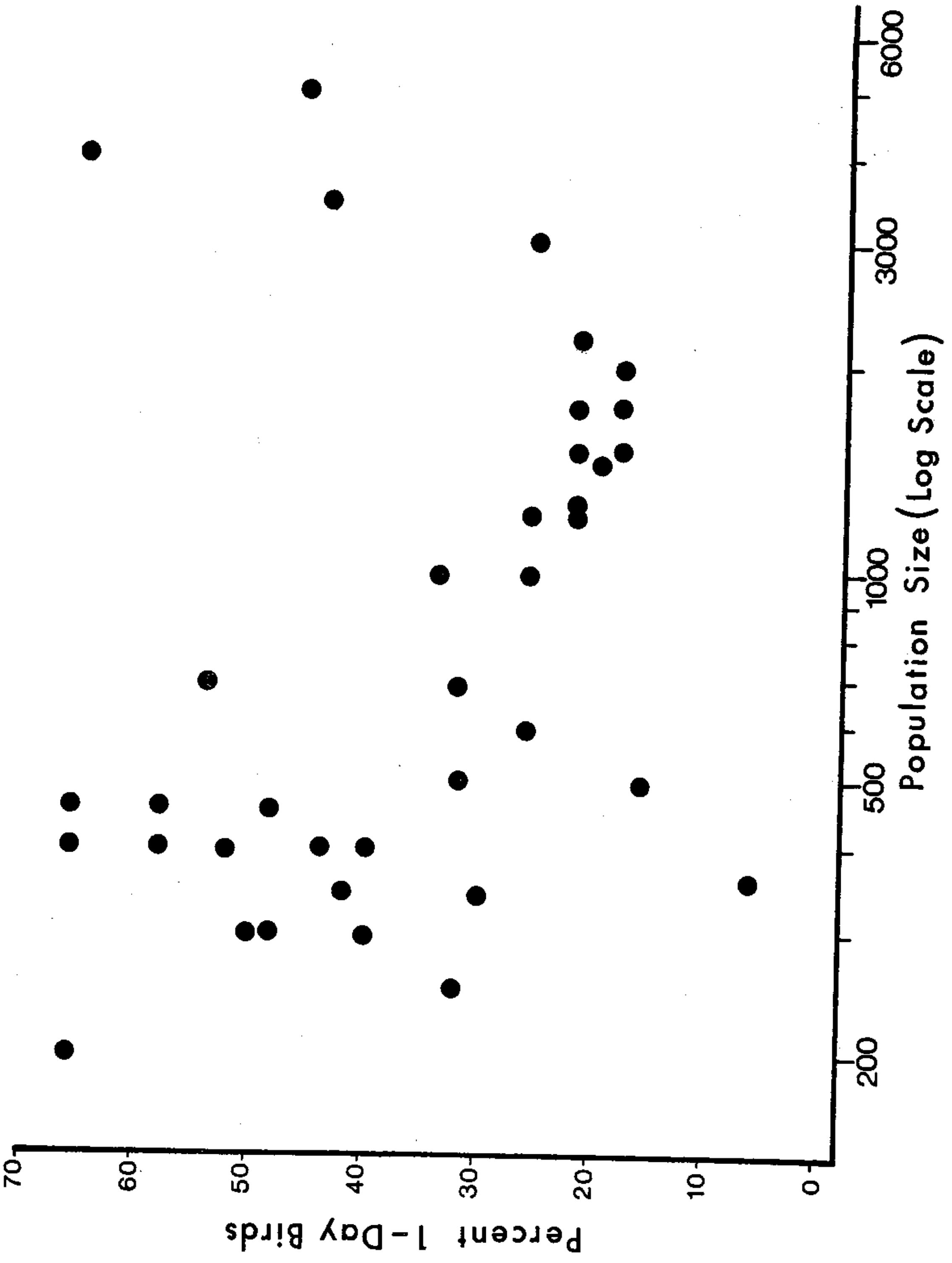
The territorial and aggressive behavior discussed above could provide a mechanism for limiting the number of birds foraging in an area. To test whether density-dependent mechanisms affected the length of time that individuals remained in the local area, I examined the percentage of birds captured daily which were never resighted after the day they were marked, hereafter called "transients". If the resource base is reasonably stable, the proportion of transients may be a measure of the relative difficulty in becoming established as a local "feeder" (Rappole and Warner, 1976; Rabøl and Hansen, 1978). As discussed earlier (Section 2.1.1), I believe that captures of birds were biased towards new arrivals unfamiliar with the local area. Since resident birds are dominant to non-residents in a wide variety of situations, transience rate should be an especially sensitive indicator of intraspecific competition.

Figure 15 plots the percentage of transients in daily cohorts at Kent Island against population size on the day caught. To control for age-specific competitive ability, the transience rates of adult birds only were considered; population sizes include both juveniles and adults. There was high variability in the percentage of birds leaving at low densities, low transience and little variability at populations from 1000-2000, and increased transience for the few points where population size exceeded 2000.

The rather constant 20% transience rate seen at intermediate population densities appears to be a "baseline" level, part of which may be a response to the trauma of capture and handling. The lack of variability in transience rates represents a consistent response of the migratory populations to this density of sandpipers. The increased level of transience of marked birds at higher population densities was consistent with emigration by the population as a whole, in that local staging populations above 2000 did not persist (Figure 14). These results point to density-dependent regulation of the number of resident foragers.

Transience rates were higher at low than at moderate population densities, despite less competition for space. This intriging observation suggests that Semipalmated Sandpipers may use the density of conspecifics in their assessment of an area, and that up to a point, higher densities are more attractive. The behavior of birds around the walk-in traps in North Dakota supports this; new birds were obviously attracted to a cage crowded with trapped birds. Dense flocking may be

Figure 15. The percentage of adult birds not seen after the day of marking (1-day birds) as a function of population density.


Percent 1-Day Birds
0
10
20
30
40
50
60
70
Population Size (Log Scale)
200
500
1000
3000
6000

taken as a signal of locally rich food and/or be related to protection from predators (Page and Whiteacre, 1975).

Transience rates at low density were highly variable. Since low density populations occurred both early and late in the season (see Figure 14), I tested whether the variance might be a response to seasonal differences in the quality of the feeding area. Schneider and Harrington (1981) showed that between July and September, migrant shorebirds, including Semipalmated Sandpipers, substantially decreased the prey available to foraging birds on mudflats at Plymouth, MA. Limited data from exclosure expermiments in the Basin showed similar effects at Kent Island in 1977 (Podolsky and Lank, unpublished data). If birds responded directly to the level of prey availability, transience rates should be lower later in the season. This was not the case. The low density points (100-700 birds) were divided into two groups: those occurring before 12 July, and those after August 11. The means of the two groups are similar ($\bar{x}$ = 44%, n=10, for early points; $\bar{x}$ = 40%, n=11 for late points), which argues against a food-abundance effect. The high variance may result from daily differences in the proportions of new arrivals caught, but remains basically unaccounted for.

I could not perform a parallel analysis of transience versus density for Sibley Lake due to the large changes in the size of the foraging habitat. However, the overall transience rates suggest a greater difficulty of establishment at Kent Island. At Sibley Lake, 26% of the marked birds were never seen locally again, while at Kent Island significantly more of the birds (36%) were never seen again ($\chi^2 = 34.03$, $p <$ .001). These rates are not excessively high. Other studies on C.

pusilla report 30-50% of marked birds disappearing within 24 hours of marking (Page and Bradstreet, 1968; Page, 1970; Harrington, personal communication). The significantly higher overall level of transience at Kent Island suggests that birds arriving on the coast may have had a more difficult time establishing themselves as feeders in the face of competition from conspecifics.

4.1.3 Local Movements

Birds failing to establish themselves as feeders on the study site must either have continued migratory movements with reduced fat stores or made local movements to areas outside the study site. Resident birds may also have moved locally, which would reflect depleted or unstable feeding conditions. Censuses made outside the study sites, and calculated daily emigration rates provide limited information about these movements.

4.1.3.1 Local Sightings of Marked Birds

At both study sites, some individuals made short-distance movements to local areas outside the primary study site. Birds marked at Sibley Lake were sighted in a large concentration of shorebirds 5.5 km. north of Sibley Lake, while Kent Island birds were reported from islands 5.5 and 18 km. north of the banding site. Since these movements were northward, rather than in the southeasterly migratory direction (Section 5.1.2), they may be clearly interpreted as dispersal in search of feeding habitat, rather than as "migratory" movements. Twenty-eight percent of the marked Sibley Lake birds seen off the study site were transients (n = 79), while 52% of such birds were so at Kent Island (n = 25). Thus significantly more birds seen off site had left immmediately and not returned at Kent Island than was the case inland ($\chi^2 = 4.96$, $p < .03$). The higher proportion of transients among off-site records suggests greater site-attachment, once established, for coastal birds. The next section examines the same question in a different way for resident birds.

4.1.3.2 Emigration Rates of Resident Birds

On the basis of sightings and resightings of marked birds, I estimated daily emigration rates from the study area (Section 2.5). These estimates exclude information from the transients considered in the previous section. Emigration rates reflect not only birds leaving on migratory flights, but also those which made local movements off the study area, and any that died. This last component is assumed to be insignificant for the daily intervals at which these rate were calculated. Thus, subtraction of migration from the estimated rates, if possible, would provide a measure of the amount of local movement which occurred at each study site.

Figure 16 plots emigration rates, computed for adults, on generalized synoptic weather maps (Section 2.3.1). The circles were placed at the location representing the weather prevailing at the modal time of daily flock departure at each site (Section 5.2.2). The symbol in the circle indicates an emigration rate class, as defined in the figure legend. The emigration rate estimates are subject to error, but grouping them into classes should provide a reliable a relative measure. The impos-

Figure 16. Daily emigration rates of adults from Sibley Lake and Kent Island in relation to weather. Darker circles represent greater emigration (see scale below). Areas of favorable and unfavorable weather are shaded as indicated below.

Emigration Rates

○ = less than -.05

⦶ = -.05 to 0.0

⊕ = 0.0 to .05

◔ = .05 to .10

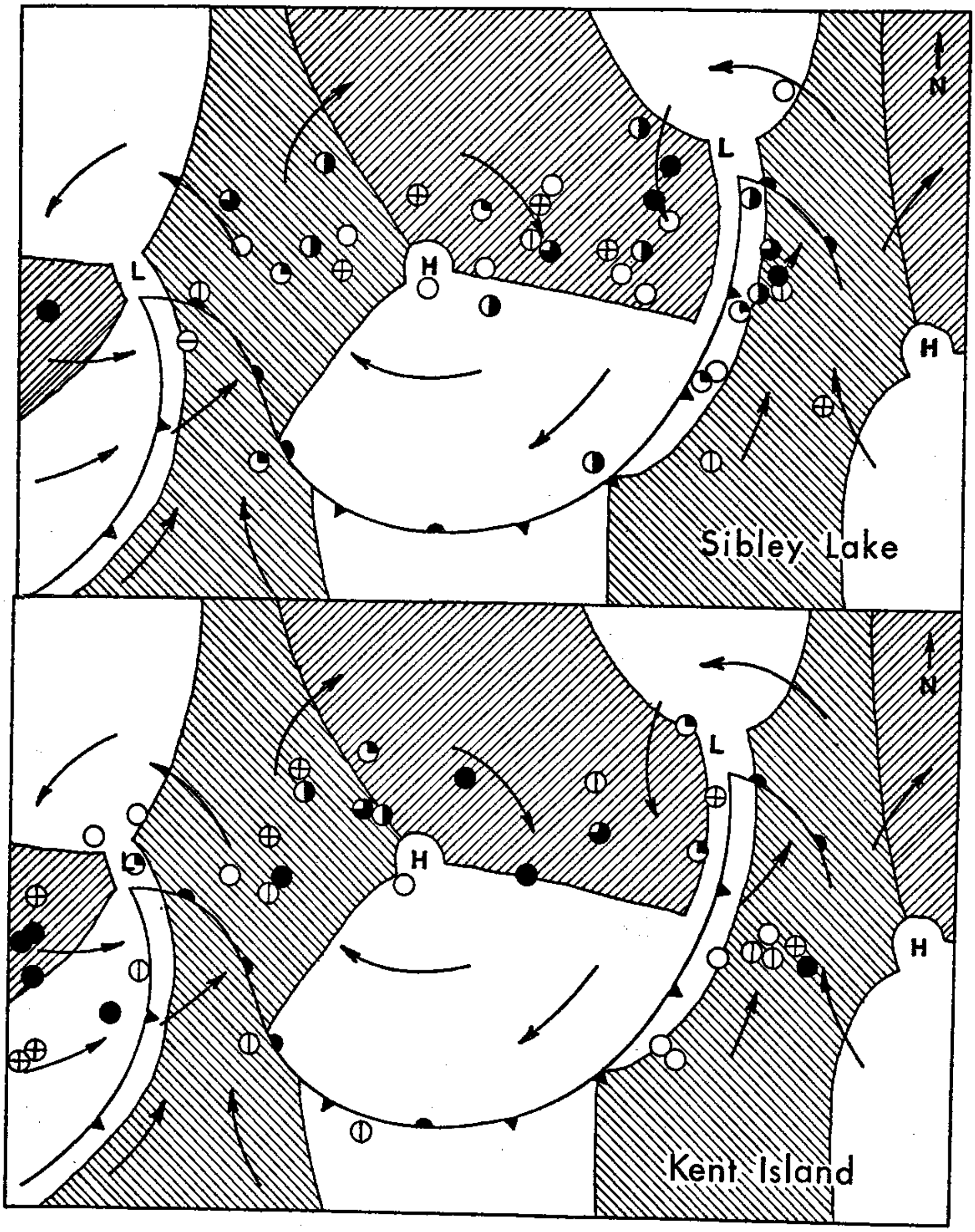
◑ = .10 to .15

◕ = .15 to .20

● = greater than .20

▨ = Favorable Migratory Weather

▧ = Unfavorable Migratory Weather



ADULT EMIGRATION RATES

sible "negative immigration" occurs because the maximum likelihood estimators of "survival" from day to day were not bounded at 1.0 (Brownie and Robson, 1980). Weather conditions that favored or hindered migratory flights, as determined in this study and elsewhere (Section 5.3.1; Richardson, 1979), are shaded accordingly.

The emigration rates do not show strong patterns of increased emigration under favorable migratory conditions and decreased rates under unfavorable conditions. The Kent Island data come closer to agreement with known departure conditions than do the Sibley Lake rates. Emigration rates are significantly higher in favorable than unfavorable weather at Kent Island, but not at Sibley Lake (Mann-Whitney U, 1-tailed tests, $p = .04$ at Kent Island, $p > .10$ at Sibley Lake).

This difference in results provides indirect information about the relative degree of migratory versus local movements made at the two sites. While it is difficult to quantify exactly, the poorer agreement between weather and the emigration estimates at Sibley Lake means either that midwestern birds were less faithful to foraging sites, making more local movements than at Kent Island, or that midwestern birds migrated under a wider variety of weather conditions. The analyses of departure weather at the two locations presented below (Section 5.3) show that while quantitative differences in migratory conditions exist, they are of insufficient magnitude to account for the differences in emigration rate patterns seen in Figure 16. Some of the movement at Sibley Lake was caused by the large changes in habitat suitability (Section 4.1.1). However, neither removal of points from days in mid-August, when habitat change was the greatest, nor restriction of the calculation of emigraton rates to birds seen only at Sibley Lake proper, produced substantially different results than those shown.

In summary, both the data on transience and on emigration rates suggest that it was more difficult to become established as a feeder on the coast, and that once established, birds remained in the area more faithfully than was the case at Sibley Lake.

4.1.4 Feeding Flock Structure

In some flock migrants (e.g. geese, Raveling, 1969), bonds between individuals affect migratory timing, since families or other groups move together. Semipalmated Sandpipers do not leave the breeding ground as family units (Section 3.1), but it seemed possible that shorebird flocks were more than the anonymous associations suggested for diurnal passerine flock migrants (e.g. West *et al*., 1968; West and Peyton, 1972). Since large numbers of the birds were marked, it was possible to observe dyadic interactions and look for constant associations between individuals. The only clear examples of this were related to the feeding territory structure. Individuals were consistently found in proximity to each other due to their holding of adjacent territories. I saw no cases of preferential treatment or toleration of any conspecifics on such territories. At Kent Island, where birds sometimes held territories in two locations (Section 4.1.2), the spatial relationships of territory holders were not maintained between areas. Thus, at least among territorial birds, there was no suggestion that individual social bonds played a role in feeding flocks, and there is no reason to believe they might be involved as part of a migratory strategy. I believe that migrant Semipalmated Sandpipers both feed and migrate in anonymous flocks. An anonymous flock stucture has been carefully documented in winter flocks of Sanderlings, Calidris alba (Myers et al., 1980). Data on the spatial relationships of individually marked birds showed that even in the more stable situation of winter residency individuals apparently associated at random.

4.1.5 Summary and Discussion

The behavior of conspecifics or, in some cases, members of other species, may affect the timing of migration through competition for local resources, social stimulation of foraging, maintenance of individual bonds, or social stimulation of flight. Individual bonds do not appear to play a role in the migratory behavior of Semipalmated Sandpipers. Social stimulation of flight will be discussed in Chapter 5.

The effects of social interactions on migratory behavior are not well documented in any species, and are more difficult to quantify than those due to inanimate effects (Wallraff, 1978). Rappole and Warner (1976) observed defense of foraging areas by migrant Northern Waterthrush (Seiurus noveboracensis), and documented the disappearance of individuals unable to establish local feeding territories. They suggested that intraspecific competition at staging areas was an important feature of migratory strategies. Rabøl and Hanson (1978) showed that the number of immigrant and resident European Robins (Erithacus rubecola) correlated positively with the probability of emigration from a local area, and attributed the effect to crowding. Among migrant shorebirds, competition for food may be inferred from reports of feeding territoriality in several species (Hamilton, 1959; Recher and Recher, 1969; Thompson, 1974; Myers _et al_., 1979).

Birds arriving after a flight must establish themselves as local feeders. _C. pusilla_ were aggressive towards conspecifics at both sites in this study. At both locations, a proportion of the population excluded other individuals from feeding territories. Twenty to 30% of the birds tagged at both locations left immediately. Censuses near both study sites showed that birds made local movements in search of available feeding habitat. Examination of the pattern of transience relative to population density at Kent Island suggested that intraspecific competition may have been one cause of such movements, at least at high population densities.

Whether failure to obtain local resources will induce migratory flights or more local movements is not clear. Rappole and Warner (1976) hypothesized that unsuccessful birds would continue migration, despite depleted fat stores. Marked sandpipers seen off the study site in this study had moved northward, rather than continuing in the migratory direction (Section 4.1.3.1). These sightings are better explained as local movements in search of available feeding habitat than as a continuation of migratory flight.

The overall rate of transience was significantly higher at Kent Island than at Sibley Lake. However, estimates of emigration rates of residents correspond better with migratory weather at Kent Island, showing less local movement among birds on the coast. Taken together, these results suggest that it was more difficult to become established as a resident feeder on the coast, and that those who succeeded in doing so were more site-faithful than inland birds. Inland migrants were feeding on a less reliable resource, both in time and space, and within and between years, than coastal birds. The increased opportunism shown in their movements between areas reflects this. The more stable environment provided by coastal areas may have been an important environmental prerequisite facilitating the evolution of regular transoceanic migration routes.

4.2 FAT LEVELS AND RATES OF FATTENING

It has long been recognized that birds engaging in long-distance migrations deposit large amounts of fat for use as flight fuel (see Berthold, 1975a, for review). Maximum or average levels of fat stores carried by different migratory populations have been used to estimate their probable flight distances (e.g. McNeil and Cadieux, 1972a, b). To understand the behavior of birds at staging areas, I addressed three questions: 1) how fat were birds at arrival, 2) at what rate could and did they put on fat, and 3) how fat were birds at departure? This section concentrates on the first two questions; the third is covered in Chapter 5 since it relates directly to migratory departures. Knowledge of these values would tell us how fat levels constrain lengths of stay at staging areas. Put simply, what was the minimum length of time needed by birds to accumulate enough fat to provide for their next migratory flight?

4.2.1 Geographical Comparisons

The top of Table 2 lists the means, standard deviations, and ranges of weights of Semipalmated Sandpipers caught during fall migration at five different locations. On average, Kent Island birds weighed more than those at more southerly or westerly locations, as might be expected for birds preparing for transoceanic flight. On the other hand, the maximum and minimum weights at each location showed about a two-fold range, suggesting that some individuals put on virtually their entire body weight as fat at all sites. This suggests flight ranges on the order of 3000 km. or more for the fattest individuals at all locations (McNeil and Cadieux, 1972a; see Section 3.4.2.2).

The bottom half of Table 2 gives the means and ranges of estimated fat levels for the four age/location classes in this study (see Section 2.4 for methods of fat estimation). In this simple analysis, Kent Island adults stand out as a singularly fatter group at initial capture. The following sections examine these data in more detail.

4.2.2 Fat Stores on Arrival

How heavy were arriving birds? Figures 17 and 18 plot the mean fat levels of birds captured daily at Sibley Lake and Kent Island. For most of the season, daily cohorts of captured birds contained an unknown proportion of new arrivals and resident birds. However, when the first birds of each age class arrived, I could measure directly the weights of new arrivals only.

At Sibley Lake early arriving adults and juveniles carried almost no fat stores. Later samples were generally heavier, although dramatic

Table 2. Weights and fat levels of Semipalmated Sandpipers during fall migration.

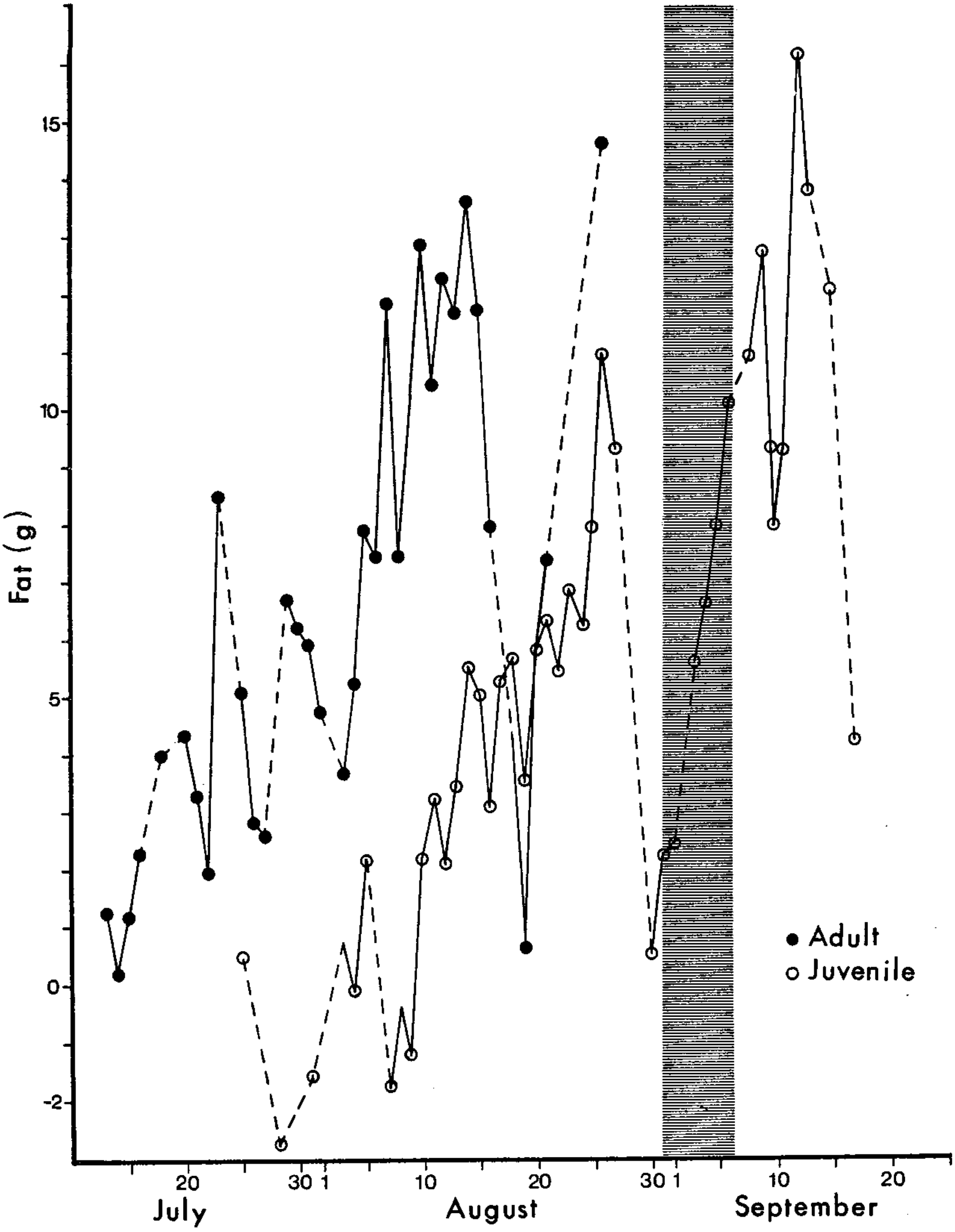
Weights

Location	$\bar{x}$ ± SD	Range	N	Source
Sibley Lake, North Dakota	29.6 ± 5.6	18.5-46.5	1476	this study
Long Point, Ontario	29.8 ± 5.3	18.0-50.0	699	Page, 1969
New Jersey shore	28.1 ± 4.0	19.8-41.3	102	Murry and Jehl, 1964
Raliegh North Carolina	29.0 ± 5.5	20.2-39.7	27	Post and Browne, 1976
Kent Island, New Brunswick	33.0 ± 5.8	18.0-49.0	1456	this study

Fat Stores

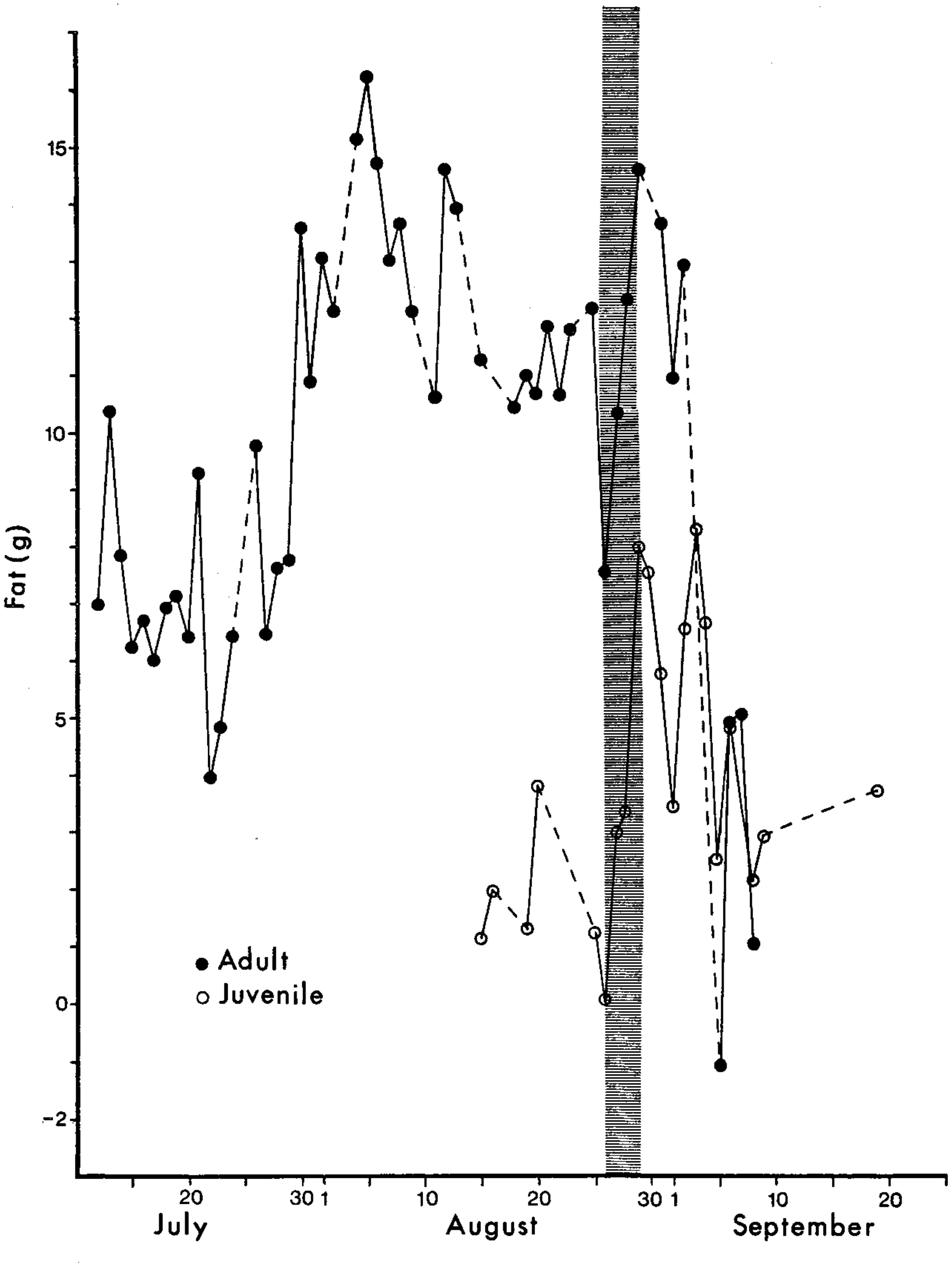
Location	$\bar{x}$ ± SD	Range	N	Source
Sibley Lake				
adults	4.9 ± 5.5	-5.2 -21.4	640	this study
juveniles	5.2 ± 5.7	-4.9 -19.3	833	this study
Kent Island				
adults	9.4 ± 5.4	-4.3 -24.1	1161	this study
juveniles	4.1 ± 4.7	-5.8 -19.2	295	this study

Figure 17. Mean fat levels of adult and juvenile birds captured each day of the season at Sibley Lake. Shaded area is the longest continuous period of weather unfavorable for migration. Solid lines connect consecutive days; a dashed line indicates that a day passed when no birds were caught.



Mean Fat Levels: Sibley Lake 1978

Figure 18. Mean fat levels of adult and juvenile birds captured each day of the season at Kent Island. Shaded area is the longest continuous period of weather unfavorable for migration. Solid lines connect consecutive days; a dashed line indicates that a day passed when no birds were caught.



Mean Fat Levels: Kent Island 1977

decreases occurred for both age classes (e.g. 16-18 August for adults, and 26-30 August for juveniles). Both of these periods corresponded to dates on which birds were observed departing in favorable migratory weather (see Section 5.3). Since the total local population size did not fall drastically during these periods (see Figure 13), new birds must also have arrived on these days. Thus, the light cohorts measured after these dates represented both previous residents that may have been too lean to leave, and new immigrants who arrived carrying little fat. Day-to-day changes in fat levels of the population will be examined further in Section 5.4.1. At present, I simply wish to establish that at least on a few days, birds arriving at Sibley Lake late in the season were as lean as the first arrivals in July.

At Kent Island, the seasonal pattern of fat levels looked quite different (Figure 18). Adults averaged six to seven g. of fat from early in the season, and maintained generally higher fat levels than their counterparts in North Dakota. A dramatic, weather-correlated drop occurred at the end of the season (September 3-4), but in general the graph shows less daily variation than does the midwest data. Although adults at Kent Island may have arrived with five to six g. of fat, juvenile birds clearly arrived light.

Lighter arrival weights of adults in the midwest may have resulted from the differences in flight paths to the two study sites, as suggested earlier (Section 3.4). Sibley Lake migrants may have flown directly from the western arctic coast to the great plains. Many Kent Island birds probably made shorter flights from Hudson's or James Bay, as 22 color-marked individuals were known to have done (Lank, 1979;

Section 3.4.2), thus arriving with some fat. The light arrival weights of coastal juveniles remain unexplained by this interpretation.

4.2.3 Rates of Fattening

The data in Figures 17 and 18 provide an unusual opportunity to measure the rates at which populations of Semipalmated Sandpipers deposit fat. As discussed above, interpretation of daily variation in fat levels is complicated by immigration and emigration. However, at both sites there were periods of several days when the weather clearly opposed emigration and total census data show that there was also no substantial immigration (Figures 13 and 14). During these periods, which are shaded in Figures 17 and 18, I was sampling daily from a relatively stable population and the mean fat levels rose fairly smoothly. I have used these means to estimate a daily rate of fat deposition for each location. Sibley Lake juveniles fattened at a rate of 1.3 g./day between 31 August and 6 September. Kent Island adults and juveniles fattened at rates of 2.4 and 2.5 g./day, respectively, between 26-29 August. These rates may not be indicative of fattening rates earlier in the season, when birds stayed for longer periods of time (see Section 4.3, below).

Two other estimates of the rates at which Semipalmated Sandpipers acquire fat reserves have been made. Page (1970), on the basis of weights of recaptured individuals, estimated average rates of 0.7 g. and 0.4 g./day for adults and juveniles, respectively, for birds at Long Point, Ont. A second estimate was based on rates of prey ingestion and estimates of metabolic costs for birds foraging in the upper Bay of

Fundy. Peter Hicklin and Peter Sherman (personal communication) estimated that gains of 1.5-1.8 g./day were normal, with 2.5 g./day, the value seen at Kent Island, being an extreme maximum.

The observed fattening rates indicate that coastal birds are able to put on fat stores at a higher rate. This may explain their greater site-faithfulness, suggested in the previous section, as birds feeding on richer resources would be expected to remain in those areas, while those feeding on poorer resources might search elsewhere.

The rates of fat deposition should affect the length of stay at the two areas. In the following discussion, I will use fattening rates to predict the average staging periods of resident birds at the two locations. I make the following assumptions:

1. Birds arrived, fattened, and left as quickly as possible.
2. The average fat of a bird at capture was 5.1 g. at Sibley Lake, and 8.3 g. at Kent Island (weighted average fat for both age classes, from Table 2).
3. The process of fattening was disrupted by capture. Page and Middleton (1972) showed that birds lost weight for the first two days after capture, returning to capture weights on the third day. I thus give birds two extra days to fatten up.
4. Birds fattened at a rate of 1.3 g./day at Sibley Lake, and 2.0 g./day at Kent Island. If the higher figure of 2.5 g./day is used for Kent Island, the estimated staging periods are obviously shorter than those computed below.
5. Birds fattened to a threshold level at which point they became likely to migrate in favorable weather. If fattening occured

independently of the weather, birds might have to wait a few days for good departure weather after they had arrived at threshold fat levels. The average bird would wait half of the average period between days with favorable weather. This amounted to 1.7 days at Sibley Lake and 2.3 days at Kent Island (Section 5.2.1).

6. The fat threshold was 18.0 g. at Sibley Lake and 20.0 g. at Kent Island. These figures are based on an analysis that does not involve staging periods (Section 5.4.2).

Under these assumptions, the average bird would stay 13.6 days at Sibley Lake and 10.2 days at Kent Island before departing. Keeping these assumptions in mind, comparison of these estimates with data on staging periods will aid in interpretation of the birds' behavior at the study sites.

4.3 STAGING PERIODS

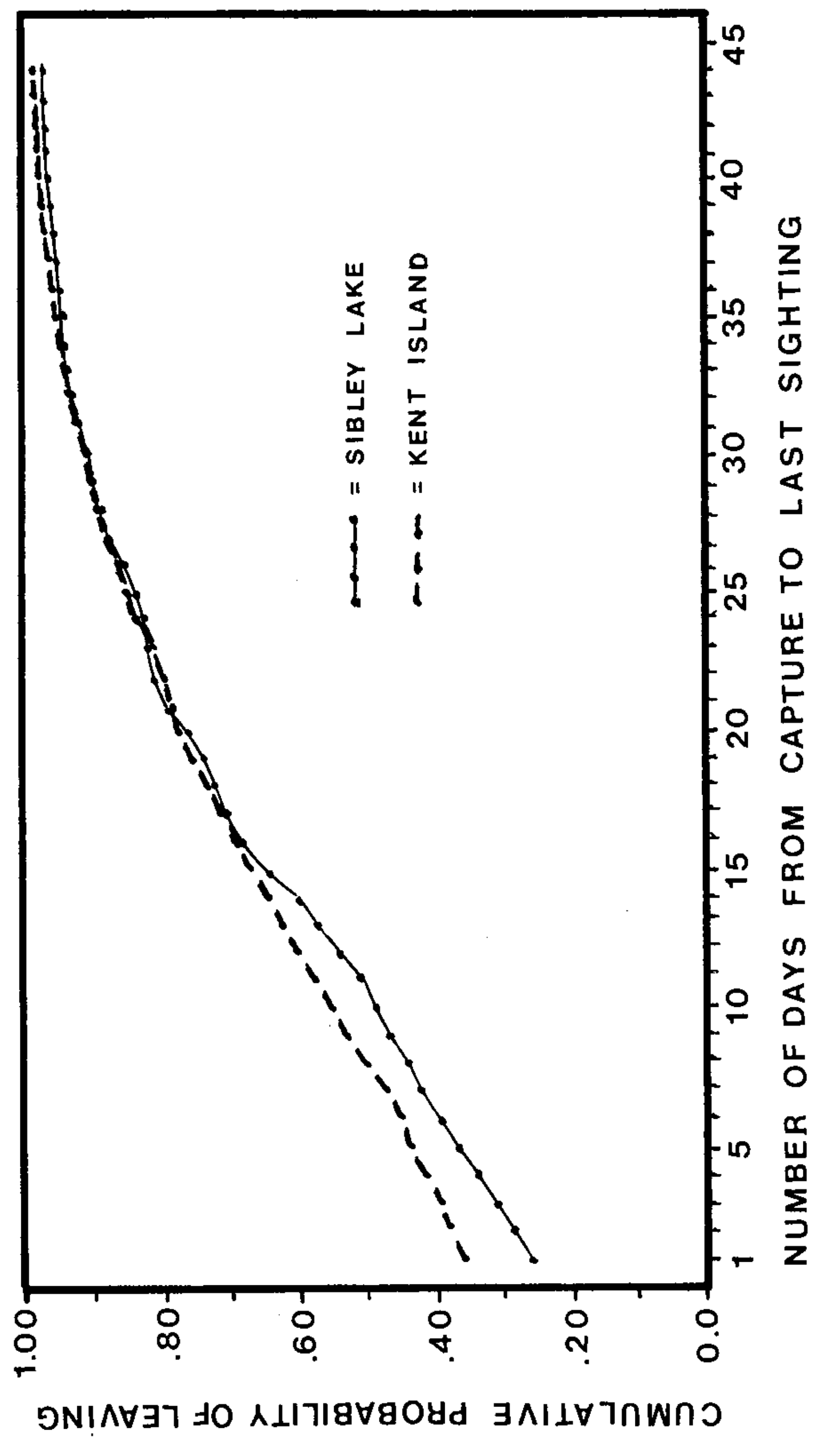
This section presents the data on how long birds remained at the study site after marking (staging periods, Section 2.2.2), concentrating on those that did not disappear the first day.

4.3.1 Overall Staging Periods

Figure 19 plots the cumulative distribution of staging periods from each area. The graph shows the total percentage of marked birds that had left, on the abscissa, versus the number of days since capture, on the ordinate. Three points can be drawn from the graph:

1. As mentioned above, 25-35% of the of birds were transients. Thus the first point on the graph (left by day 1) is high for both areas.

Figure 19. The cumulative probability of leaving as a function of days since marking at Sibley Lake and Kent Island.


CUMULATIVE PROBABILITY OF LEAVING
1.00
.80
.60
.40
.20
0.0
NUMBER OF DAYS FROM CAPTURE TO LAST SIGHTING
1
5
10
15
20
25
30
35
40
45
= SIBLEY LAKE
= KENT ISLAND

2. In contrast to this, the proportions of birds leaving after the first day were quite similar from day to day, with 1-2% of the total birds marked disappearing daily for the first two weeks after capture, and generally less than 1% per day thereafter. On the basis of this graph, I concluded that transients formed a separate class and ought to be excluded from analyses involving average length of stay, and from the calculation of daily emigration rates. It was also clear that the distribution of staging periods greater than one was extremely even. Birds marked three days previously had a chance of leaving similar to those marked ten or 20 days previously.
3. At both locations many birds stayed for surprisingly long periods of time. Excluding transients, half the birds remaining at each location stayed 15-16 days, and many stayed much longer.

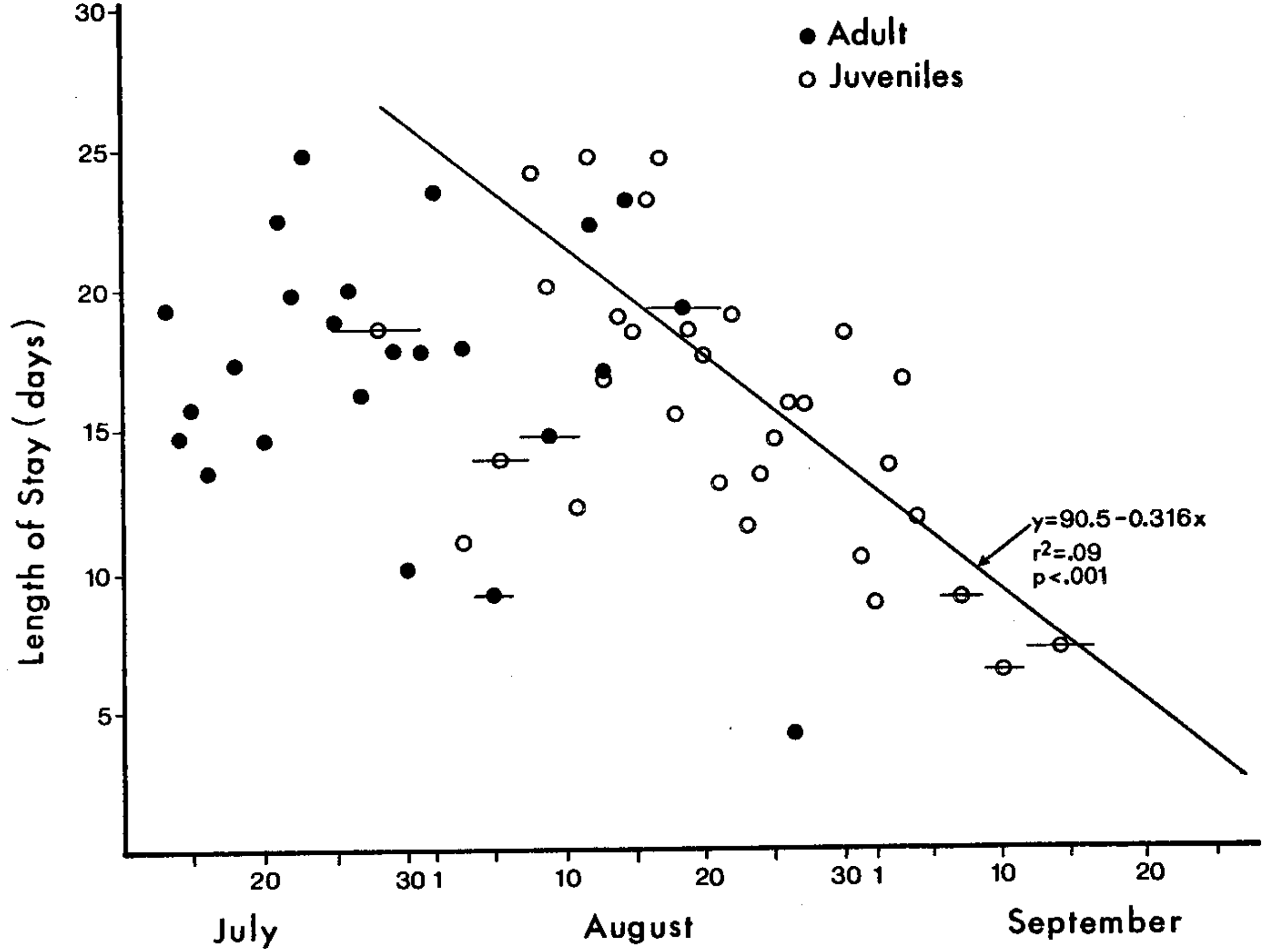
Such long staging periods imply that the estimates made in the previous section were substantially low. Before searching for faulty assumptions that might have led to such poor predictions, we will examine the data on staging periods in more detail.

4.3.2 Seasonal Trends in Staging Periods

Figure 19 plotted data averaged over the whole season. Figures 20 and 21 plot the mean staging periods of cohorts of adult and juvenile residents captured daily at the two sites.

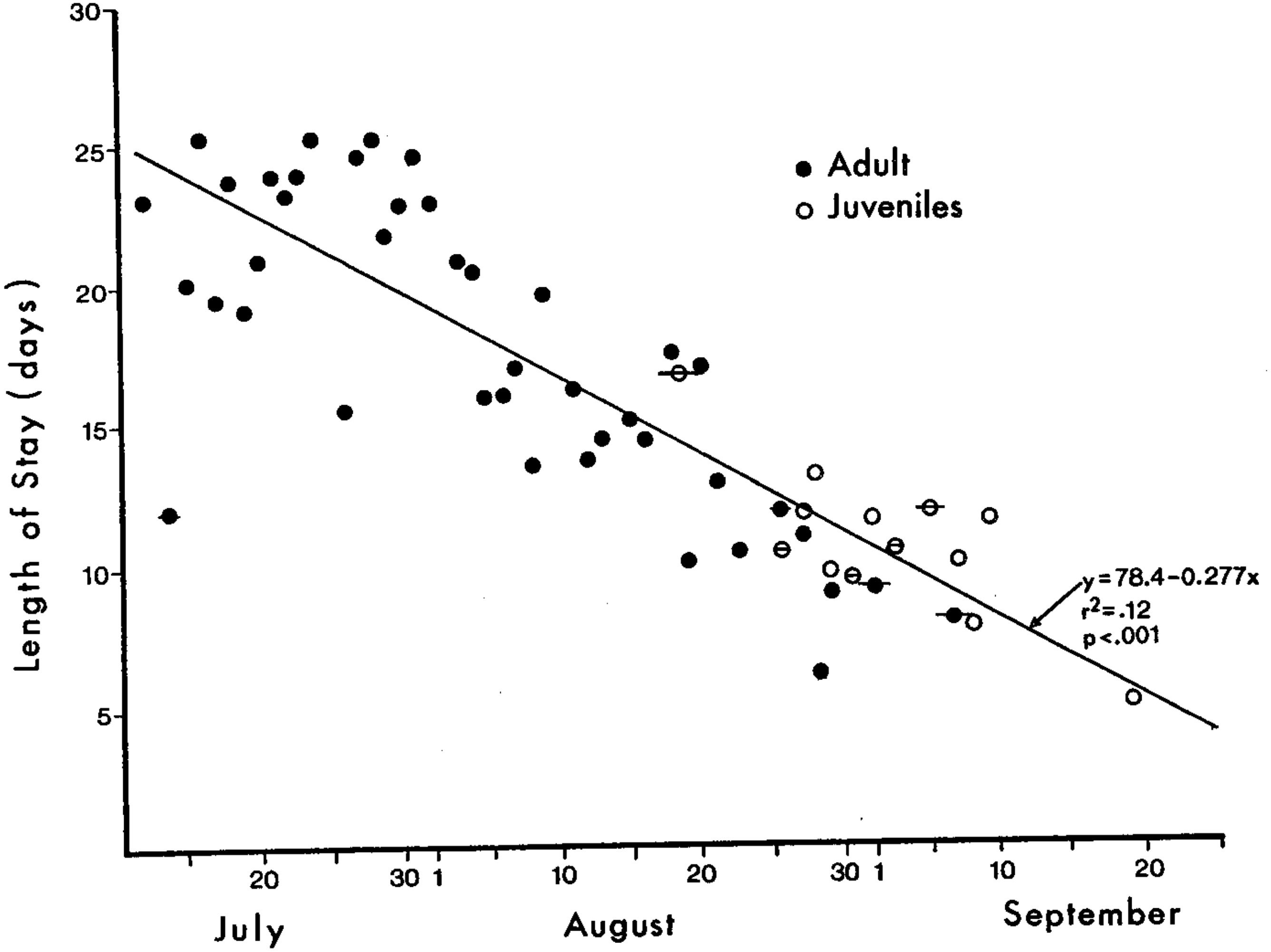
At Sibley Lake, adults stayed for 15-20 days, on average, for most of the season. Early arriving juveniles stayed for similar periods. Those caught in late August and September, however, had significantly shorter

Figure 20. Length of stay of marked birds during the season at Sibley Lake. Dots with horizontal lines through them represent pooled means combining samples from days within the length of the line. Days were pooled to bring the sample sizes for each point to at least 7. The regression line was plotted for juveniles only on the original data, not the means.



NORTH DAKOTA 1978

Figure 21. Length of stay of marked birds during the season at Kent Island. Dots with horizontal lines through them represent pooled means combining samples from days within the length of the line. Days were pooled to bring the sample sizes for each point to at least 7. The regression line was plotted for adults only on the original data, not the means.



KENT ISLAND 1977

residence times, with the latest birds staying only seven to ten days (Figure 20). Since early birds, which show no seasonal trend, are for the most part adults, and later birds, which do show a trend, are mostly juveniles, I cannot conclusively attribute the presence and absence of trends to date or age. However, early arriving juveniles stayed as long as adults caught at the same time, suggesting that date, rather than age, was the important factor. The slope of the regression of juvenile staging periods on dates shows a decrease of about a third of a day per day. While the means fit the line fairly well, the variance accounted for by the regression, calculated from individual points, is small ($r^2 = .09$). Thus the within-day variation was large despite the obvious seasonal trend.

At Kent Island the picture was quite different (Figure 21). Adults show a significantly decreasing seasonal trend in the length of staging periods. Birds arriving in July stayed 21-24 days, while those arriving in late August only stayed about ten. As at Sibley Lake, the total amount of variance accounted for was low ($r^2 = .12$). Although I have computed a simple linear regression, the relationship between staging period and date appears flat through the last two weeks of July, and then begins a linear decline. Juveniles, all of which migrated late in the season, showed no significant trend, but appear to fall on the same line as the adults. Disregarding the flat period at the beginning of the season would steepen the line and give it a rate of change close to that at Sibley Lake, about a third of a day per day decrease.

Failure of Kent Island juveniles to show a significant seasonal trend in staging period may be an artifact of their short seasonal spread.

But Sibley Lake adults differ strikingly from their coastal counterparts by their failure to show any seasonal trend. In the midwest between mid-July and mid-August, date provided no information about probable length of stay; it did so on the coast.

4.3.3 Fat Levels and Staging Periods

Did fat levels at capture predict subsequent staging periods, as expected if birds simply came, fattened, and left? Table 3 presents regressions that used date, fat at capture, and both variables together as predictors of staging periods for all four age/location classes. Fat is an extremely poor predictor, and is significant only in cases where date is also so. Use of both variables is little better than using date alone, although the increase in the percentage of variance accounted for is greater for Kent Island adults than for other groups. Since birds were generally fatter later in the season (Figures 17 and 18), and since there is little improvement over date alone when both date and fat are used, the relationship with fat alone is in part a consequence of its correlation with date. Restriction of the fat-only regressions to cases with 1) staging periods of less than 8 or 12 days, and/or 2) first capture dates after 10 August produced slightly higher r^2-values, but in no case was more than 10% of the variance accounted for. These results imply that fat levels had a greater effect on the staging periods of birds that left within 12 days than was the case for those staying for longer periods, and was of more use late than early in the season. However the relationship was still a weak one.

Table 3. Bivariate regression analyses of length of stay against Julian date of capture and fat stores at capture. One-day birds were excluded from these analyses.

Group	Variables	r^2	F	sig.
Sibley Lake				
Adults	Date	.002	1.26	ns
n=521	Fat	.000	0.02	ns
	Date + Fat	.003	0.71	ns
Juveniles	Date	.090	54.45	$P < .005$
n=558	Fat	.033	18.83	$P < .005$
	Date + Fat	.093	28.41	$P < .005$
Kent Island				
Adults	Date	.118	89.99	$P < .005$
n=675	Fat	.038	26.29	$P < .005$
	Date + Fat	.125	48.05	$P < .005$
Juveniles	Date	.029	5.04	ns
n=168	Fat	.008	1.27	ns
	Date + Fat	.034	2.91	ns

The finding that fat is a poor predictor of length of stay agrees with Page and Middleton's (1972) finding for Semipalmated Sandpipers at Long Point, Ontario. It also implies that some of the assumptions involved in the prediction of length of staging periods are seriously incorrect. It does not mean, however, that fat levels of birds could not affect their probability of migratory departure, which they did (Section 5.4.2). If fat levels provide little information about staging periods, however, and fat does affect a bird's chance of leaving, then birds must not simply be putting on fat at a linear rate during the staging period.

4.4 DISCUSSION

The staging periods seen in Semipalmated Sandpipers are longer than those reported for other shorebirds, and for passerine migrants, where periods over two weeks are unusual (e.g. Middleton, 1939; Nisbet *et al*., 1963; Mascher, 1966; Rabol and Petersen, 1973). However they agree, roughly, with those found by Page (1970) for Semipalmated Sandpipers at Long Point, Ontario. This discussion will concentrate on why staging periods change over the season, and what might be most seriously wrong with the predictions of staging periods, based on fattening rates, made in Section 4.2.3.

4.4.1 Seasonal Trends in Staging Periods

Data from a variety of sources, in lab and field, show that date in the season is important to migratory birds. The most common field data involve recurring phenological patterns of migration in spring and fall (e.g. Hinde, 1951; Hilden, 1979), and laboratory studies of seasonal patterns of migratory activity in caged birds, under both natural and artificial environmental conditions (see Berthold, 1975a; Meier and Fivizzani, 1980, for reviews).

The data on length of stay indicate that the pace of migration is faster for birds migrating later in the season. Daily examination of the relationship between date and the length of migratory stopovers has not been previously presented for any species. Mascher (1966) found that the percentage of Dunlin (_Calidris_ _a_. _alpina_) recaptured during a migratory stopover was lower for birds banded later in the season, suggesting shorter staging times. Rabøl and Petersen (1973) found similar recapture trends in several passerine species.

The seasonal trends in staging periods seen at the two sites might not reflect seasonal rhythms _per_ _se_ (be they endogenously or exogenously controlled), but may result from changes in another factor that correlated with date. The most likely ones are 1) the length of time birds had been at the staging area prior to capture, 2) the frequency of favorable weather, 3) availability of foraging habitat, 4) food levels within available habitat and the amount of local versus migratory movements, 5) fat at arrival or fattening rates, or 6) fat departure threshold.

1. If birds caught later in the season had been at the study site for longer periods prior to capture, the apparent trend might be produced by this capture bias. I cannot provide convincing evidence to eliminate this possibility. The strongest arguement against its importance is the similarity in the behavior of

late-captured adults and early-captured juveniles. The juveniles had only been present for short periods of time, implying that such a bias was unimportant at least at that time of the season.

2. Favorable weather occurred at fairly regular intervals throughout the season (Section 5.2.1). It is thus unlikely that birds had to wait different lengths of time to depart during the season.
3. The drastic changes in habitat in North Dakota might have truncated the staging periods of birds at Sibley Lake. Staging periods for birds caught in early August, prior to Alkali's complete dessication, appear shorter than those before and after that period (Figure 13). However, adults and juveniles caught during the habitat deterioration, which could not establish themselves on Alkali, stayed for full-length periods. At Kent Island, while the size of foraging habitat remained constant throughout season, its quality may have decreased. This possibility is discussed below.
4. If _per capita_ food levels increased during the season, birds might fatten faster, which could produce shorter staging periods. On the coast, there is evidence that shorebirds deplete their food source during the migratory season (Schneider and Harrington, 1981; Hicklin, personal communication), thus longer, rather than shorter staging periods might be expected. If the local decline in food were great enough, one might interpret the shorter staging periods as reflecting local movements in response to unsuitable local feeding conditions later in the season. If this were the case, transience and emigration rates would be

expected to increase during the season. Transience rates, controlled for density, did not do so (Section 4.1.2.2); nor did emigration rates (F = 1.15, r^2 = .02, ns for Sibley Lake; F = 0.70, r^2 = .01, ns for Kent Island). The food situation in the midwest is complex and unknown. However, the clear inapplicability of this hypothesis to Kent Island eliminates it as a general explaination.

5. Birds caught later in the season were, in general, fatter (Figures 17 and 18), and fatter birds might stay for shorter periods. However, this was not strongly the case (Table 3). Fattening rates might have increased during the season; this would seem unlikely if food levels decreased, but *per capital* food levels might not have decreased since fewer birds were present late in the season. When population levels were low early in the season, however, and food would have been most abundant (at least at Kent Island), the staging periods were longest.
6. Finally, the threshold for migration might be lower later in the season. I calculated migration thresholds in Section 5.4.2., but I did not have enough data to look for seasonal changes. It seems highly unlikely that the threshold level for transoceanic flight could change drastically, since the distance to be covered is large and unchanging.

I conclude that the seasonal trends observed in staging periods are real, date-related phenonmena. The key within-site question is why do birds early in the season stay as long as they do? The estimates of length of stay made in Section 4.2.3 best match the behavior of birds near the end of the season, when birds stayed the shortest periods, despite the effects of assumptions that lengthened the estimates (e.g. assumptions 3, 4, and 5). Despite all of the uncertainties involved in both analyses, the most erroneous assumption may have been the first one, that birds were motivated to fatten and depart as quickly as possible after arrival. Semipalmated Sandpipers apparently pause at temperate staging areas longer than necessary simply to refuel for the next flight. Date in the season affects the length of this pause, producing the seasonal changes in staging periods.

The effects of handling and marking may also be involved in the long staging periods of some birds. Page and Middleton (1972) found that recaptured sandpipers did not return to their original capture weight, on average, until three days after capture. Harrington found a similar pattern at Manomet, MA (personal communication). Data from both of these studies were mostly from birds marked only with leg bands. Some authors have interpreted similar data from other species as reflecting natural changes after migratory flights (e.g. Nisbet _et al_., 1963; Mascher, 1966; Rappole and Warner, 1976). However, Morrison and Gratto, who marked the breasts of _C. pusilla_ with picric acid at James Bay, Ontario, found no consistent weight gains until from five to ten days after original capture, with large samples from five years (personal communication). I had few recaptures of birds at Kent Island, and few from the early cohorts at Sibley Lake, which stayed for long periods. However, most birds recaptured shortly after initial capture showed a weight loss, and even those with a longer interval between captures showed little weight gain, on average (Lank, unpublished data). Page

(1970) also reports instances of birds at Long Point staying for long periods of time without gaining weight.

In interpreting these data, it is important to remember that birds that leave the area (after fattening up?) cannot be caught, so the recapture samples do not provide unbiased data on the fate of the initial cohorts marked. Capture and marking nonetheless seem to have a substantial effect on some Semipalmated Sandpipers, and more drastic marking methods (wing-tags and picric acid, versus leg-bands) seem to have a greater effect, although the studies cited above were done at different places and times. While handling and marking may have lengthened staging periods, seasonal patterns cannot have been caused by it, since the treatment of birds did not vary throughout the season. We can thus discuss seasonal patterns independently of handling effects.

If staging schedules exist, they differ between locations, with inland adults following a more flexible schedule than coastal migrants, at least during July and early August. Laboratory studies, mainly on young European warblers, have documented the presence of internal rhythms of migratory activity that correlate with geographical features of species' migration routes (e.g. Berthold, 1973; Gwinner, 1977). The field data on sandpipers do not provide evidence of such internal rhythms, but they do show that different seasonally-specific staging periods exist for each population.

I can only speculate on what might be driving date-specific staging periods at the two sites. The larger numbers of birds migrating through the coastal areas (see Figure 9) may produce greater competition for suitable habitat. Greater competition was suggested by the patterns of transience and residency discussed above. Predictable large influxes of competitors may have selected for more rapid movement through congested staging areas at an earlier time on the coast.

On the other hand, the shortest staging periods occurred late in the season, when density was low. Fall migration schedules of sandpipers have recently been related to seasonal patterns of food availability at staging areas, with decreases late in the season (Schneider and Harrington, 1981; Schneider, 1982), or to sexual differences in migration distances (Myers, 1981). Since females predominate among the early migrants, physiological differences resulting from the pattern of parental care could conceivably be involved, with the later-arriving males staying for shorter periods. The occurrence of tropical storms late in the season might also be one factor advancing the migratory timing of coastal migrants. For whatever reason, the longer duration of a seasonal trend represents greater specialization of staging periods on the coast. Although I have shown a behavioral difference between the two populations, its adaptive signficance, if any, remains unclear.

4.4.2 Fat Levels and Staging Periods

While increased fat levels and migratory activity are often correlated in the field, laboratory studies of passerines have shown that they may be controlled separately (King and Farner, 1963; Lofts *et al.*, 1963; Berthold, 1975b, 1976; Gwinner, 1977). In the field, a positive relationship between fat levels and the probability of leaving a local study area have been found in some cases (e.g. Helmes, 1959; Nisbet *et al.*, 1963; Mueller and Berger, 1966; Mascher, 1966; Dolnik and Blyumental, 1967; Rabøl and Hansen, 1978; Demong and Emlen, 1978), but not in others (Helms and Drury, 1960; Odum *et al.*, 1961; Szulc-Olech, 1965; McNeil and Carrera de Itriago, 1968; Rappole and Warner, 1976). Among shorebirds, Mascher (1966) found a negative relationship between fat content and length of stay in Dunlin (*Calidris a. alpina*); however Page and Middleton (1972) found length of stay independent of fat in autumn migrant Semipalmated Sandpipers at Long Point, Ont.

The failure of fat as a predictor of staging periods in this study may be due to noise from other factors, including weather, handling effects, censusing efficiency, local movements, fattening rates and so on. However, real adaptive responses may also be involved. Some lean birds may have stayed for short periods because they were unsuccessful local competitors that went elsewhere in search of food, as suggested for other species (Szulc-Olech, 1965; Rappole and Warner, 1976). The migratory pause hypothesized above might result in some fatter individuals staying for longer periods. Questions remain about the fattening behavior of birds at the study site, but a different approach will show that the migratory departures of birds are not independent of fat levels (Section 5.4.2).

Chapter V

THE PROXIMAL REGULATION OF MIGRATORY FLIGHT

The staging behavior described in the previous chapter ends with departure on the next migratory flight. Migratory departures, defined as one or more birds taking flight and disappearing from view against the sky, were distinct and infrequent events. Nearly all departures were in the appropriate migratory direction. This chapter examines the proximal regulation of migratory flight. Sections cover departure behavior; flight directions; the size of departing flocks; the timing of departures with regard to date, sunset, and stage of the tidal cycle; meteorological conditions at departure; and the fat stores carried by departing birds.

5.1 DEPARTURE BEHAVIOR, DIRECTION, AND FLOCK SIZE

This section describes the behavior of Semipalmated Sandpipers prior to and at migratory takeoff. It goes into detail on the direction and size of departing flocks.

5.1.1 Pre-flight and Takeoff Behavior

The behavior of staging sandpipers usually enabled prediction of departures several hours prior to their occurrence. Prior to migratory departure, foraging birds became more aggregated and less aggressive, fed more rapidly, moved more frequently, and were more easily startled into flight by observers than was the case at other times. The "rat-tat-tat-tat" aggressive call given as birds defended foraging sites was heard less often, and a pre-flight and flight call note became the dominant auditory signal. The calling of departing flocks was conspicuous to human observers, and no doubt also to conspecifics. No departures were observed to begin silently.

Several accounts of shorebirds initiating migratory flights describe extensive pre-departure circling by flocks of calling birds (e.g. Henshaw, 1910; Svardson, 1953; Sauer, 1962; Johnson and McFarlane, 1967). I observed circling only twice. In all other cases birds left the ground headed in the direction in which they eventually disappeared, as has been described by others (Van Tyne and Trautman, 1945; Johnson and McFarlane, 1976; Grimes, 1974). Departing flocks often flew low over other foraging birds, some of which might join the flock, and then began to climb. At Sibley Lake, small flocks sometimes made short, low flights southward along the eastern shore, aggregating at the south end prior to departure. Lack (1930) describes the pre-departure behavior of shorebirds, including brief, noisy ascending and descending flights, prior to eventual takeoff.

As flocks ascended, they often "accordioned"-- spread and collapsed in basically a horizontal plane-- as individuals or sub-flocks headed in slightly different directions. Accordioning was especially prominent in large flocks, and the largest separated into two or three groups. Eventually most flocks collapsed into a compact bundle and disappeared from view, still climbing.

The departing flocks were not exclusively composed of Semipalmated Sandpipers, although they were usually the numerically dominant species. Least Sandpipers (*Calidris minutilla*), Sanderlings (*C. alba*), and Semipalmated Plovers (*Charadrius semipalmatus*) mixed in with Semipalmated Sandpipers at Kent Island; Least and Baird's Sandpipers (*Calidris bairdii*), and Piping Plovers (*Charadrius melodus*) departed with Semipalmated Sandpipers at Sibley Lake. Larger shorebirds, such as Stilt Sandpipers (*Micropalama himantopus*) at Sibley Lake and Short-billed Dowitchers (*Limnodromus griseus*) at Kent Island, departed in separate flocks. Cases considered in the analyses below contained at least 70% *C. pusilla*; six departures of flocks including Semipalmated Sandpipers fell below this proportion and were excluded.

If body mass is an important determinant of energetically optimum flight speed (e.g. Pennycuick, 1975), it is surprising that birds as small as Least Sandpipers (18-22 g.) flocked with birds as large as Semipalmated Plovers (50-60 g.) and Sanderlings (60-80 g.). Perhaps birds sort themselves out into more homogeneous groups *en route*.

The departures of shorebird flocks were dramatic events. At these moments some individuals began what might be two-day-long flights, while others remained feeding on the ground, failing to respond to the repeated calling of their airborne conspecifics. The heritability and consequences of a bird's behavior at that moment-- whether it flew or fed-- are the ultimate source of the adaptations of populations that are the focus of this chapter.

5.1.2 Departure Directions

Flocks were observed until they vanished from view against the sky. Figure 22 shows the distributions of vanishing bearings from the two sites, which are in excellent agreement with the expected migratory direction from each area. The mean vanishing bearing at Sibley Lake is only 10° different from the recovery pattern shown in Figure 12 for birds banded in the midwest. The mean bearing at Kent Island, 144°, may be compared with the departure directions of shorebird flocks seen by radar. Richardson (1979) gives 134° as a mean track of departing shorebirds, although his analysis excluded all tracks west of south. Similar treatment of the Kent Island departure data shifts the mean vanishing bearing from 144° to 138°, almost a perfect match.
All but three flocks left on courses that would take them out over the ocean. The agreement between departure and known migratory directions provides strong support for interpretation of departures as the beginnings of migratory flights.

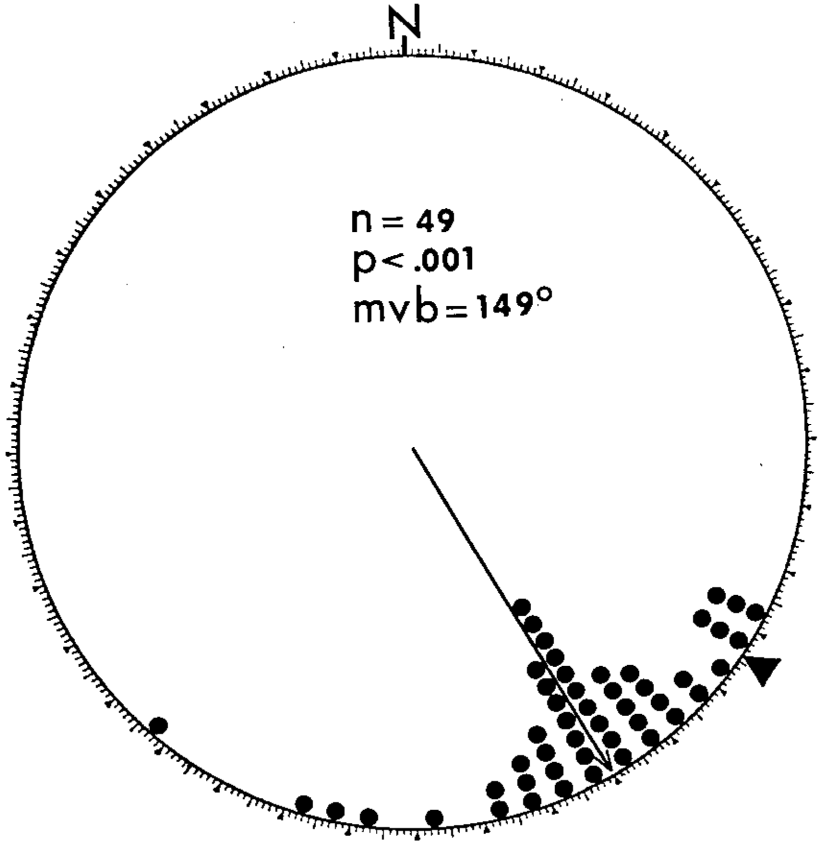
There was no significant difference in the mean bearings of the two populations (F-test, $f = 0.856$, $p > .10$). The notion of parallel migratory routes from breeding grounds to staging areas (Section 3.4.1) might be extended to include parallel flights from temperate zone staging areas towards the wintering grounds.

5.1.3 Departing Flock Size

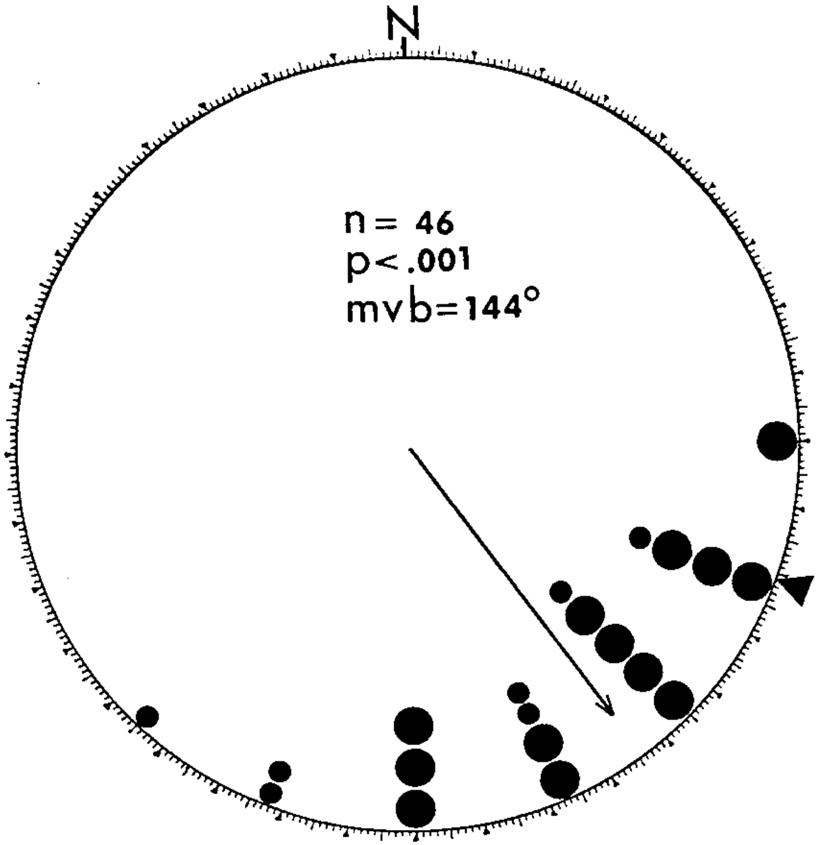
Birds departed in flocks ranging in size from three to 200 individuals. Flocks leaving Sibley Lake were smaller, on average, than those departing Kent Island (Figure 23; Wilcoxsin Rank-Sums test, $p < .02$).

Figure 22. The distribution of vanishing bearings of departing flocks at Sibley Lake and Kent Island. Each dot at Sibley Lake represents one flock, plotted to the nearest 5 degrees. Two points were omitted due to thunderstorms. Large dots at Kent Island represent 3 flocks, and small dots one flock. Data at Kent Island were taken to the nearest 1/16th of a circle. The arrow is proportional to the length of the mean vector (Batschlet, 1965), and the triangle on the outside of the circle is the mean direction of the surface wind at hours when flocks departed.

DEPARTURE BEARINGS

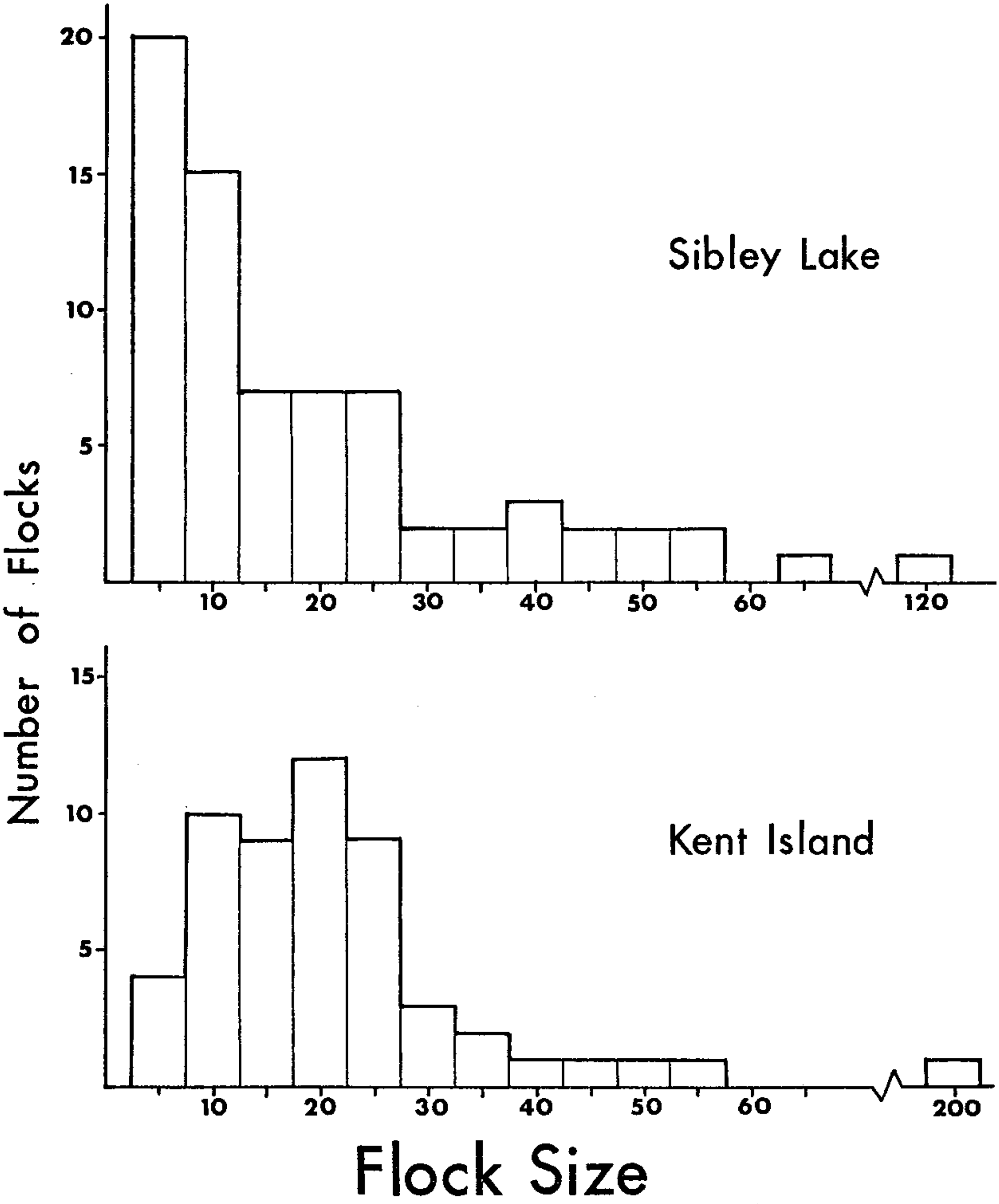


Sibley Lake



Kent Island

Figure 23. The distributions of departing flock sizes at Sibley Lake and Kent Island.


Sibley Lake
20
15
10
5
10
20
30
40
50
60
120
Number of Flocks
Kent Island
15
10
5
10
20
30
40
50
60
200
Flock Size

The histograms show the greatest difference in the proportions of small flocks at the two sites. Whereas flock sizes of three to seven form the modal size class at Sibley Lake, and the distribution falls away from that peak, the Kent Island data are more nearly normal, with a mode in the 18-22 class. Flocks of one or two were not seen departing at either location.

Why did so few Kent Island birds leave in small flocks? Are there advantages to flying in larger flocks that are more important on the coast, does the difference relate to differences in pre-flight behavior, or does it simply reflect differences in the numbers of birds in the migratory pool at each location?

The first hypothesis tested was that flock size simply varied with population size (or some function of population size and "migratory condition"), and that Kent Island birds left at higher local population levels. This was not the case; at neither location was there a significant correlation between local population size and flock size (Spearman Rank Correlation tests, $p > .10$).

Several other processes might account for the difference. The populations may have differed in the variability of individual probabilities of departure under prevailing conditions. If it were possible to poll individuals independently, this hypothesis would predict greater agreement among Kent Island than Sibley Lake birds about acceptable or "optimal" departure weather. Thus, more birds might leave at the same time, resulting in larger flock sizes, even if no advantage were gained by flying with more birds.

The populations may have differed in the importance of social processes in determining an individual's probability of departure ("communal decision making", Emlen, unpublished manuscript). By reaching a collective decision on the timing of flights, birds could reduce the chances of migrating at inappropriate times. The pre-flight behavior of birds is interpreted as social signaling that leads to such decisions. Like the previous hypothesis, social stimulation could result in the formation of larger flocks, or eliminate the formation of small ones, even if there were no direct advantages in flight. If this process occurs, the larger flock sizes at Kent Island would reflect an increased importance of socal signaling on the coast.

Finally, there may be direct aerodynamic or navigational advantages to flying in larger flocks, and these may have been more important to coastal populations. Noer (1979) found that low-flying diurnal shorebird flocks showed a positive relationship between flock size and air speed. Although it is not well established, a body of theory has predicted, and some evidence suggests, that larger flocks will be more accurately oriented than small ones (Bergman and Donner, 1964; Hamilton, 1976; Rabøl and Hansen, 1973; Wallraff, 1978; Tamm, 1980; but see Keeton, 1970). If either of these processes were important, birds should not depart unless joined in the air by a sufficient number of others.

I cannot clearly reject any of these hypotheses; indeed, they all may operate in concert. Meteorological conditions at departure are somewhat less variable at Kent Island than at Sibley Lake (Section 5.3.3), but since this result was based on flock departures, it provides no evidence with regard to the variance in weather preference among individuals. Pre-flight behavior patterns that might enable communal decision making were described in Section 5.1.1. Observations of aborted takeoffs--situations where small flocks began ascending flights, failed to recruit a sufficient number of birds, and returned to the ground-- might favor interpretations for the direct advantages of larger flocks. I saw no flights that clearly fit this pattern (including ascending flight), but pre-departure birds were "flightier", making short low flights that might have been aborted recruitment flights of this sort, but also may have served as a social signal.

There is evidence that larger flocks were better oriented. I tested the relationship between flock size and accuracy of orientation using the data from Sibley Lake. Bearings from six flocks that were rapidly changing direction when lost to sight were omitted from data prior to analysis. Figure 24 shows the vanishing bearings of 41 flocks plotted as a function of flock size. The variance in bearings appears to decrease with increasing flock size. I tested the signficance of this by dividing the data into three size clases: 3-14, 15-25, and 26 or more birds (Table 4). Since all of the bearings were within 180° range, I have used normal, rather than circular statistics in this analysis. The largest flocks have significantly lower variance than smaller ones. If three outlying points are removed (with a large decrease in within-group variance), all three groups have significantly different variances. These data are the first from migratory birds to show that variance in orientation decreased over this large range of flock sizes.

Figure 24. Vanishing bearings of flocks in relation to flock size. Bearings from 6 flocks which were rapidly changing direction when lost to sight were omitted.

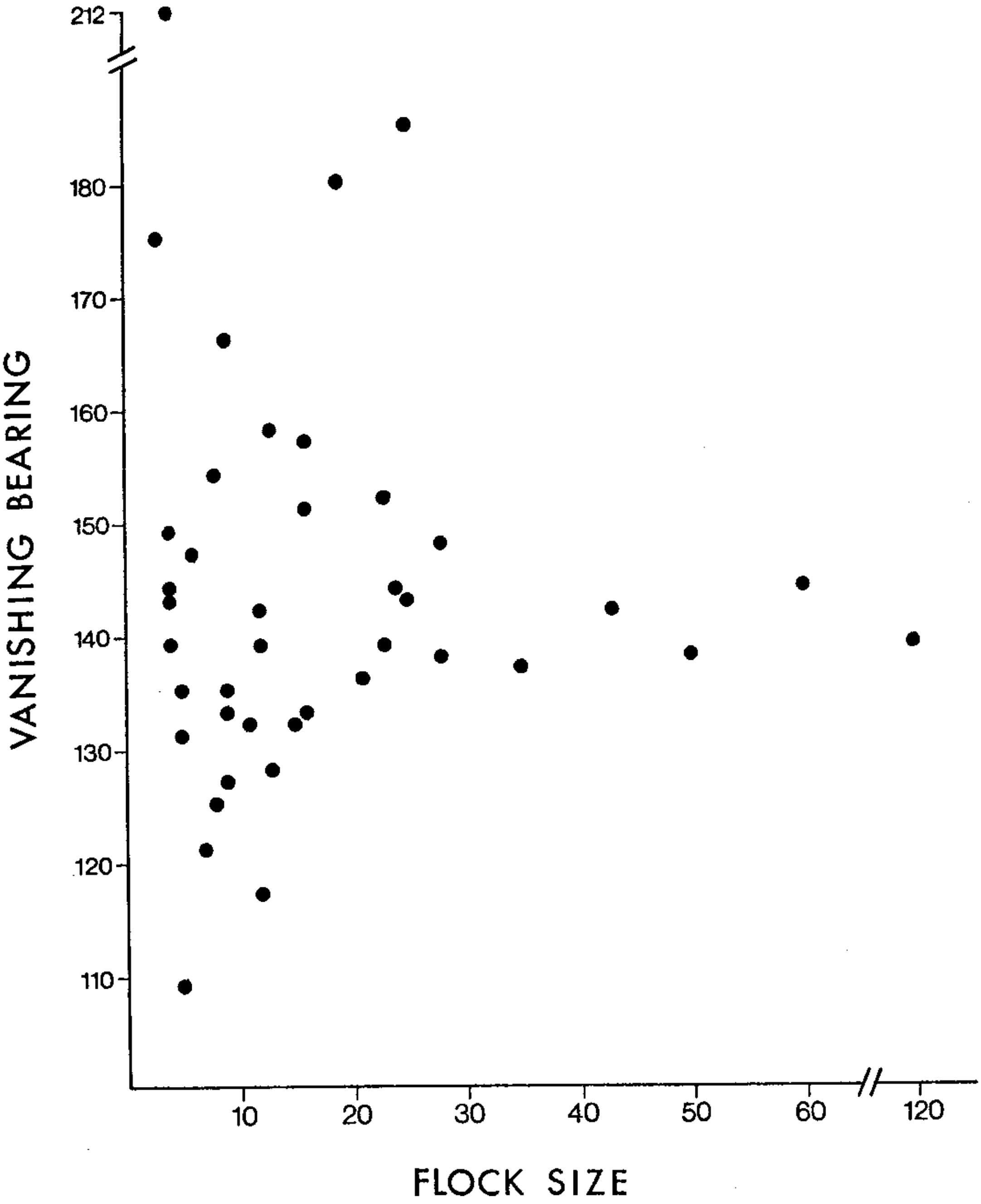

212
180
170
160
150
140
130
120
110
VANISHING BEARING
10
20
30
40
50
60
120
FLOCK SIZE

Table 4. Variances of flock bearings.

N	Flock size		Direction	F	p
	$\bar{x}$	SD	s^2		
			All data		
23	7.7	3.3	469.4		
				1.47	$> .10$
11	20.3	4.0	319.4		
				17.11	$< .01$
7	52.0	32.2	18.6		
			Outliers excluded		
22	7.8	3.3	246.3		
				3.14	$< .05$
9	19.9	4.1	78.5		
				4.21	$< .05$
7	52.0	32.2	18.6		

Unfortunately, the data from Kent Island cannot be examined in parallel fashion due to the imprecision of the directional data. The relationship between flock size and accuracy of orientation may also hold true on the coast. If so, the absence of small flocks at Kent Island might mean that a lower variance in headings has been of stronger selective advantage on the coast than inland. This does not imply that the other hypotheses proposed above are not also operating and of importance. I conclude that selection against departing in small flocks has been more severe prior to transoceanic than overland migration.

5.2 TIMING OF DEPARTURES

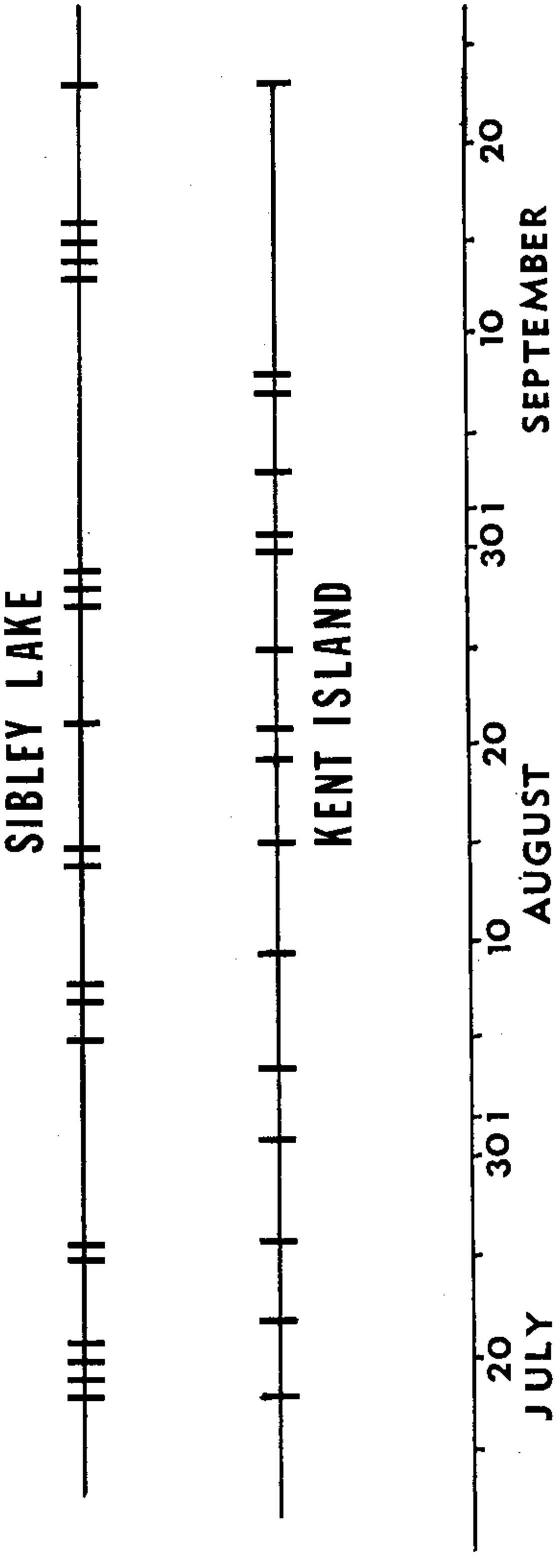
When did birds initiate migratory flights? This section examines the temporal occurrence of departures with respect to date in the season, hours prior to sunset, and, on the coast, stage of the tidal cycle.

5.2.1 Seasonal Distribution of Departures

Departures were observed on 24% of the days of the study. During the 77-day field season at Sibley Lake, 67 departures were observed on 20 different days (26%). During 74 days at Kent Island, 65 departures were observed on 16 different days (23%). There is no significant difference between locations in the frequencies of days with departures (GO days) and days without them (NOGO days) ($\chi^2 = 0.601$, $p > .05$).

The seasonal timing of departure days is shown in Figure 25. The occurrence of departures was largely determined by the weather (Section 5.3). The interval between GO days averaged 3.2 3.3 days at Sibley Lake, and 4.5±3.4 days at Kent Island. If the unusually long last

Figure 25. Occurrence of departures during the season at Sibley Lake and Kent Island. Vertical bars indicate days on which one or more flocks were seen departing.


SIBLEY LAKE
KENT ISLAND
20
JULY
30 1
10
AUGUST
20
30 1
10
SEPTEMBER
20

interval at Kent Island is excluded, the average interval was 3.8±1.8, which more accurately represents the periodicity and variability throughout most of the season. For the most part, GO days were more clumped at Sibley Lake.

The clumping at Sibley Lake is due to two factors: 1) the larger size of some cyclonic and anticyclonic weather systems meant that favorable and unfavorable conditions often persisted for more than one day, and 2) the faster rate of movement of smaller pressure systems that did occur in the midwest allowed meteorological conditions to become favorable again within 24 hours. In contrast, weather systems on the coast were more uniformly sized and moved more slowly than those in the midwest. Thus, favorable conditions occurred at more regular intervals, but rarely persisted for more than a day.

5.2.2 Hourly Distribution of Departures

The previous section showed that departures were observed on some days but not others. The next section (5.3) will show that weather patterns were the primary source of the daily variation. Despite the fact that suitable departure weather occurred at all times of day, there were strong hourly patterns of departures within a day. Thus, while favorable weather appears to be a necessary condition for departures, time of day is also influential.

5.2.2.1 Results

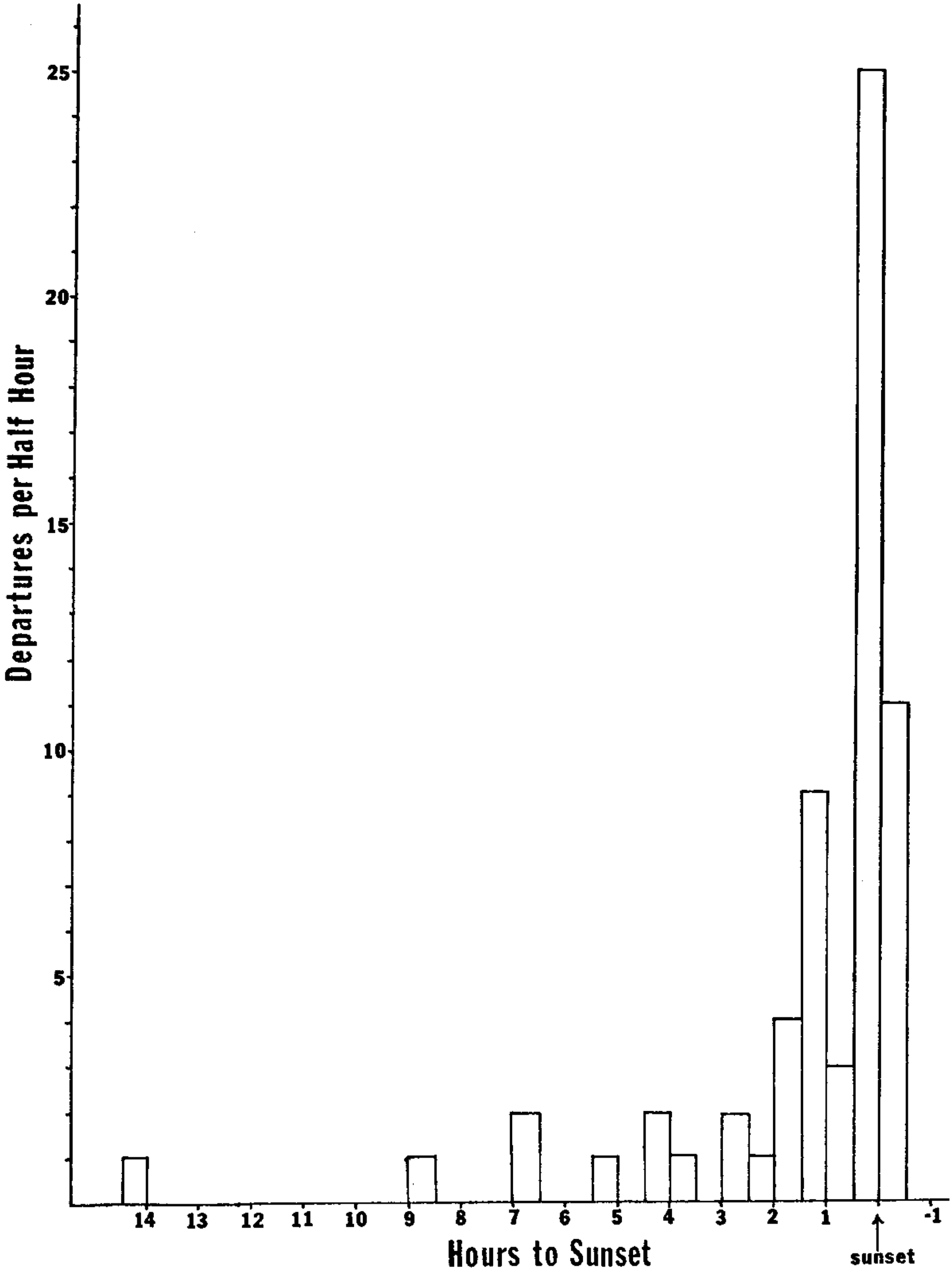
In North Dakota, departures occurred primarily during the hour just prior to sunset, although a few were scattered throughout the day

(Figure 26). At Kent Island the hourly pattern was much more variable, and the mode occurred two hours before sunset (Figure 27 a). The hourly scatter at Kent Island results from the influence of the tides on departure timing (Figure 27 b). Only a few departures occurred at low tide, with the bulk taking place during the ascending tides, as feeding areas were flooded.

The principal feeding areas at Kent Island were flooded 1-2 and 3-4 hours prior to high tide (Section 2.1.2, Figure 2). As the tide rose, many birds flew from earlier-flooded areas and continued foraging on later-flooded sites (see Section 4.1.2). Nearly all feeding habitat was covered one hour before peak tide, when birds moved to high tide roosting areas. The two peak departure times shown in Figure 27 b correspond to times when birds took flight as feeding areas flooded, while the few departures seen 2.5-3 and 0-1 hours before high tide correspond to times when feeding areas were not being flooded. Thus, most flocks departed at times when they normally took flight to make short within-island movements.

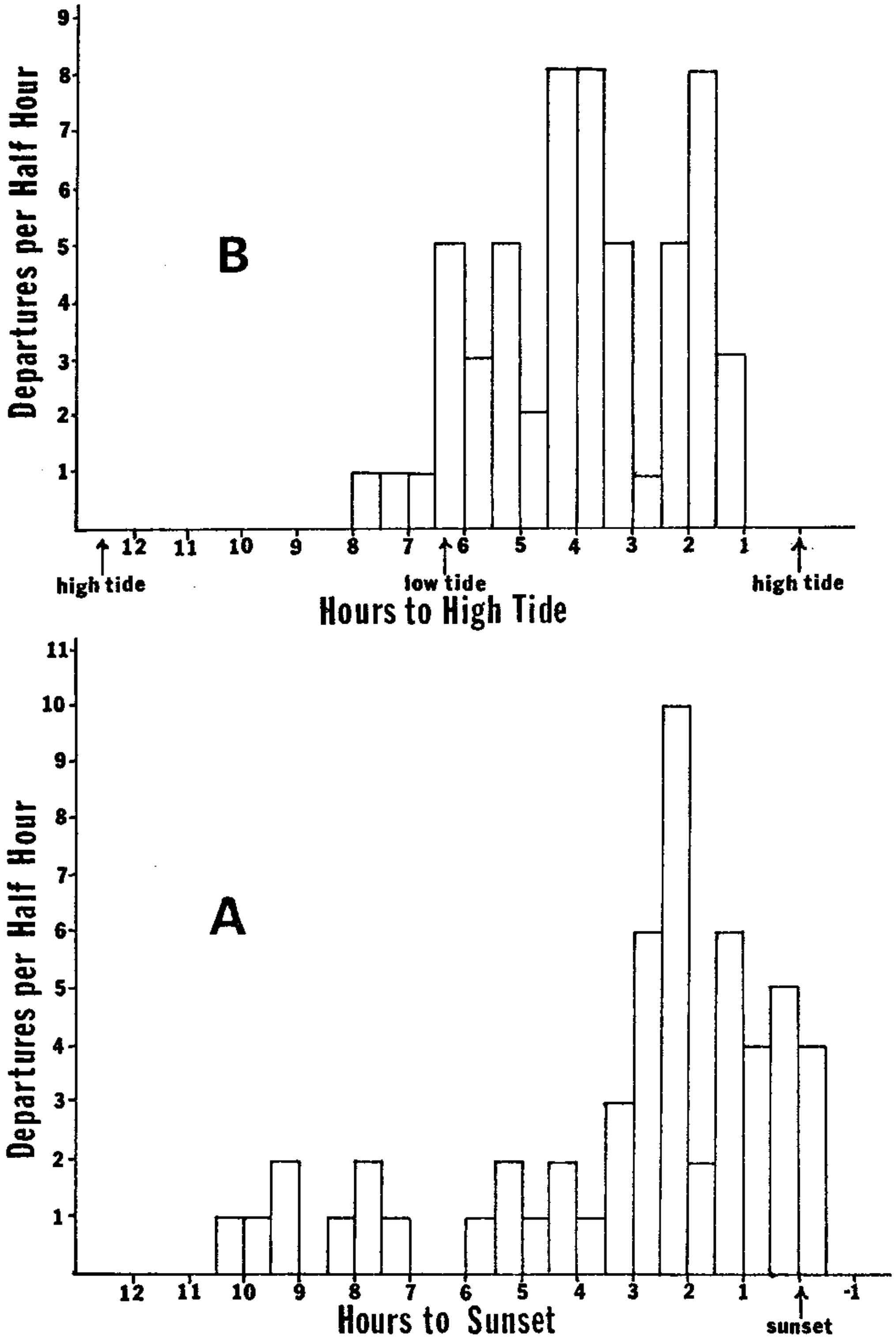
The interaction of tidal cycle and sunset in determining the timing of departures is shown in Figure 28. Time of day is on the vertical scale, with morning at the bottom, and date in the season is shown on the horizontal. The times of sunset and high tides are shown by solid lines, although they actually are sets of discrete points for each day. Shaded areas cover "departure windows": one three hours around sunset, the other one to four hours prior to high tide. Horizontal bars were placed at the time of departures. The graph shows that 1) departures early in the day were associated with the "tidal window", and 2) depar-

Figure 26. The timing of departures relative to sunset at Sibley Lake.



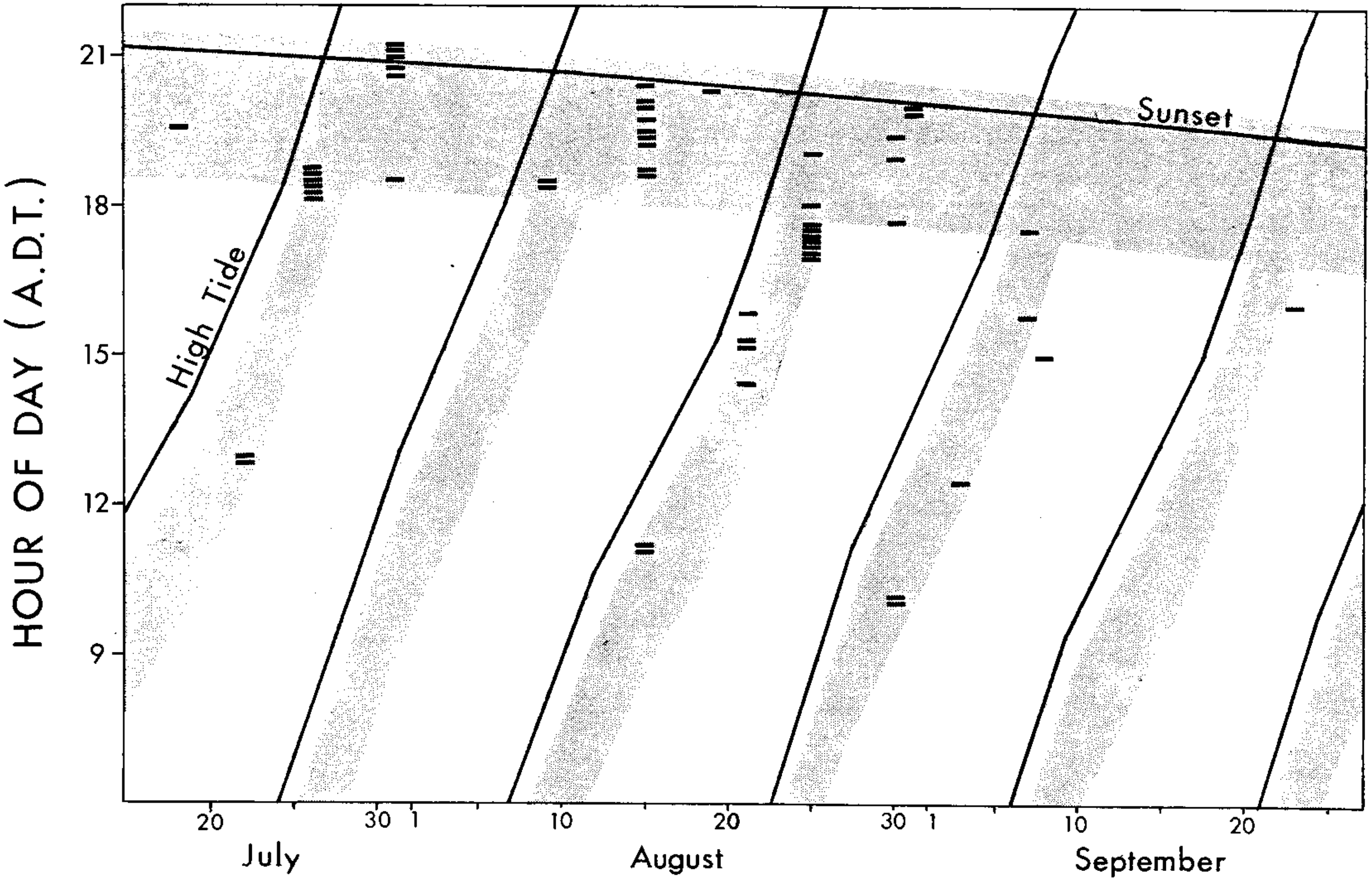
SIBLEY LAKE, 1978

Figure 27. The timing of departures relative to sunset (A) and tidal cycle (B) at Kent Island.



KENT ISLAND, 1977

Figure 28. The interaction of sunset and tidal cycle in the timing of departures at Kent Island. Each departure is noted by a short, horizontal, black line. Solid lines indicate the time of sunset or of high tide. Both are shown as continuous lines, although they actually changed in discrete steps from day to day. Shaded areas are "departure windows" - 3 hours during the late ascending tide and 2 hours around sunset.



KENT ISLAND 1977

tures not occurring during the tidal window occurred around sunset. The latest departures occurred when low tide coincided with sunset (31 July; 15, 21, 30 and 31 August). On these days, the hourly departure distribution resembles that of Sibley Lake. On two days, departures were observed both during an ascending tide in late morning and prior to sunset (15 and 30 August).

5.2.2.2 Discussion

A tendency for shorebirds to depart at sunset has been documented previously at coastal locations (Drury and Keith, 1963; Lack, 1962, 1963; Drury and Nisbet, 1964; Evans, 1968; Feeny *et al*., 1968; Grimes, 1974; Richardson, 1979). Most of these studies report that the first shorebird departures occurred one or two hours before sunset. However some flocks were known to have initiated flights both earlier in the day, as was seen with *C. pusilla*, and at night, on which I have no information.

No systematic study of the effects of tidal cycles on departure timing has previously been presented (Richardson, 1978a), however Drury and Keith (1962:473) reported this pattern of shorebird echos in radar studies on Cape Cod, MA:

> Maximum density coincides with rising tide, and echo counts rise during the afternoon to a peak one to two hours before sunset.

This pattern matches almost exactly that documented at Kent Island. Tidally mediated departures also occur at Plymouth, MA (Harrington, personal communication).

The patterns of departure times seen here raise several questions. Why do birds concentrate departure times just prior to sunset? Why do birds leave on ascending tides at Kent Island? What caused some flocks, even in North Dakota, to depart earlier in the day?

The first question usually has been posed: why do birds migrate at night? If the 50 hour flight time estimated for transoceanic flight (Section 3.4.2.2) is accurate, birds departing the east coast will fly both day and night in roughly equal proportions. Thus, the question of interest is in part "why fly at night?", but also "why initiate flight at sunset?", which is slightly different.

Nocturnal migration was first addressed by Brewster (1886). From a tabulation of groups of birds that migrated by day, night, and both, he suggested that

> Timid, sedentary, or feeble-winged birds migrate at night because they are either afraid to venture on long, exposed journeys by daylight, or unable to continue these journeys day after day without losing much time in stopping to search for food. By taking the nights for traveling they can devote the days entirely to feeding and resting in their favorite haunts . . . . The remainder of the wading. . . birds . . ., as far as I can ascertain, migrate indifferently, and more or less equally, by both night and day. This again was to be expected when we consider that they feed (again without exceptions, I believe) more or less indifferently and freely at all hours, and are not accustomed to seek safety in concealment. (p.20-21).

Brewster thus proposed that nocturnal migration enabled small birds 1) to fly by night and feed by day, and 2) to obtain protection against diurnal predators. Wetmore (1926), Thompson (1926), and Lincoln (1931) repeat both theories, and favor the advantages of feeding on arrival in the morning after a night flight. More modern authors retain this view (e.g. Griffin, 1964). However two additional hypotheses have been advanced: 3) nocturnal migrants gain by flying under cooler conditions, which reduces potential heat stress and enables greater retention of water, which might be a limiting factor for long distance migrants (Dorka, 1966; Hart and Berger, 1972; Pennycuick, 1975), and 4) certain orientational or navigational cues, such as the stars (e.g. Sauer and Sauer, 1960; Emlen, 1967) or the setting sun (e.g. Vleugel, 1954; Emlen and Demong, 1978; Bingman and Able, 1979; Emlen, in press) would be available only in the evening or during the night. A view of the setting sun, or polarization patterns associated with it, appear to be necessary for nocturnal orientation in Savannah Sparrows. If these cues are necessary, they could constrain migratory timing (Moore, 1978, 1980, 1982).

What do the sandpiper data suggest with regard to these theories? The potential constraints on orientation mechanisms are apparently not important, since flocks are well-oriented when departing both during the day and in the evening. With regard to water loss, the timing of flight initiation should make little difference to transoceanic migrants, who fly both day and night, unless there are significant differences in water loss as birds make their initial climb to migratory altitude during the day or evening. Shorebirds are probably more vulnerable to predators while on the ground than on the wing; in any case, given the height of shorebird migration, predation does not seem especially relevant. The flexibility in departure timing seen in Semipalmated Sandpipers shows that all three of these proposed advantages for nocturnal flight may be overridden by other factors, such as weather (Section 5.3.1.4).

This leaves the feeding hypothesis, which is really two separate propositions. The first is that by feeding until sunset birds may depart with a maximum amount of stored food. The second is that by flying at night, birds will arrive with stores depleted at a time when they can forage well visually, as opposed to landing in the evening. While Brewster suggested that waterbirds feed equally well by day or night, Semipalmated Sandpipers are in part visual foragers, and would be expected to be more efficient foragers by day.

The departure patterns shown on the coast provide a unique source of data consistent with the first food hypothesis, but possibly also with the second. Birds leaving on ascending tides are departing as food becomes unavailable. They would face, at Kent Island, a period of poor feeding lasting two to four hours. At some point in the day, it might be advantageous to depart fully fueled, rather than roosting through the high tide to resume foraging until sunset. Lowered food availability is a common environmental feature that follows both tidal and sunset departure windows shaded in Figure 28, and occurred at no other times. Thus, decreased access to food is closely associated with the onset of migratory flight.

With regard to feeding conditions on arrival, birds leaving the coast earlier in the day would seem to be at an advantage compared with those departing at sunset. If transoceanic flight averages 50 hours (Section 3.4.2.2), and the birds land at about the same longititude as they started (they don't change "time zones"), they will arrive, on average, about two days and two hours later than they left. Thus birds departing early in the day would have several hours of daylight foraging upon arrival, while those departing at sunset would arrive during the night. This suggestion is admittedly speculative and obviously dependent on the true duration and amount of variability in flight times. Since the majority of flocks leave near sunset, this hypothesized effect is apparently not an overriding selective force.

This discussion of the influence of food availability on migratory timing has ignored some of the most intriguing observations in the study: early departures in the midwest. In the next section, I will propose that the diurnal flexibility shown in departure times, especially in North Dakota, suggests that the availability of favorable migratory weather can be a key resource that influences even the hourly timing of migration.

5.3 METEOROLOGICAL CONDITIONS AT DEPARTURE

The relationship between shorebird migration and weather appears somewhat different from that found in passerines. Studies with search radars find fewer shorebirds in the air with strong opposing winds (e.g. Lack, 1962, 1963b; Evans, 1968; Able, 1973; Richardson, 1979), but also find that the volume of shorebird migration is less predictable from local weather variables than that of passerines. In extensive radar studies in the Maritimes, Richardson found that meteorological variables accounted for 53% of the nocturnal and 51% of the diurnal variances in the volume of migration in passerines, but only 27% and 43% of the respective variances for shorebirds (Richardson, 1974, 1976a, 1979). These estimates for explained shorebird variance may even be exaggerated, due to methodological limitations (Richardson, 1978a: Table 1).

Other studies of "waterbird" migrations have also found lower correlations with local weather than the 35-55% common for studies of passerines (Nisbet and Drury, 1968; Beason, 1978; see Richardson 1978a, for review). Gauthreaux and Able (1970), and Able (1974) stress that the faster flight speeds of shorebirds and waterfowl would enable them to fly in stronger crosswinds, with less deflection, than passerines.

Radar studies have shown a poorer correlation between weather and migration for shorebirds than for passerines, suggesting that shorebirds are less particular in choosing when to migrate. However, the local weather conditions at the radar station may differ substantially from the weather in which the birds began their flight. This section examines departure weather at the study sites where the departures occurred. I describe departure conditions, compare departure weather to that prevailing at other times, and compare the meteorological selectivity of the two populations. The analyses include both a synoptic approach (e.g. Richardson, 1970), and analysis of local weather variables.

5.3.1 Synoptic Analysis of Departure Conditions

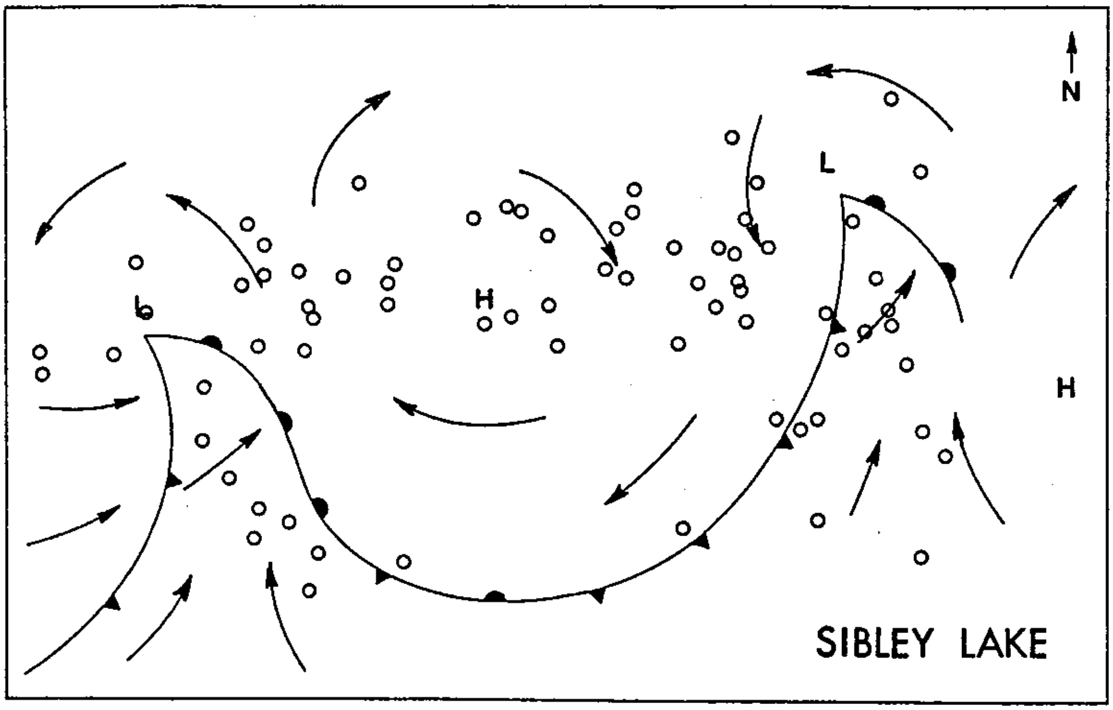
The generalized synoptic weather map was introduced in section 2.3.1. Three types of maps will be presented in this section: the "expected" distribution of the weather, derived from a systematic sampling; summary maps plotting synoptic situations at departures; and "path diagrams", showing the movement of the weather for several days before, during and after departures. Following these sections, the frequencies of synoptic categories (Section 2.3.1, Figure 6) in both locations for five years prior to the study will be examined to determine whether the study years were "typical" years, and to get an idea of the relative frequency of occurrence of favorable weather at the two locations.

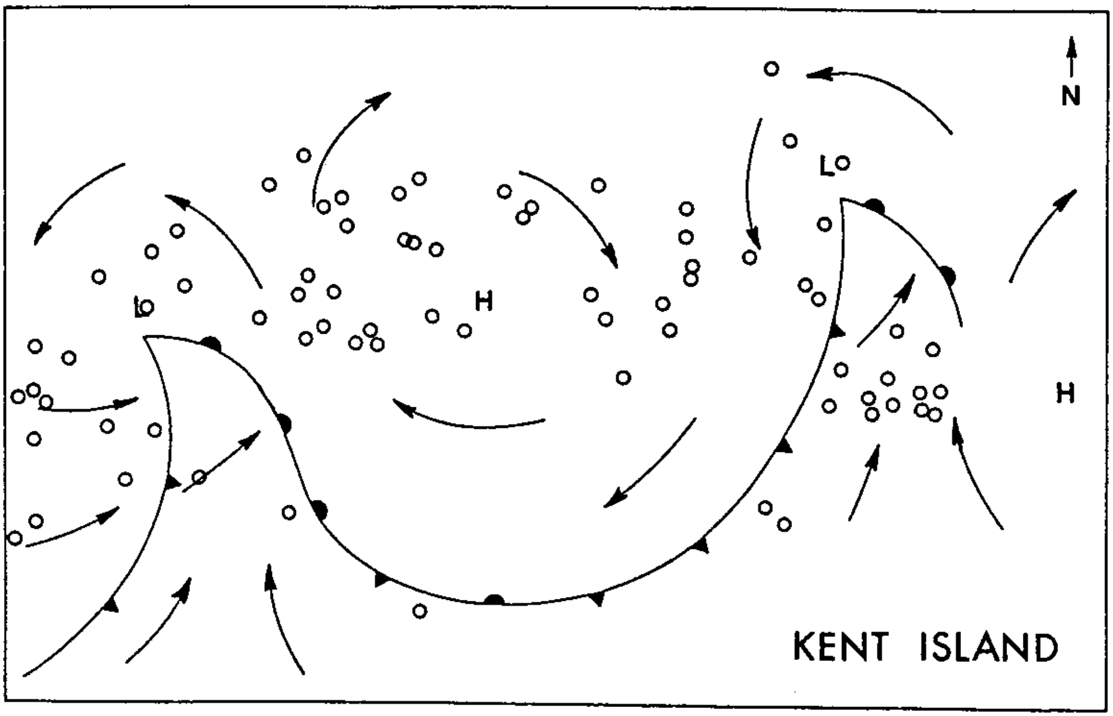
5.3.1.1 Background Distributions of Synoptic Conditions

To provide a background against which the variability in departure weather may be judged, I will first examine the distribution of weather conditions systematically sampled throughout the season. This sampling allows determination of the "expected distribution" that would be obtained if flocks left at random with respect to weather conditions. Figure 29 shows the background distributions of the weather on synoptic maps for Sibley Lake and Kent Island. One dot was plotted per location per day of the study season, showing the prevailing synoptic situation at the modal time of flock departures (Section 5.2.2).

The maps show a relatively even spread of points in an arc between the centers of the pressure systems. Few points are present south of highs or around stationary fronts (at the bottom). Two differences between the weather patterns at the study sites are visible. While cold fronts at Sibley Lake were almost invariably followed by northwesterly winds (points to the left of the cold fronts), about half of the points behind cold fronts at Kent Island had west or southwesterly prevailing winds (plotted on the left side of the maps). In addition, warm fronts were better developed in the midwest, as seen by the greater proportion of warm sector dots (southeast of lows) plotted on the right hand side of the Sibley Lake map (see Figure 6).

Figure 29. The background distribution of the weather at Sibley Lake and Kent Island. One dot is plotted per day representing the prevailing weather over the study site at the modal time of takeoff at each location.


N
L
L
H
H
SIBLEY LAKE


N
L
L
H
H
KENT ISLAND

5.3.1.2 Synoptic Conditions at Departure

Figures 30 and 31 plot the prevailing synoptic situation at all hours during which departures were observed at Sibley Lake and Kent Island. The numbers inside the circles indicate the number of flocks leaving within an hour of each other. Shaded circles show departures that occurred more than four hours prior to sunset.

The departures at both locations are obviously clumped relative to the background distributions shown in Figure 29. Departures occurred almost exclusively in the zone to the west and southwest of lows and east and northeast of highs. These areas are characterized by westerly to northerly geostrophic winds. It is clear that at both sites Semipalmated Sandpipers initiated migratory flights when winds aloft favored movement in the appropriate migratory direction (Section 5.1.2).

5.3.1.3 Path Diagrams

To provide a clearer picture of the dynamic situation under which migratory departures occurred, I have constructed "path diagrams" that show the changing weather conditions before, during, and after particular GO days. Since weather systems in both areas typically moved from west to east, these maps plot the "movement" of the study site relative to the weather, from east to west.

Figure 32 shows the weather at Sibley Lake during a typical departure situation. The study site is plotted at 3-hourly intervals from the early morning of 21 July to after sunset 22 July, 1978. The variability in spacing between 3-hourly fixes reflects a combination of the size, speed, and shape of the actual weather systems vis-a-vis their represen-

Figure 30. Prevailing weather at the hours of flock departures at Sibley Lake. The number in each circle represents the number of flocks which left within an hour of each other. Departures which occurred more than 4 hours before sunset are shaded.

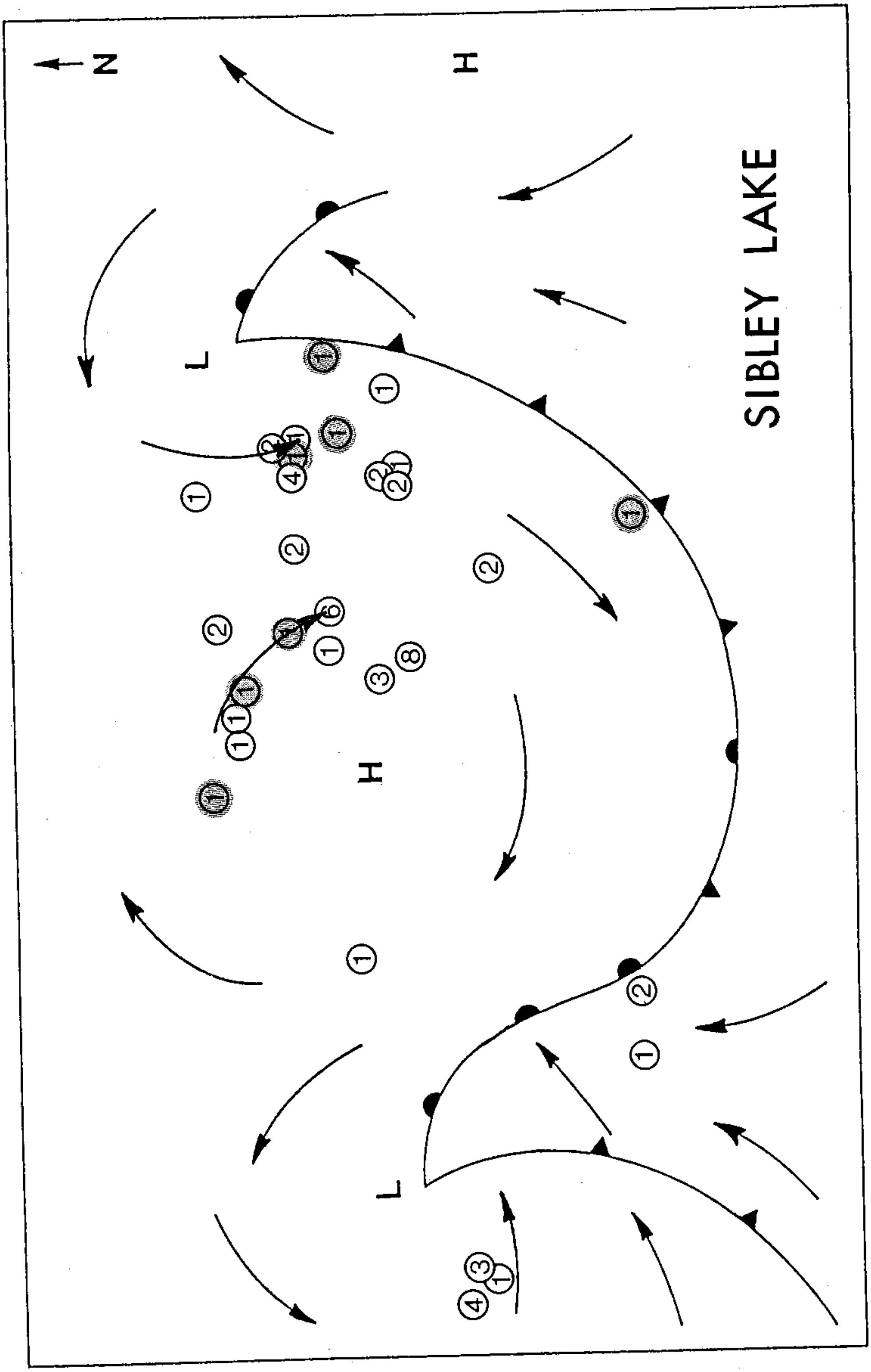

N
H
L
H
L
SIBLEY LAKE

Figure 31. Prevailing weather at the hours of flock departures at Kent Island. The number in each circle represents the number of flocks which left within an hour of each other. Departures which occurred more than 4 hours before sunset are shaded.

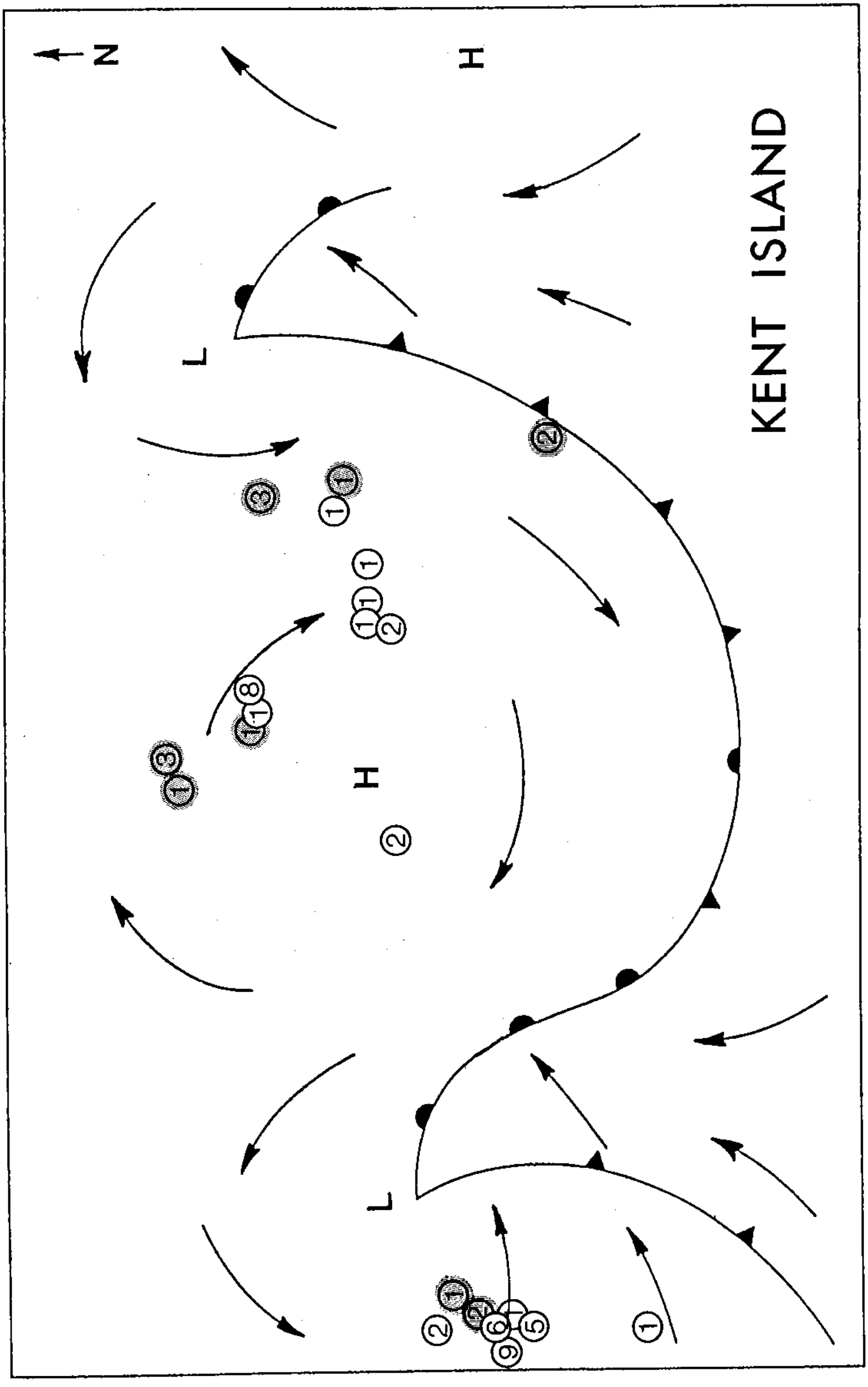
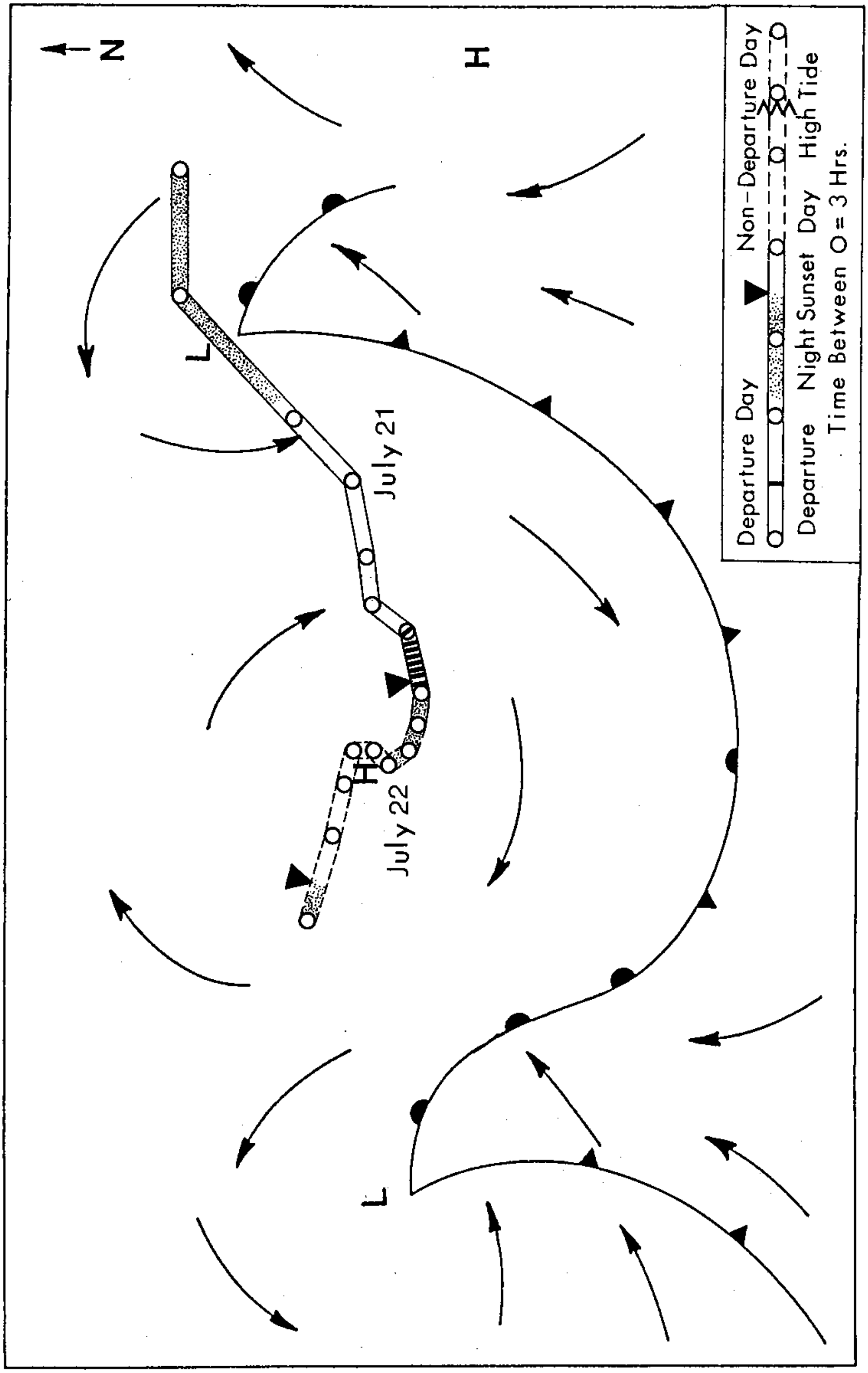

KENT ISLAND
N
H
L
H
L

Figure 32. The weather prevailing over Sibley Lake on 21 and 22 July, 1978, and the timing of flock departures.


N
H
L
July 21
H
July 22
L
Departure Day
Non-Departure Day
Departure
Night
Sunset
Day
High Tide
Time Between O = 3 Hrs.

tations on the generalized map. The path shows a low pressure system passing over Sibley Lake during the morning of the 21st, and a high approaching around noon. The cold front did not actually pass over the area; nevertheless Sibley Lake experienced the weather conditions that typically follow cold fronts. Northwesterly winds associated with the backside of the low, and leading edge of the high, blew all day, and eight flocks departed around sunset. During that night and the next day, a large high pressure system moved over the site, and unfavorable winds prevailed the next evening, when no departures were observed.

Figure 33 shows a less typical pattern of weather movement in the midwest. Warm sector conditions prevailed on 13 August as a low pressure system approached from the north. The cold front passed through on the early morning of the 14th, followed by favorable migratory conditions. However, instead of a high pressure system moving in, as in the previous example, the low maintained its influence over Sibley Lake. Upper level winds became more northerly, and even northeasterly during the afternoon and night. Flocks departed that afternoon and evening, including one "early" flock (shaded in Figure 30). When this flock left, conditions had been favorable for six to seven hours and the weather was actually becoming less favorable, a trend that continued during the night. On the 15th a high pressure system did move in, passing south of the study site, and flocks departed during favorable conditions around sunset.

Turning to Kent Island, Figure 34 shows two departure sequences. The timing of high tides has been added to the diagrams. The righthand path (24-26 August) represents a weather situation similar to that shown at

Figure 33. The weather prevailing over Sibley Lake on 13-15 August, 1978, and the timing of departures.

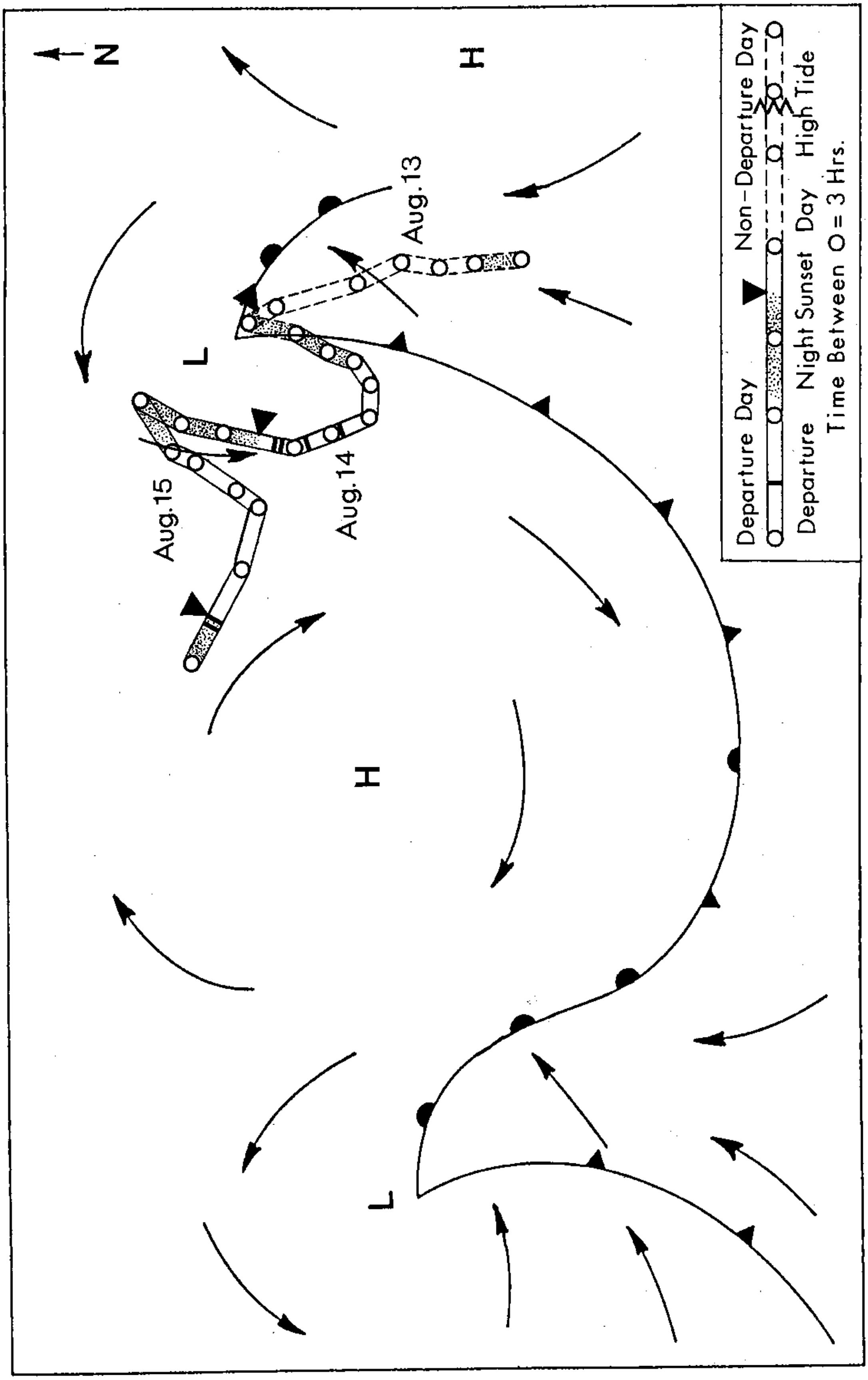
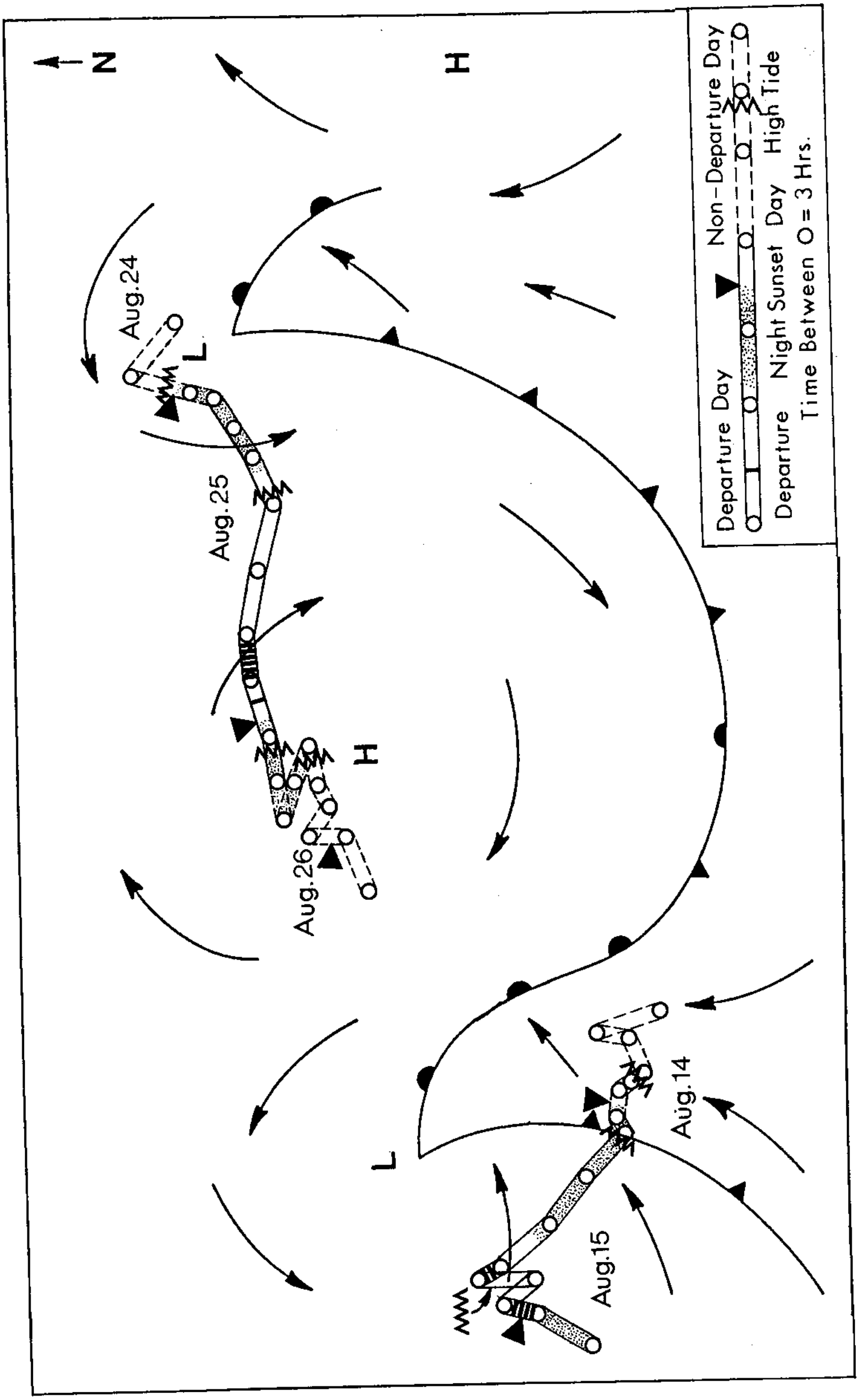

N
H
L
Aug.13
Aug.14
Aug.15
H
L
Departure Day
Non-Departure Day
Departure
Night
Sunset
Day
High Tide
Time Between O = 3 Hrs.

Figure 34. The weather prevailing over Kent Island on 14-15 August and 24-26 August, 1977, and the timing of departures.


N
H
L
Aug.24
Aug.25
Aug.26
H
L
Aug.14
Aug.15
Departure Day
Non-Departure Day
Departure
Night
Sunset
Day
High Tide
Time Between O = 3 Hrs.

Sibley Lake in Figure 32 - a low pressure system followed by favorable conditions during most of the day, with a group of departures prior to sunset. Since high tide occurred shortly after sunset, it did not affect the timing of flights (see Figure 28). The path on the left side shows a sequence in which departures were stimulated by the incoming tide. A cold front moved through on the night of 14 August, and favorable weather conditions prevailed just prior to a late-morning high tide, when flocks left. The weather remained favorable throughout the day, and flocks also left during the low tide prior to sunset (see Figure 28).

5.3.1.4 Departures Early in the Day

Departures that occurred early in the day are of particular interest. These are shown as shaded circles in Figures 30 and 31.

Looking first at Sibley Lake, two of the seven early departures immediately followed the movement of a cold front through the area. Although the "passage of a cold front" is commonly cited as the prime stimulatory factor for autumn bird migration in North America (e.g. Richardson, 1978a), the prevailing conditions behind the front, rather than its passage *per se*, can be sufficiently stimulatory (Figure 32). These two observations imply, however, that the rapid changes in conditions associated with the passage of a cold front may indeed directly stimulate departures.

Three early departures occurred as the weather changed from favorable to unfavorable conditions. Two are southwest of a low, with the winds changing from northwesterly to north or northeasterly, as was shown in

Figure 33. The third was north of a high. In this latter case, the weather "moved" north from the shaded dot into the warm sector of an adjacent system. The single departure shown in the warm sector in the lower left of the map occurred at sunset of the same day. By leaving early, the shaded flock departed in more favorable weather than did the one that waited until sunset. The two remaining early departures, northeast of the high, are apparently early departures under favorable conditions on days when birds also left around sunset.

The relationship between weather and early departures at Kent Island is complicated by concurrent tidal effects. There were 14 early departures. All but one of the shaded circles in Figure 31 occurred within four hours prior to high tide. However, there are parallels with the early departure conditions seen inland. Two flocks departed Kent Island in the same hour, just after the passage of a cold front. Seven flocks departed when the weather was becoming less favorable. Three of these left during the same hour when winds were shifting from northwesterly to north-northeasterly, a situation similar to that shown at Sibley Lake in Figure 33 (three flocks southwest of the eastern low). Four flocks (three and one, straight north of the high) left on the same day prior to a shift to less favorable southwesterly winds by sunset. This leaves five departures that occurred on rising tides during continuously favorable weather.

In summary, if we lump the two locations, 21 flocks were seen departing more than four hours prior to sunset. Ten of these departures (48%) occurred when weather conditions had been favorable for several hours but were becoming less so, either with shifts in geostrophic winds towards the northeast (5 cases) or towards the southwest (5 cases). Four (19%) occurred when the weather rapidly became favorable immediately after the passage of a cold front. The seven remaining cases (33%) show the same dynamic synoptic conditions as the evening departures.

5.3.1.5 Ecological Correlates of Daily Flexibility

Although few flocks were observed leaving early in the day, the cases presented demonstrate a sensitivity to meteorological conditions and a flexibility with regard to hourly timing that makes the dynamic weather picture important in determining in which hour, as well as on what day, birds depart. I previously argued that the normal departure timing was related to the availability of food supplies (Section 5.2.2.2). These exceptional cases, where birds left while food was still available, show that exploitation of favorable weather may at times override the benefits of continued foraging.

While numerous studies have discussed the correlation of cold front passages and increased autumn bird migration, there has been little discussion of whether birds might benefit by leaving at the beginning, during, or at the end of a period of weather that is energetically favorable for migration (but see Drury and Nisbet, 1968). Since birds flying downwind within a pressure system will move relative to that system, they will eventually fly out of it. This means that sandpipers leaving behind a cold front will catch up with the front, and encounter less favorable flight conditions as they fly through it and into warm sector conditions on the other side. Richardson (1976a, 1979) describes examples of shorebirds in the Maritimes doing this as they flew southeastwardly out over the ocean.

From an energetic point of view, the optimal time to leave would be at the end of the period of favorable weather. This would allow maximum flight time with following winds. In contrast, those flocks leaving immediately after the passage of a front will have only a short period of favorable flight conditions. While a few flocks took off directly after a front's passage, and others left as conditions worsened, the bulk of the departures are scattered throughout the period of favorable weather. For the most part, departure weather within the range of acceptable conditions was determined by what conditions happened to be present at sunset.

Why aren't the birds more precise with regard to the weather? Why do relatively few flocks leave much before sunset? On days when birds took off at two distinct times, such as those shown in Figure 28, birds departing later in the day ran the risk of missing favorable winds. Twice at Sibley Lake, flocks that waited until sunset departed in weather no longer energetically favorable, although they may have caught up with it. The birds, of course, may not know the size of the system passing overhead, which would make waiting for the last moment difficult. The advantage of feeding until sunset may also be involved (Section 5.2.2.2). While departures in favorable weather have been selected for, the daily feeding rhythms, also adaptive, may result in departures occurring at less than optimal moments with respect to the weather.

The effect of tides in increasing the variance of departure times on the coast may now be reinterpreted slightly. By forcing birds into the air several times during the day, rising tides may have facilitated departures that more closely tracked changes in weather conditions. The fact that shorebirds must feed on tidal cycles may have preadapted flexible daily patterns of behavior in other respects. Thus, the tides may provide a mechanism that promotes flexibility in departure timing and increases specialization with regard to meteorological conditions at departure.

The studies cited earlier, and the quote from Drury and Keith (1963) (Section 5.2.2.2) indicated that a degree of hourly flexibility is characteristic of shorebirds at coastal sites. Are other groups of birds as opportunistic in their migratory timing with respect to weather as are the sandpipers? For the most part, I restrict the discussion that follows to studies in which the investigators measured numbers of birds they believed to be beginning migratory flights, rather than measuring "traffic rates" of migrants that initiated flights at unknown times of day.

The initiation of migratory flight by "nocturnal" passerines appears to be a much less variable behavior pattern than that of shorebirds. Richardson (1978b:727) reviews studies on the timing of initiation of "landbird" migration, and places it at a precise 28±5 minutes after sunset. In his paper on shorebird migration, by contrast, Richardson (1979) states that "shorebird densities often increased gradually from one to two hours before sunset to sunset or shortly thereafter", although these data include migrants of unknown origin. Moore

(1980:685) reviews numerous studies, and concludes that for passerines, "the actual night's migration usually commences prior to the end of twilight within the first hour after sunset." Richardson (1978a) states there is little evidence of passerines beginning migratory flights when cold fronts pass overhead during the night in autumn. Nocturnal passerines are sometimes observed flying by day, but recent analyses of these movements do not suggest that the birds begin migratory flights during daylight hours (for review, see Richardson, 1978b; Bingman, 1980).

Studies of White-throated Sparrows (*Zonotrichia albicollis*) in activity cages under natural light conditions, or in the laboratory with gradual changes in light levels, show a period of inactivity (*Einschlafpause*, Palmgren, 1949) at the end of daytime activity, prior to the beginning of *Zugunruhe* during twilight periods (e.g. Weise, 1956; Helms, 1963; Riker, 1977). This has also been observed in the wild for nocturnally migrant passerines (e.g. Hebrard, 1971). Thus, radar, field, and laboratory studies identify a "twilight window" as a specialized time for the initiation of nocturnal passerine migration.

Zugunruhe exists in shorebirds, as shown by successful nocturnal orientation experiments performed with Golden Plovers (*Pluvialis dominica*) (Sauer, 1963, 1964), Semipalmated Sandpipers (Lank, 1973), and other calidrids (Emlen, unpublished data; Lank, unpublished data). Lank (1978, unpublished data) showed that nocturnal activity in freshly caught Semipalmated Sandpipers was significantly greater on nights with favorable weather (synoptic category 2, Figure 6) than at other times. Considering the limited success that many workers have had in correlating cage activity with weather conditions in passerines (see Richardson, 1978a, for review), these last data suggest that more flexible patterns of Zugunruhe may be present in shorebirds.

Among "diurnal" passerine migrants, the best data on daily rhythms of migratory departures are for Starlings, (Sturnus vulgaris), both in Europe and America. Richardson and Haight (1969), using radar, recorded departures only on mornings with seasonally favorable winds. However, Harper (1959), Lack (1963a:476), and Eastwood (1963) report occasional nocturnal departures of starlings from roosts in eastern England. Eastwood (1963:394) states "this took place on nights in the early spring when a suitable following wind prompted the birds to join the general migrant stream eastward to the Continent."

Waterfowl seem to have flexible daily patterns of departure timing, and, at least in some cases, weather is known to be involved. The most detailed studies are those of Blokpoel et al. (1975) and Blokpoel and Gauthier (1975) on the departure timing of Snow Geese (Chen caerulescens atlantica) from migratory staging areas in both central and eastern Canada. The bulk of the Snow Goose population moves in a relatively small number of waves, which coincide with favorable winds. In this highly social, long-distance migrant, flocks begin migratory flights at all hours of the day and night while favorable weather persists (Blokpoel et al., 1975). As Ogilvie (1978:294) states in a review of the Snow Goose literature:

> The timing of any migratory flight seems more dependent on weather conditions than time of day, but there does seem a preference, observed in a number of different populations, for a departure in daylight, though with some tendency for the afternoon or early evening.

Other waterfowl may have similar, if less well documented, patterns of daily departures. Miskimen (1955) referred to "evening" migratory departures of Mallards (Anas platyrhynchos), Black Ducks (A. rubripes), and Lesser Scaup (Aythya affinis) in Ohio, and stressed the importance of pre-flight social behavior. Hochbaum (1955) described spring waterfowl departures at Delta, Manitoba, as occurring during the long twilight period from sundown until dark. But both authors mention that other departures occurred during the day.

In summary, shorebirds, waterfowl, and diurnally migrant passerines appear to have greater flexibility in the hourly timing of their departures than do nocturnal passerines, and some of this flexibility is related to the weather. Despite their stronger flight abilities, shorebirds and waterfowl may actually be more selective about weather conditions at departure than are passerines. This conclusion agrees with that of Able (1974:229), who found that:

> it is difficult to obtain data on the flight orientation of shorebirds and waterfowl over a broad spectrum of wind directions because they appear to select favorable winds for their specific goal-directed fights.

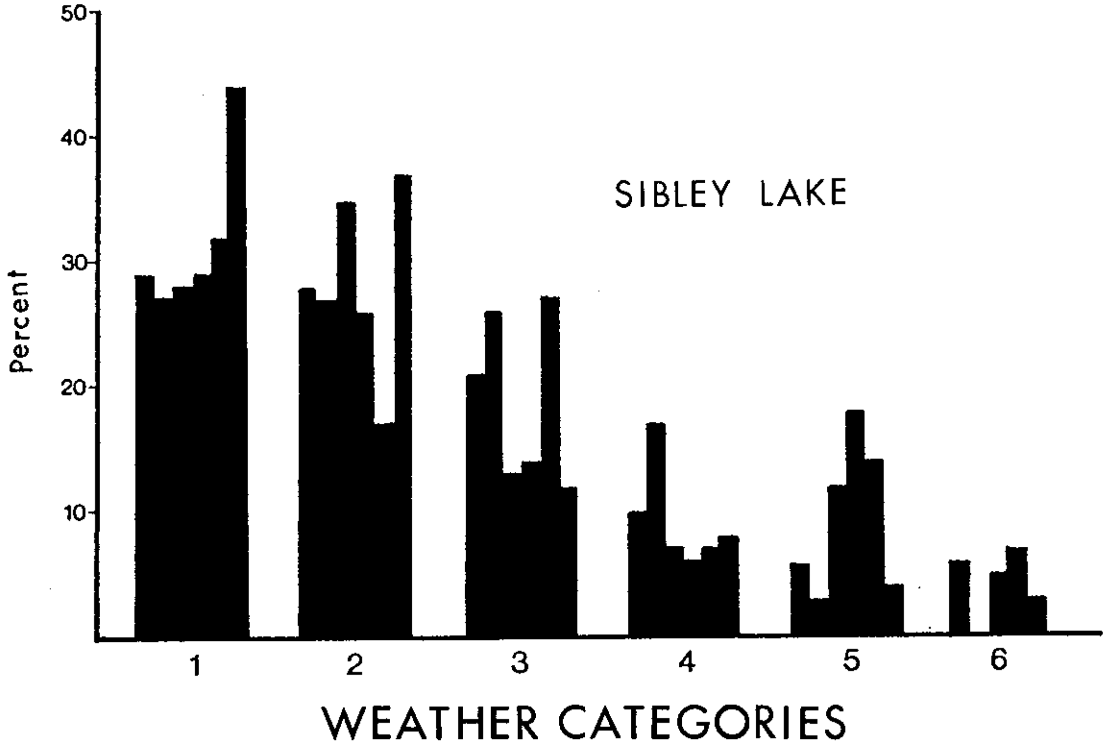
The greater selectivity of waterfowl and shorebirds may be due to the length of the migratory flights made by these groups. The poorer correlation between meteorological conditions at radar sites and the volume of shorebird migration discussed at the beginning of this section is not indicative of lesser selectivity of departure conditions. Rather, it reflects shorebirds maintaining the same course as they fly out of the weather in which they began their flights. Since passerines make shorter flights, local conditions at a radar site are more likely to be similar to those in which the birds initiated flight than is the case for shorebirds. The groups with more temporal flexibility are also those that migrate in flocks. This strengthens the possiblity that "decision making" is an important adaptive feature of migration in flocks (see Section 5.1.3), since these groups have a greater "choice" of times in which to fly. Flocking might also be considered as a cause of the flexibility, with mutual stimulation during periods of favorable weather overriding any internal rhythms of flight activity. One might argue that the strong rhythms in passerines are related to the relative lack of social stimulation.

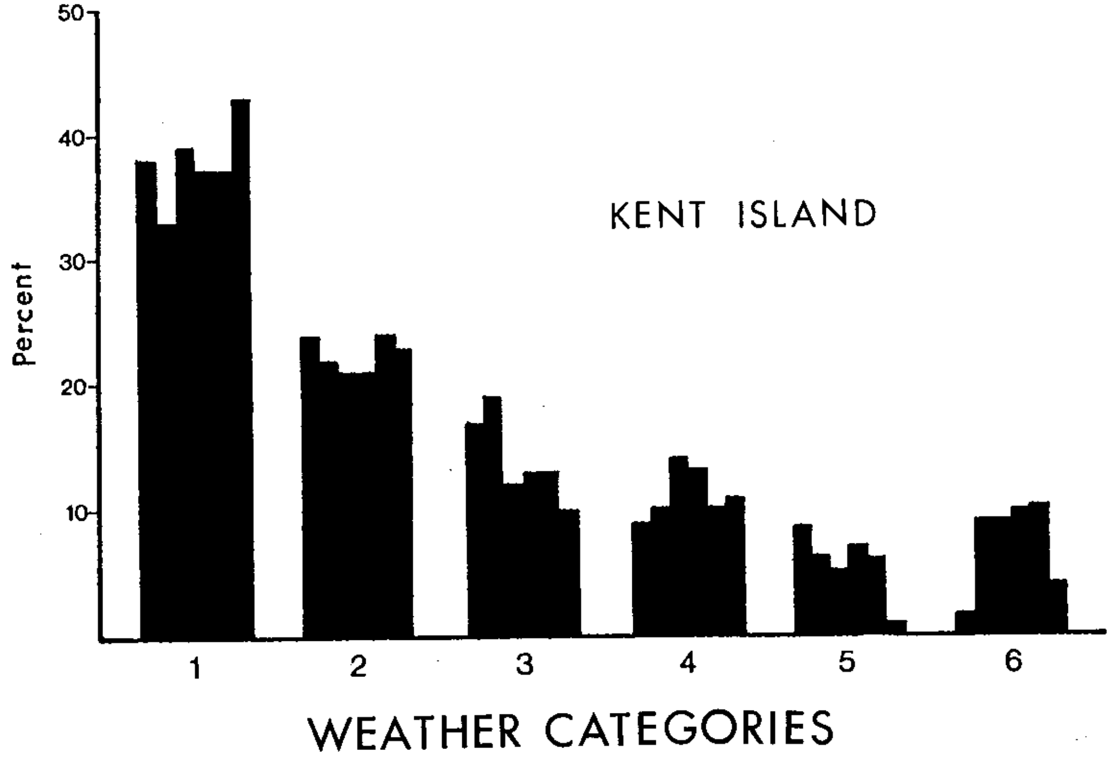
Favorable weather is an important and ephemeral resource for migrating birds. It has played a key role in determining not only the daily occurrence, but also the hourly timing of migration in Semipalmated Sandpipers. The next section examines the dependability of this resource for inland and coastal populations.

5.3.2 Frequencies of Favorable Migratory Weather

To evaluate whether the weather during the study years was "normal" in terms of the frequency of favorable migratory conditions, and to examine how important it might be for a migrant to take advantage of favorable weather, I determined the frequencies of six synoptic conditions for the five years preceding the study, 1972-1976. The synoptic map was divided into six areas, shown in Figure 6, and the number of days falling into each category per season was determined. Since category 2 weather encompasses nearly all departures (compare Figures 6, 30, and 31), it will be considered as "favorable weather". Figure 35 presents the distributions of weather categories at each location in

Figure 35. The frequency distributions of six weather types during six fall migratory seasons at Sibley Lake and Kent Island. The six weather categories and this analysis are explained in detail in Section 2.3.1. The set of vertical bars for each category represent different seasons; each bar represents the proportion of the season's weather that fell into that category. The years are 1972-1977 for Kent Island, and 1972-1976 and 1978 for Sibley Lake.


50
40
30
20
10
Percent
SIBLEY LAKE
1
2
3
4
5
6
WEATHER CATEGORIES


50
40
30
20
10
Percent
KENT ISLAND
1
2
3
4
5
6
WEATHER CATEGORIES

each year, including the study years. Favorable weather occurred about one day in four to five at both locations; slightly more often on average in the midwest. The study year at Sibley Lake was unusual in the high frequencies of favorable and strongly unfavorable (category 1) weather.

Overall, the occurrence of weather in different categories was more stable at Kent Island than at Sibley Lake. Statistically, the distributions from Sibley Lake differ among years, while those from Kent Island do not ($\chi^2 = 50.91$, $p < .005$ at Sibley; $\chi^2 = 13.31$ at Kent Island, $p > .10$). Thus, while favorable weather occurs at about equal frequencies on average at the two sites, it may be a more reliable feature of the coastal environment. Dependable periods of favorable weather are an essential resource for populations making such long migratory flights.

5.3.3 Local Conditions at Departure

While the synoptic analysis gives a general picture of departure conditions, analysis of local weather examines the conditions experienced by birds on the ground. Thus, it may be possible to determine which weather variables directly influence the initiation of migratory flight. The analysis enables more precise quantification and comparison of background and departure conditions. Having shown that favorable weather may be slightly more reliable on the coast, we can ask whether coastal migrants are more selective about departure conditions. Section 2.3.2 detailed the treatment of specific meteorological variables, the definitions of GO and NOGO hours, and the sampling used to produce the background distribution of the weather. Univariate (t-tests for means and F-tests for variances) and multivariate (discriminant function analysis, DFA) analyses involved four comparisons: 1) GO vs. NOGO at Sibley Lake, 2) GO vs. NOGO at Kent Island, 3) GO at Sibley Lake vs. GO at Kent Island, and 4) comparison of the background distributions at the two locations. In addition, the correlation matrices of weather variables within both locations were examined to aid in interpretation of the results. These comparisons allow examination, either for single variables or for the weather as a whole, of 1) whether departure (GO) conditions differed from non-departure (NOGO) conditions at each site, 2) whether departure conditions were different between sites, and 3) whether any differences found in departure conditions simply reflected differences in the prevailing weather from which the birds could "choose", rather than real preferences for different departure weather.

5.3.3.1 GO-NOGO Comparisons Within Locations

The impression of clumping of departure conditions relative to the background weather distribution seen in the synoptic analysis (Sections 5.3.2.1 and 5.3.2.2) was confirmed in the analyses of local weather conditions. Table 5 presents the univariate comparisons of GO and NOGO conditions within Sibley Lake and Kent Island. The only variables showing significant differences of the means at both locations were the Tail-Headwind Component of the wind (THC) and the 24-hour trend in THC. The GO and NOGO values of THC were 4.7 vs. 0.0 knots at Sibley Lake and 6.6 vs. -0.3 at Kent Island. Thus birds flew with tailwinds. Variances of both these variables were significantly lower at GO than NOGO hours at Sibley Lake, but not at Kent Island.

Table 5. Mean and standard deviations of weather variables at Sibley Lake and Kent Island with univariate comparisons [a] between GO and NOGO hours within locations.

	Sibley Lake				Kent Island			
Variables	GO n=36	NOGO n=140	s^2	$\bar{x}$	GO n=26	NOGO n=135-139[b]	s^2	$\bar{x}$
Tail-headwind (THC)	4.8 ± 4.8	0.0 ± 7.7	**	***	6.6 ± 6.9	-0.3 ± 6.5	ns	***
Side wind (SWC)	0.8 ± 5.9	1.4 ± 4.8	ns	ns	2.2 ± 4.4	4.8 ± 7.7	***	*
Absolute SWC	4.7 ± 3.5	3.9 ± 3.1	ns	ns	3.9 ± 2.8	7.6 ± 5.1	***	***
9 hr. THC trend	-0.2 ± 6.9	0.3 ± 7.2	ns	ns	0.6 ± 7.3	-0.2 ± 5.6	ns	ns
9 hr. SWC trend	0.3 ± 6.0	0.5 ± 5.1	ns	ns	2.1 ± 5.7	3.1 ± 5.9	ns	ns
24 hr. THC trend	4.8 ± 7.5	-0.5 ±11.4	**	***	8.6 ± 8.9	-1.0 ± 9.2	ns	***
24 hr. SWC trend	-1.4 ± 8.0	0.0 ± 6.9	ns	ns	-4.1 ± 7.5	0.5 ± 8.0	ns	**
Temperature (TMPR)	21.1 ± 5.1	22.9 ± 5.9	ns	ns	18.7 ± 2.5	16.8 ± 4.2	**	**
24 hr. TMPR trend	-1.5 ± 3.7	0.1 ± 4.2	ns	*	0.4 ± 4.0	-0.3 ± 3.2	ns	ns
Relative humidity	48.5 ±16.8	48.1 ±16.9	ns	ns	54.9 ±14.9	75.5 ±18.4	ns	***
12 hr. humidity trend	-32.9 ±23.0	-25.3 ±17.8	*	-	-40.0 ±14.7	-14.1 ±17.7	ns	***
Opacity	5.0 ± 4.1	4.5 ± 3.9	ns	ns	4.2 ± 2.6	6.1 ± 3.6	ns	*
Visibility	4.0 ± 0.0	3.9 ± 0.2	ns	ns	4.0 ± 0.2	3.4 ± 1.1	***	***
Precipitation	0.1 ± 0.7	0.1 ± 0.6	ns	ns	0.0 ± 0.0	0.2 ± 0.6	ns	-
Barometric Pressure	14.0 ± 5.3	12.7 ± 6.7	ns	ns	15.6 ± 4.4	15.8 ± 6.0	ns	ns
6 hr. pressure trend	-0.3 ± 2.3	-0.2 ± 2.5	ns	ns	1.0 ± 1.6	-0.3 ± 2.5	**	***

a) Significance of difference in variances and means are indicated by: ns for $P > .10$; - for $.05 < P < .10$; * for $P < .05$; ** for $P < .01$; *** for $P < .001$.

b) Sample sizes varied slightly due to missing data for particular variables.

At Sibley Lake, there were only three other univariate differences between GO and NOGO hours with significance levels less than .10, and these were all weak ($p > .01$). The 24-hour temperature trends differed, with temperature decreasing slightly at GO hours, and GO hours had a lower variance in the 12-hour humidity trend. By contrast, at Kent Island all variables except 9-hour wind component trends, precipitation, and barometric pressure showed significant differences in means, and five variables had significantly smaller variances at GO hours. When birds left Kent Island, sidewinds were weaker and showed decreasing 24-hour trends, humidity was lower and had fallen, pressure had risen, skies were clearer (opacity lower), and visibility was higher: all features associated with passage of and/or weather behind cold fronts. Interestingly, the absolute temperature was actually higher at GO hours. At Kent Island, "cold fronts" often brought west and southwesterly winds that moved warm continental air to the cool Bay of Fundy.

The univariate results show that at both locations birds left with strong tail winds, and that hours in which they did not leave averaged weak tail winds or slight head winds (negative values of THC). In addition, the univariate results suggest either that Kent Island birds responded to a wider range of meteorological variables, or that the variables themselves were much more intercorrelated at Kent Island. The fact that birds left Kent Island with significantly weaker sidewinds is especially intriguing, since strong sidewinds will affect the amount of wind drift the birds experience and/or must compensate for (Hinde, 1951; Evans, 1966a; see Emlen, 1975 for review). Intercorrelations among weather variables, however, could account for the differences without any more careful meteorological timing by coastal sandpipers. Further analyses will help resolve these possibilities.

The discriminant function analysis attempted to use meteorological information to classify the GO and NOGO cases within each location. The classifications achieved were significant, but not spectacular. They are summarized in the top half of Table 6. The canonical correlation coefficient, which measures overall classificatory success, showed only moderate success in classification; using its square as the percent of variance explained gives values of 28% at Sibley Lake and 35% at Kent Island. Its failure to do better may relate to sampling problems: flocks may have left but not been observed in some NOGO hours, or perhaps the local populations were simply too small to assure departures during all favorable weather conditions. Additionally, time of day was specifically not included in this "weather only" analysis, since time of day effects were stronger in one area than the other.

As in the univariate comparisons, Tail-Headwind Component, its 24-hour trend, and the 12-hour trend in humidity were important predictors at both locations. Table 7 gives the canonical coefficients and the correlations between individual variables and the discriminant function (DF). The latter number maybe used to assess the significance of each variable in the predictive model. While five variables had correlations with the DF of 0.2 or more at Sibley Lake, 11 did so at Kent Island.

Despite the much larger number of univariate differences seen at Kent Island, DFA achieved only slightly better success on the coast. This suggests that the variables themselves were probably more intercorrelated on the coast. Table 8 shows the correlation matrices for weather

Table 6. Summary of Discriminant function analyses of meteorological conditions.

Analysis	Canonical correlation	% Cases correct	5 most correlated variables
Sibley Lake: Go vs. NOGO	.526	83	Tail-headwind (THC), 24 hr. THC trend, 12 hr. humidity trend, 24 hr. temperature trend, temperature.
Kent Island: Go vs. NOGO	.589	87	12 hr. humidity trend, relative humidity, 24 hr. THC trend, THC, absolute sidewind.
Sibley Lake GO vs. Kent Island GO	.751	87	6 hr. pressure trend, temperature, 24 hr. temperature trend, 24 hr. THC trend, relative humidity.
Background distributions	.702	79	Relative humidity, temperature, absolute sidewind, visibility, sidewind.

Table 7. Canonical coefficients [a] and correlations [b] of weather variables with the discriminant function: Within location comparisons of GO and NOGO distributions for Sibley Lake and Kent Island.

	Sibley Lake n=36GO, 140NOGO			Kent Island n=26GO, 135NOGO		
Weather variable	coefficient	correlation	p[c]	coefficient	correlation	p
Tail-headwind (THC)	-1.111	-.429	**	-0.201	-.527	**
Sidewind (SWC)	0.289	.080		-0.066	.210	**
Absolute SWC	-0.325	-.167	*	0.324	.375	**
9 hr. THC trend	0.647	.046		0.387	-.066	
9 hr. SWC trend	-0.244	.020		0.244	.089	
24 hr. THC trend	-0.327	-.322	**	-0.548	-.536	**
24 hr. SWC trend	-0.031	.131		-0.017	.294	**
Temperature (TMPR)	-0.335	.202	**	0.010	-.229	**
24 hr. TMPR trend	0.375	.254	**	0.147	-.111	
Relative humidity (RH)	-0.887	-.017		0.127	.581	**
12 RH trend	0.792	.262	**	0.775	.756	**
Opacity	-0.066	-.082		-0.363	.270	**
Visibility	-0.240	-.140		0.004	-.315	**
Precipitation	0.019	-.012		0.043	.197	*
Barometric pressure	-0.158	-.124		-0.203	.008	
6 hr. pressure trend	0.707	.015		0.170	-.278	**

a) Standardized canonical discriminant function coefficient.

b) Pooled within-group correlations between variables and canonical discriminant function.

c) * $p < .05$; ** $p < .01$

Table 8. Correlation matrix for weather variables at Sibley Lake (above diagonal) and Kent Island (below diagonal). Significant Pearson correlations (P ≤ .05) are indicated by an asterix.

	THC	SWC	ABSWC	THC9	SWC9	THC24	SWC24	TMPR	TMPR24	RH	RH12	BP	BP6	PCT	OPAC	VIS
Tail-headwind (THC)				*	*	*		*				*	*			
Sidewind (SWC)	*		*		*		*		*	*				*		
Absolute SWC (ABSWC)	*	*			*		*							*		
9 hr. THC trend (THC9)	*		*			*							*		*	
9 hr. SWC trend (SWC9)	*	*	*	*		*	*									
24 hr. THC trend (THC24)	*		*	*	*								*			
24 hr. SWC trend (SWC24)	*	*	*		*	*			*							
Temperature (TMPR)		*				*			*	*	*	*	*		*	*
24 hr. TMPR trend (TMPR24)			*			*		*		*	*		*	*	*	*
Relative humidity (RH)	*				*			*			*			*	*	*
12 hr. RH trend (RH12)	*				*	*		*	*	*			*	*	*	*
Barometric pressure (BP)				*		*	*	*					*			
6 hr. BP trend (BP6)	*	*	*	*	*	*				*		*				
Precipitation (PCT)	*	*			*		*	*		*	*	*	*		*	*
Opacity (OPAC)	*		*			*		*	*	*	*		*	*		*
Visibility (VIS)	*							*		*	*		*	*	*	

variables within each location. The weather at Kent Island was indeed more intercorrelated. Of 120 possible dyadic comparisons, 69 were significant at Kent Island, while only 47 were so at Sibley Lake. Most of the difference is due to correlations among the wind variables themselves, and to correlations between wind and non-wind variables. Together, 44/83 of the correlations involving wind variables were significant at Kent Island, while only 22/83 were so at Sibley Lake. All variables except temperature and barometric pressure were correlated with the Tail-Headwind Component at Kent Island.

The impression given by the univariate analyses that Kent Island birds responded to a wider range of meteorological variables than the inland population may be due to the greater intercorrelation among weather variables at Kent Island. Birds departed Kent Island in weather that was distinct in more variables from NOGO weather than was the case at Sibley Lake. Factors that were less variable at Kent Island included the strength of sidewind components, which will certainly play an important role in determining the course flown. But multivariate analysis and direct examination of correlation matrices of the weather variables themselves show that response to the Tail-Headwind Component alone could probably produce the departure behavior seen at both sites. This analysis does not support a less variable response to weather conditions on the part of Kent Island birds.

5.3.3.2 GO-GO and Background Comparisons Between Locations

There is no evidence thus far that Kent Island birds were responding more selectively to the existing weather. Sandpipers departed the two sites in similar areas of the synoptic weather map (Figures 30 and 31). Differences in meteorological departure conditions might be expected, however, due to the different en route options available to overland and overwater migrants. Comparisons between GO conditions at the study sites involve relatively small samples (36 departure hours at Sibley Lake, 26 at Kent Island), but are of great interest. Interpretation of any differences found must be made within the context of systematic meteorological differences in the background weather distributions at the two sites.

Table 9 compares the GO conditions at Sibley Lake with those at Kent Island, and also compares the background distributions at the two sites. It is immediately clear that the background distributions differ in more dimensions than do the GO hours. There are nine significant differences in mean values of background variables, but only two among the GOs. The number of significant differences in variances are seven for background and three for GO hours. The smaller number of differences in means and variances indicates that Semipalmated Sandpipers at Sibley Lake and Kent Island selected similar departure weather from dissimilar background weather.

Which variables show between-site differences under GO conditions? Temperature differs in both mean and variance, but it also does so between background distributions. Thus, temperatures differ systematically between sites, and the difference at GO hours may be attributed to this, rather than to differences in response to temperatures by the birds at the two sites. However, three features differed under GO conditions that did not do so in the background distributions. Relative

Table 9. Means and standard deviations of weather variables for GO and for Background hours with univariate comparisons [a] between Sibley Lake (SL) and Kent Island (KI).

	GO hours				Background			
Weather variables	SL n=36	KI n=26	s^2	$\bar{x}$	SL n=150	KI n=144-148[b]	s^2	$\bar{x}$
Tail-headwind (THC)	4.8 ± 4.8	6.6 ± 6.9	-	ns	0.5 ± 7.7	0.4 ± 7.0	ns	ns
Side wind (SWC)	0.8 ± 5.9	2.2 ± 4.4	ns	ns	1.2 ± 4.8	4.6 ± 7.6	***	***
Absolute SWC	4.7 ± 3.5	3.9 ± 2.8	ns	ns	3.9 ± 3.1	7.3 ± 5.1	***	***
9 hr. THC trend	-0.2 ± 6.9	0.6 ± 7.3	ns	ns	0.4 ± 7.1	0.2 ± 6.0	*	ns
9 hr. SWC trend	0.3 ± 6.0	2.1 ± 5.7	ns	ns	0.3 ± 5.1	2.8 ± 6.1	*	***
24 hr. THC trend	4.8 ± 7.5	8.6 ± 8.9	ns	-	-0.1 ±11.2	-0.0 ± 9.9	ns	ns
24 hr. SWC trend	-1.4 ± 8.0	-4.1 ± 7.5	ns	ns	-0.2 ± 6.8	0.0 ± 8.0	-	ns
Temperature (TMPR)	21.1 ± 5.1	18.7 ± 2.5	***	*	22.8 ± 5.8	17.0 ± 4.1	***	***
24 hr. TMPR trend	-1.5 ± 3.7	0.4 ± 4.0	ns	-	0.0 ± 4.2	-0.1 ± 3.2	***	ns
Relative humidity (RH)	48.5 ±16.8	54.9 ±14.9	ns	ns	47.9 ±16.7	74.2 ±19.0	ns	***
12 hr. RH trend	-32.9 ±23.0	-40.0 ±14.7	*	ns	-26.1 ±17.9	-15.9 ±19.0	ns	***
Opacity	5.0 ± 4.1	4.2 ± 2.6	*	ns	4.4 ± 3.9	5.9 ± 3.6	ns	***
Visibility	4.0 ± 0.0	4.0 ± 0.2	ns	ns	4.0 ± 0.2	3.4 ± 1.1	***	***
Precipitation	0.1 ± 0.7	0.0 ± 0.0	ns	ns	0.1 ± 0.6	0.2 ± 0.6	ns	-
Barometric Pressure (BP)	14.0 ± 5.3	15.6 ± 4.4	ns	ns	12.9 ± 6.7	15.7 ± 5.8	ns	***
6 hr. pressure trend	-0.3 ± 2.3	1.0 ± 1.6	ns	*	-0.1 ± 2.5	-0.2 ± 2.5	ns	ns

a) Significance of difference in variances and means are indicated by: ns for $P > .10$; - for $.05 < P < .10$; * for $P < .05$; ** for $P < .01$; *** for $P < .001$.

b) Sample sizes varied slightly due to missing data for particular variables.

humidity trends and opacity were of similar magnitudes, but were significantly less variable during GO hours at Kent Island than at Sibley Lake. The 6-hour pressure trends had different mean values, with the pressure actually dropping, on average, at Sibley Lake. These three differences, although small, might represent real differences in departure weather preferences.

Evidence of differences in meteorological preference would be stronger if the mean or variance of the variable involved were also significantly different between GO and NOGO conditions. Finding a between-site difference in a variable that appears to be involved in discriminating departure from non-departure conditions is more convincing than a difference in a variable that is not involved orginally. Of the three differences identified above, only the mean of the 6-hour pressure trend at Kent Island was of significance in the univariate GO-NOGO analysis (Table 5). Were Kent Island birds responding to pressure trends while Sibley Lake birds were not? The correlation coefficient between THC and 6-hour pressure trend at Kent Island was 0.53, a strong correlation. Thus, the difference in pressure trend may be an indirect result of the correlation between THC and pressure trend at Kent Island, coupled with the lack of such at correlation at Sibley Lake. Strong evidence for the use of pressure as a cue, or of differences in meteorological preferences, is not found in these analyses.

The multivariate analysis achieved better separation in both comparisons between study sites than it did GO-NOGO hours within each site (Table 10). The DFAs accounted for 56% of the GO-GO variance and 49% of the variance between backgrounds. Pressure trend again emerged as a

Table 10. Canonical coefficients [a] and correlations [b] of weather variables with the discriminant function: between location comparisons of GO and of Background distributions.

	GO vs GO			Backgrounds		
Weather variable	SL n=36 coefficient	KI n=26 correlation	p[c]	SL n=150 coefficient	KI n=144 correlation	p
Tail-headwind (THC)	0.212	.156		0.602	-.007	
Sidewind (SWC)	0.108	.130		0.333	.264	**
Absolute SWC	-0.207	-.120		0.311	.347	**
9 hr. THC trend	0.092	.059		-0.228	-.008	
9 hr. SWC trend	0.730	.152		-0.322	.195	**
24 hr. THC trend	0.051	.238	*	-0.145	.000	
24 hr. SWC trend	-0.564	-.176		-0.322	.014	
Temperature (TMPR)	-0.126	-.291	*	-0.006	-.496	**
24 hr. TMPR trend	0.070	.259	*	0.190	-.013	
Relative humidity (RH)	1.310	.203		1.385	.651	**
12 hr. RH trend	-1.095	-.178		-0.447	.242	**
Opacity	-0.183	-.110		-0.309	.172	**
Visibility	-0.130	-.154		-0.007	.346	**
Precipitation	-0.147	-.111		0.001	.090	
Barometric pressure	0.146	.164		0.159	.186	**
6 hr. pressure trend	0.338	.305	*	-0.010	-.006	

a) Standardized canonical discriminant function coefficient.

b) Pooled within-group correlations between variables and canonical discriminant function.

c) * $p < .05$; ** $p < .01$

strong GO-GO discriminator. Temperature, also significant, was also important in the backgrounds, and thus may be discounted. The 24-hour THC and temperature trends, which approached significance in the univariate comparisons (Table 9), were also significantly correlated with the GO-GO, but not the background, DF (Table 10). Twenty-four hour THC trend was a significant uni- and multivariate predictor of departures at both Sibley Lake and Kent Island; the temperature trend was signficant at Kent Island only.

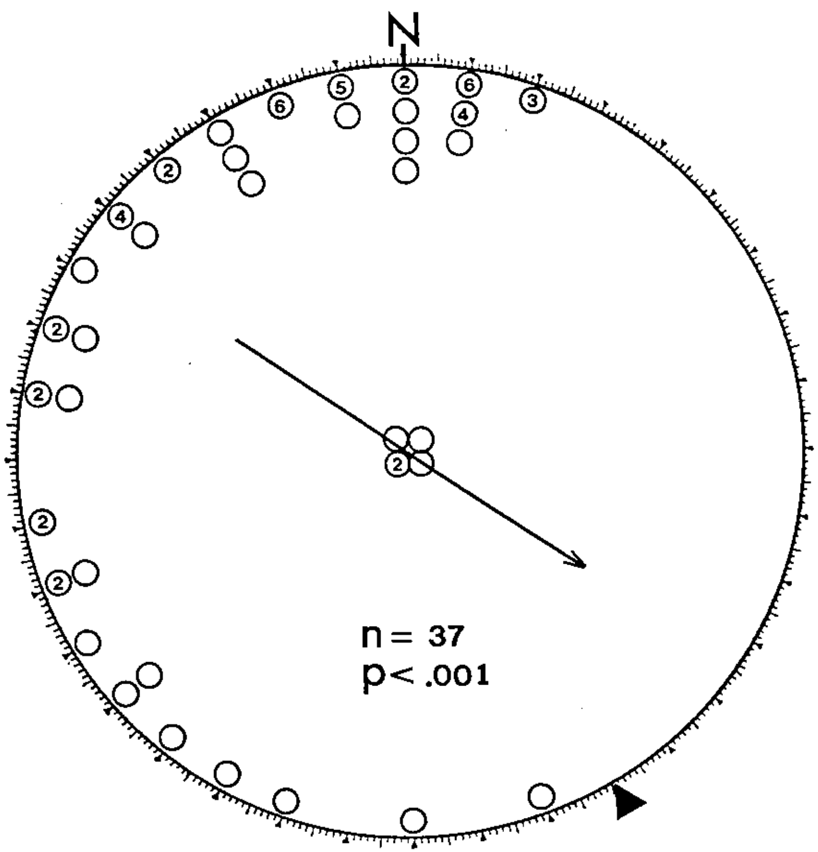
In summary, on the basis of correlation, 24-hour trend in THC emerges as the only variable that 1) is involved at both sites in discriminating GO and NOGO weather, and 2) is not different in the background distributions at the two sites, but 3) is involved in discriminating GO-GO conditions. The mean value of the 24-hour trend in THC at GO hours was 4.8 knots at Sibley Lake and 8.9 knots at Kent Island, although both were quite variable (Table 9). If midwestern and coastal birds differed in departure behavior with regard to meteorological conditions, it was in their response to 24-hour changes in the strength of winds along the NW-SE axis. It took a larger increase to stimulate coastal than inland birds to begin migratory flight. The 24-hour change in THC is, not surprisingly, very closely correlated with the value of THC. The correlation coefficients were 0.71 and 0.70 for Sibley Lake and Kent Island, respectively, the largest and third largest values in the correlation matrices listed in Table 8. The final section of the meteorological analysis takes a closer look at wind directions at departure.

5.3.3.3 **Winds at Departure**

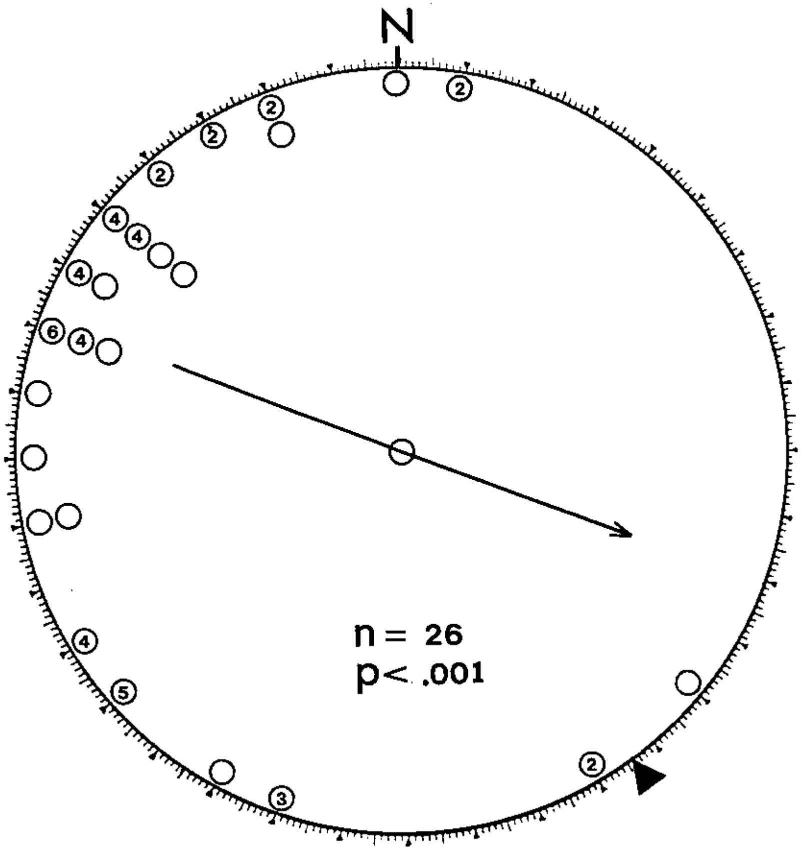
Figure 36 plots the surface wind directions at hours when flocks departed. As was true of departure directions (Section 5.1.2), there was no difference between locations in the mean directions of the surface wind distributions (Watson U^2 test, $p > .05$). There is also no significant difference in the variance of the two distributions, although it is lower at Kent Island (F-test, $p > .05$). No flocks at either site left when winds were blowing from the northeast, east, or southeast. Interestingly, the means of both distributions were rotated about 30° counterclockwise from the mean departure bearings, shown by the black triangles outside the circles (from Figure 22). This is of significance because at north temperate latitudes, winds tend to shift clockwise about 30° and become more parallel to isobars at increased altitudes. Most of this shift occurs within the first 500 meters (Neiburger _et_ _al_., 1971). Thus birds were probably flying more nearly downwind when vanishing bearings were obtained than the plots suggest. This also implies that if they were departing in the migratory direction, which appears to be the case from independent evidence (Section 5.1.2), they left the ground when winds were systematically shifted counterclockwise $25\text{-}35^{\circ}$ from that direction. In short, rather than depart when surface winds are blowing in the migratory direction, selection appears to have favored birds that departed with surface winds slightly to the left (in autumn) of the appropriate flight direction. If shorebirds respond directly to surface wind direction as a stimulus, they apparently compensate for the probable shift in wind direction with altitude.

Figure 36. Wind direction at hours of departure at Sibley Lake and Kent Island. Numbers within circles indicate multiple departures per hour. The length of the mean vector is shown by the length of the arrow from the center of the circle. The triangle on the outside of the circle shows the mean vanishing bearing of flocks. Circles in the center indicate flocks which left calm conditions.

WIND DIRECTION AT DEPARTURE



Sibley Lake



Kent Island

Radar studies have shown overwhelmingly that migrant passerines fly downwind (see Able 1980). This is true despite variations in wind direction from night to night, although the number of birds in the air is greater when winds are in a seasonally appropriate direction (Richardson, 1976a, 1978a, 1982). Some workers (e.g. Gauthreaux and Able, 1970; Able, 1974, 1980) proposed that this correlation reflected a "downwind orientation" mechanism in passerine migrants, which might be used as a primary orientation cue at some locations or under particular environmental conditions (Able, 1978). Others (e.g. Evans, 1966a; Nisbet and Drury, 1967; Alerstam _et al_., 1974; Alerstam, 1978) suggested that variation in the preferred direction of populations taking off on different nights could account for the phenomenon. The observations presented here are relevant to this discussion in showing that an individual species of bird may possess the degree of selectivity postulated by the latter group of researchers.

5.3.3.4 **Summary and Discussion**

The results of the local weather analysis agree with those in the synoptic analysis (Section 5.3.1), and with the findings of Brooks (1965), Woeller (1971), and Richardson (1979), in showing that populations left staging areas under particular weather conditions. In general, birds at both sites selected similar departure weather from background distributions that differed in many variables. In the direct comparison of GO weather at the two locations, only the 6-hour pressure trend differed in mean value between sites. The strengthening and strength of tailwinds (from the northwest) were the most consistent predictors of migration at both study sites.

Brooks (1965:51) concluded that "a clockwise wind shift toward north is the primary or even sole weather stimulus to continuing migration in the Midwest". In the section on synoptic weather (5.3.1.4) I showed that both clockwise and counterclockwise shifts towards northwesterly winds could stimulate departures. While clockwise shifts are more common, it is the strength of the northwesterly wind, rather than the direction of change, that seems to be the operative factor. In Richardson's (1979) study in the Maritimes, the density of nocturnal shorebird migration was related to the Tail-Headwind Component (THC), the 24-hour change in THC, and precipitation (negatively) in univariate analyses, and with THC, Side-Wind Component (SWC), 24-hour change in SWC and the absolute value of SWC, and preciptation in multivariate analysis. Twelve hour humidity trend, which emerged as a good predictor at Kent Island in this study, was not used by Richardson.

Examination of the distribution of surface winds at takeoff showed a systematic 30° counterclockwise shift from the mean departure bearings. This may be adaptive because of systematic clockwise shifts in wind directions that occur with increasing altitude.

Despite the overall similarity in the departure weather at the two sites, it appears to take a stronger 24-hour increase in tailwinds to stimulate departures at Kent Island. This effect was not due to systematic differences in the strength of this variable between sites. This difference is clearly interpreted in terms of stronger selection for more energetically favorable weather prior to transoceanic flight.

5.4 FAT LEVELS AT DEPARTURE

In the descriptions of departure behavior that opened this chapter, I focused on the moment when some individuals took flight while others remained on the ground. Departures occurred only under particular meteorological conditions, but not all birds departed at the same time. Although the amount of fat carried by a bird at initial capture was an extremely weak predictor of its subsequent length of stay (Section 4.3.2), I pointed out that this did not mean that birds departed without regard for their fat content. The analysis below examines the relationship between fat and departures in two steps. First, it establishes that the mean weights of birds caught on days after favorable migratory weather were lower than the day before, whereas they were higher after unfavorable weather. This "weight loss" means that heavy birds left in higher proportions on departure days and/or that lighter birds arrived. Similar comparisons of mean weights of local populations before and after migratory events have been made in other studies (e.g. Helms, 1959; Nisbet *et al*., 1963). The second part of the analysis involved detailed examination of changes in the proportions of the population represented in a series of fat classes before and after departure days. This comparison enabled estimation of the shape of the relationship between fat and migration for different age and location classes in this study.

5.4.1 Changes in Fat with Synoptic Weather

Sections 4.2.2 and 4.2.3 (Figures 17 and 18) showed that large changes in the fat levels of daily cohorts could be related to several days of favorable or unfavorable migratory weather. I now examine fat changes on a day-to-day basis in relation to synoptic weather patterns. Figures 37 and 38 plot changes in the mean fat levels of cohorts of birds captured on two successive days. The symbols are placed at the location representing the weather on the evening of the first day. In general, fat levels decreased following evenings with favorable migratory weather, increased during unfavorable weather, and were intermediate in intermediate conditions. Table 11 summarizes and compares changes in fat levels under favorable and unfavorable weather (synoptic categories 2 and 1, Figure 6, respectively). In general, changes in fat were more positive during unfavorable than favorable weather, but the differences were significant only for juveniles at both locations. Failure to find a difference at Sibley Lake may be a function of the small sample size, but reasonable samples were available at Kent Island. Examination of the data for Kent Island adults (Figure 38) shows that the birds generally did gain weight during unfavorable weather, but a loss of weight during favorable weather was less clear. This suggests that Kent Island adults may have arrived with more fat stores than other groups, a conclusion reached earlier from examination of daily mean weights (Section 4.2.2).

These results may be compared with a methodologically similar analysis of variation in weights of Swainson's Thrushes (*Hylocichla ustulata*) in relation to weather by Mueller and Berger (1966). They found

Figure 37. Change in the mean fat of samples of birds caught on consecutive days at Sibley Lake, plotted at the location of the weather on the evening of the first day.

Change in mean fat (g.)

● = -2 or less

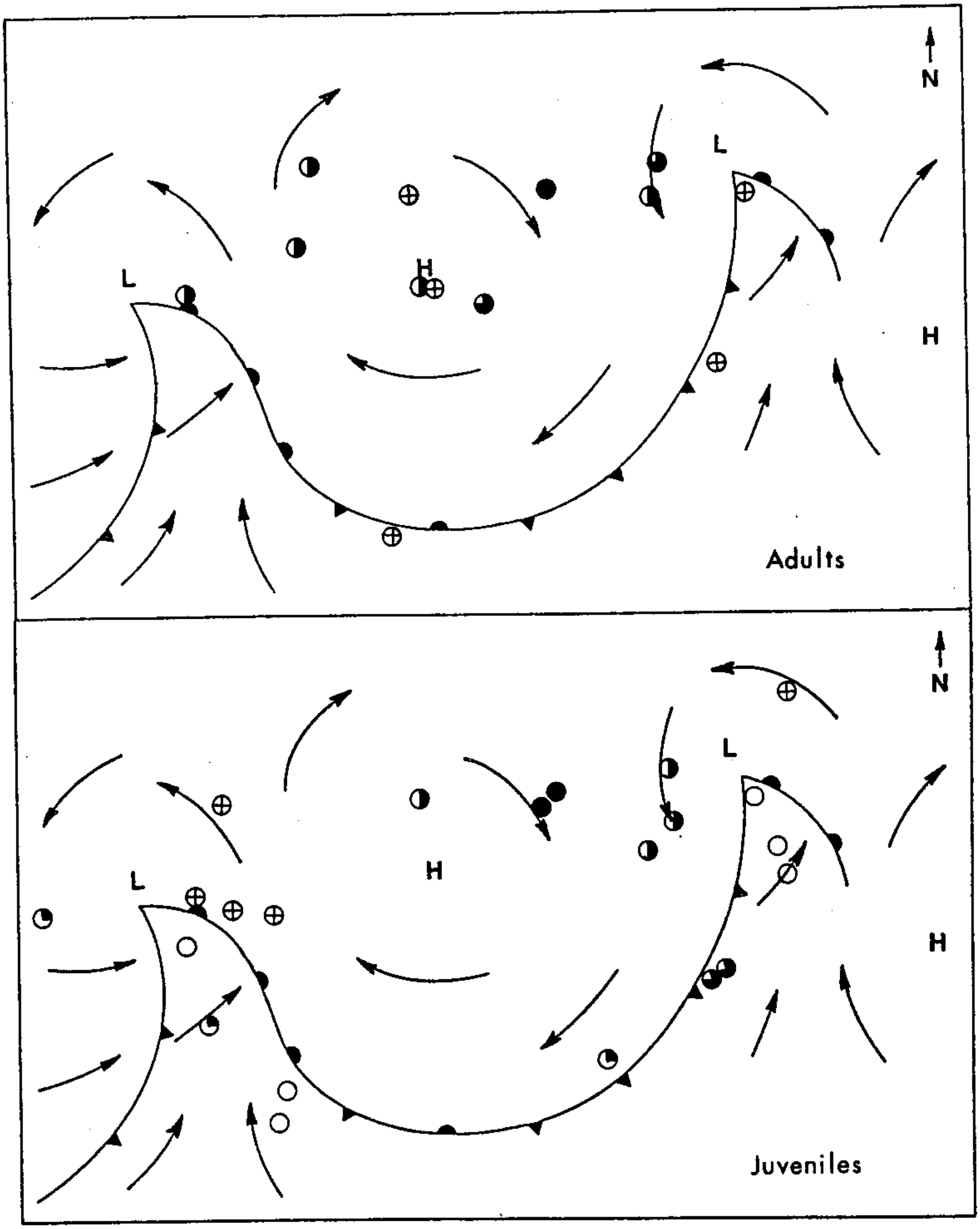
◕ = -2 to -1

◑ = -1 to 0

◔ = 0 to +1

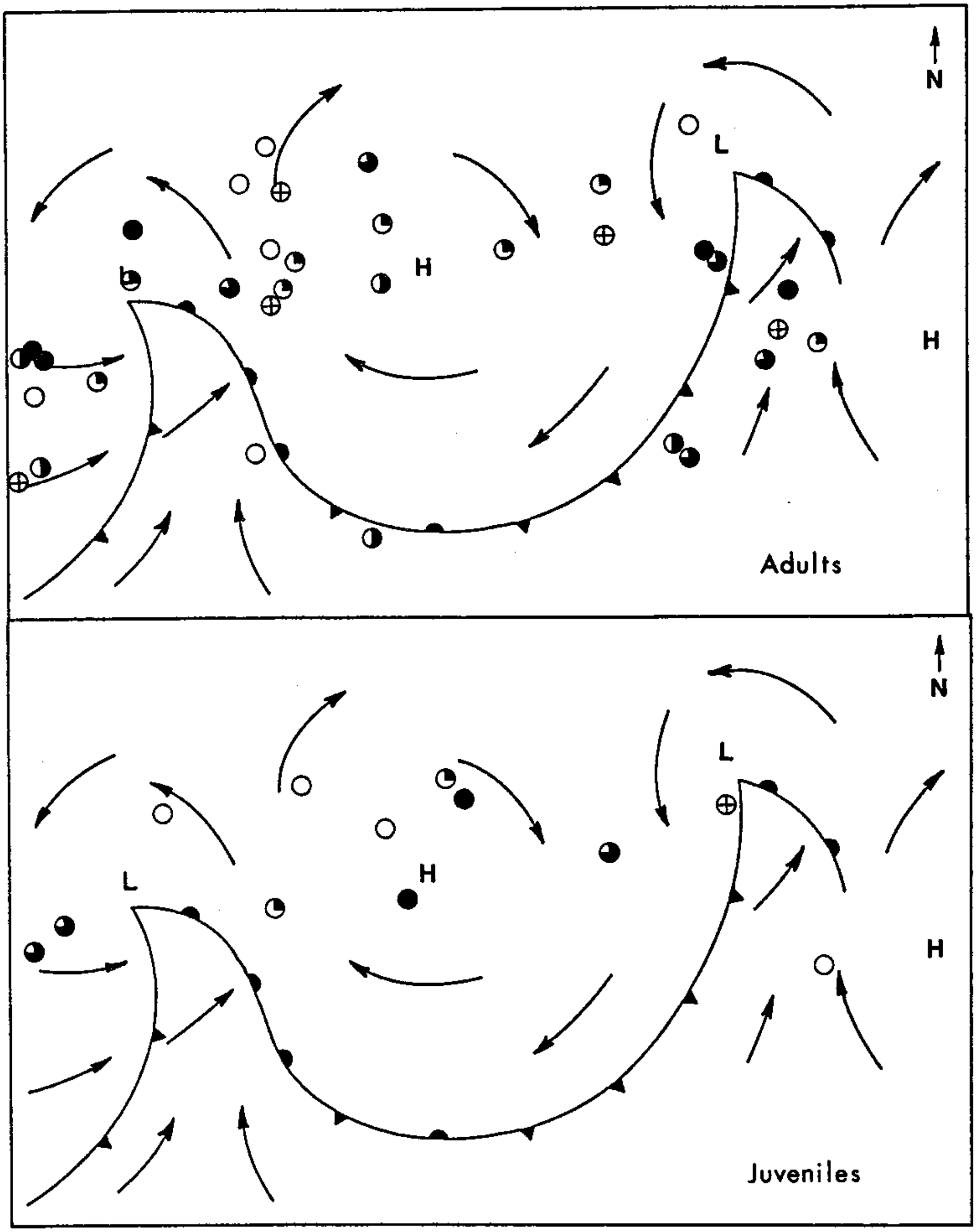
⊕ = +1 to +2

○ = more than +2



SIBLEY LAKE

Figure 38. Change in the mean fat of samples of birds caught on consecutive days at Kent Island, plotted at the location of the weather on the evening of the first day. For Key see Figure 37.



KENT ISLAND

Table 11. Day-to-day changes in mean fat levels following favorable and unfavorable synoptic weather.

	Favorable weather		Unfavorable weather		Wilcoxin rank-sums test	
	n	$\bar{x}$ change in fat (g.)	n	$\bar{x}$ change in fat (g.)	s	p
Sibley Lake						
Adults	4	-1.1	4	-0.4	19.0	ns
Juveniles	7	-0.7	11	1.8	28.0	$< .001$
Kent Island						
Adults	8	-0.7	16	0.8	82.0	ns
Juveniles	5	-1.5	4	1.9	29.0	$< .05$

that unfavorable fall migration weather (southerly winds, low pressure) was followed by catches of heavier birds, while favorable weather (following frontal passage, northerly winds) was followed by captures of significantly lighter birds. Mueller and Berger suggested that the increases in fat following poor weather were due to early landings by birds upon encountering poor flight conditions. This is probably not the case for the sandpipers in this study. Few thrushes stayed in Mueller and Berger's study area for periods longer than a week. The mean weights and variances of their birds suggest that thrushes migrate in a series of comparatively short flights. Cochran (1972) reports following radio-tagged migrant Swainson's Thrushes in Illinois for flights ranging up to 600 km. In contrast, the sandpipers in this study remained at staging areas much longer, and were preparing for flights up to five times as long as were the thrushes. I attribute the weight gains on poor nights to fattening by a static population, rather than to an influx of birds that aborted flights upon hitting poor weather. This difference in interpretation ties in with the previous discussion of differences in the flight strategies of shorebirds and passerines (Section 5.3.1.5).

The turnover of birds with favorable weather lowers the mean fat value of the population on the ground the next day. These data may also be used to examine whether this effect is likely caused by arrival of light birds or the departure of heavy ones, or a combination of the two. This question is examined in the next section.

5.4.2 Levels of Fat at Takeoff

The fat levels of birds captured before and after migration dates may be used to determine the relationship between fat levels and the probability of migration. One strength of this analysis is that it utilizes only information from birds that had not previously been captured. Thus post-handling effects are not a problem. As a control for the methodology used, I performed the analysis on dates when migration was, and was not, thought to occur. In the latter cases, changes in the weight distribution should only reflect the daily fattening rate of a stable population (Section 4.2.3).

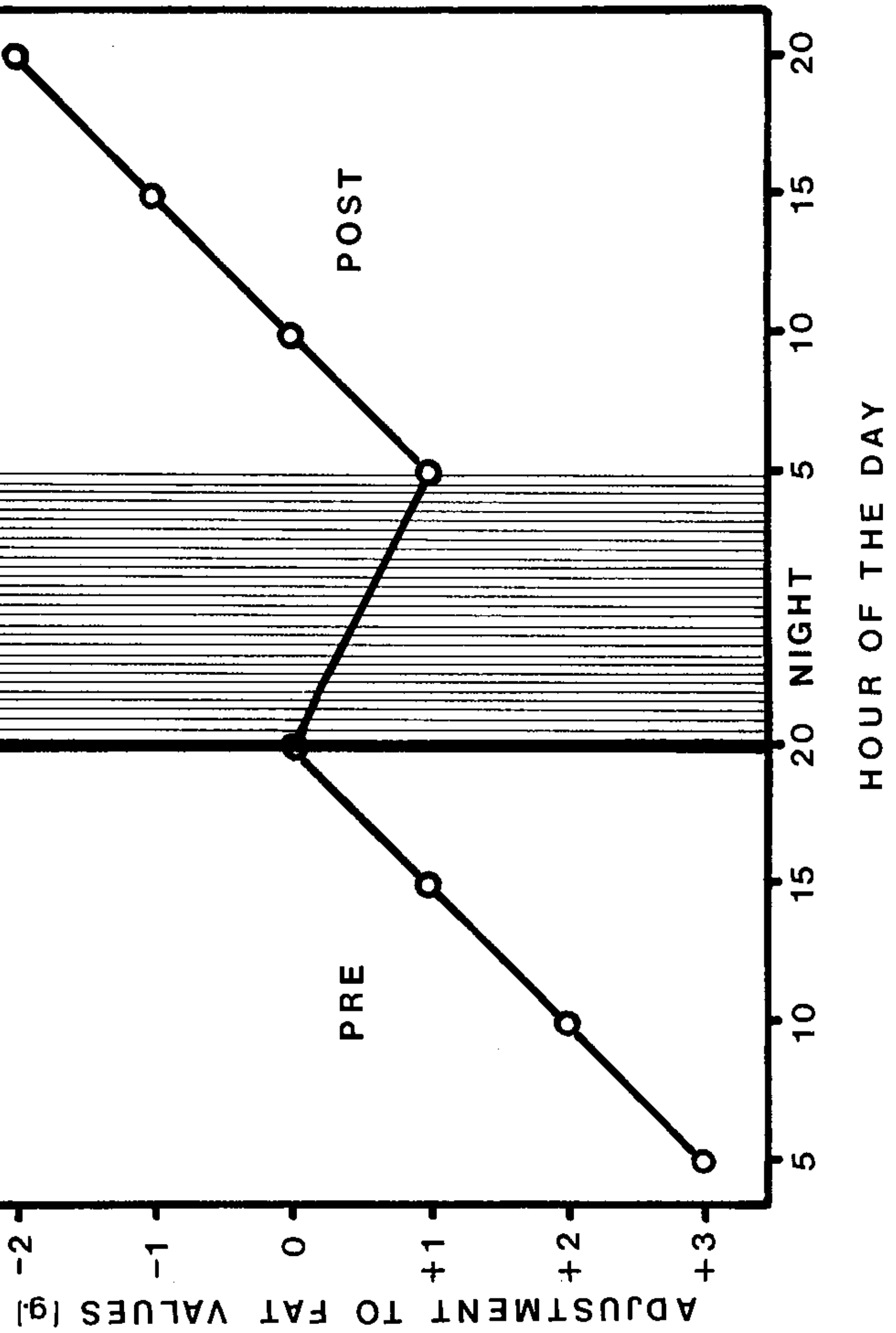
5.4.2.1 Methods

The first step in the analysis was to identify migratory ("GO") and non-migratory ("NOGO") dates. A date was classified as GO if it met one of the following criteria: 1) flocks were seen departing on that date, or 2) its weather path plotted on the synoptic map was entirely within category 2 (Figure 6), or 3) it had an emigration rate, calculated for both juveniles and adults, of 0.15 or more. A day was classified as NOGO if no flocks were seen leaving on that date and it met either of the following criteria: 1) its weather path plotted on the synoptic weather map was entirely within category 1, or 2) it had an emigration rate, calculated for both juveniles and adults, below 0.05. Emigration rates calculated for Sibley Lake during the week that Alkali dried up were not considered when classifying dates.

Having identified GO and NOGO dates, I tabulated the numbers of birds weighed on those dates (PRE) and on the following dates (POST). I combined the data from all GO (or NOGO) dates into single PRE and POST samples for each age/location class. Since there were strong seasonal trends in fat levels (Section 4.2.2), it was also necessary to have reasonably equal-sized PRE and POST samples from each pair of dates. The potential bias introduced when combining data from pairs of dates with different mean fat levels should be clear from an example. Suppose that early in the season, when birds were generally light, a sample date had 50 PRE and 20 POST observations. When combined with samples from latter dates, the resulting PRE distribution would be biased towards light birds. To minimize this bias, I systematically eliminated every 2nd, 3rd, 4th or 5th data point from the larger data set of each pair of days. This resulted in PRE and POST data sets no more than 20% different in size. Data were eliminated systematically rather than randomly to preserve as much as possible the shape of the distributions. Table 12 shows the number of dates and birds included in the analysis for each age/location class.

The object of this analysis was to determine how fat affected the behavior of birds at the "moment of decision" with regard to migratory departure. Since most departures occurred in the evening (Section 5.2.2), the desired comparison was of the weights of birds that did and did not depart <u>at that time</u>. Using the model of daily weight changes presented in Figure 39, I estimated what the fat level of individuals in both the PRE and POST samples would have been at sunset of the PRE date. The differences between PRE and POST distributions were thereby attributable to the effects of immigration and emigration. Fat levels for both the GO and NOGO analyses were adjusted with this model.

Figure 39. Model of daily changes in fat levels. The thick diagonal line shows the hypothesized changes in a bird's fat level during a two-day period. Birds are assumed to be gaining 1 g./5 hours during the day, and losing 1 g. during the night. These rates of fat deposition and loss were used to estimate what the fat levels of birds caught at different times on PRE and POST days would have been at sunset of the PRE day (heavy vertical line). All data were adjusted by using the adjustment value (-2 to +3) shown for the hour nearest to the time of capture of the bird.


ADJUSTMENT TO FAT VALUES (g.)
-2
-1
0
+1
+2
+3
PRE
POST
NIGHT
5
10
15
20
5
10
15
20
HOUR OF THE DAY

All edited and adjusted data were tabulated and placed into 2-gram fat classes (-1 g., -0.9 to 1.0, 1.1 to 2.9, 3.0 to 4.9, etc.). A contingency table was constructed for each age/location class under GO and NOGO conditions, with PRE and POST in columns, and fat classes as rows. A chi-square test was used to look for differences in the fat distributions of the PRE and POST samples.

This analysis is sensitive to the net changes between PRE and POST dates. A lack of difference indicates either stable populations that had an increase of one fat class per day (as per model, see Figure 39), or balanced immigration and emigration that produced a similar effect. Any changes detected also reflect the sum total of immigration and emigration, and thus cannot be directly interpreted as being due to birds either arriving or departing.

To facilitate visualization of the relationship between fat levels and migration, the data were treated in two ways. First, histograms of the PRE and POST distributions are presented for direct comparison, and second, a "migration index" was calculated for each fat class. The index reflected the proportion of each fat class that departed (or arrived) and was calculated as:

$$(\text{pre}_i - \text{post}_i) \ / \ \text{pre}_i$$

where pre_i and post_i represented the proportions of the PRE and POST distributions in fat class i. The migration index thus varied from 1, indicating that birds in that fat class were only present before migration (if $\text{POST}_i = 0$, the formula is $\text{PRE}_i/\text{PRE}_i = 1$), to "negative infinity" for fat classes where birds were present only after migration (since division by zero is not defined).

5.4.2.2 Results

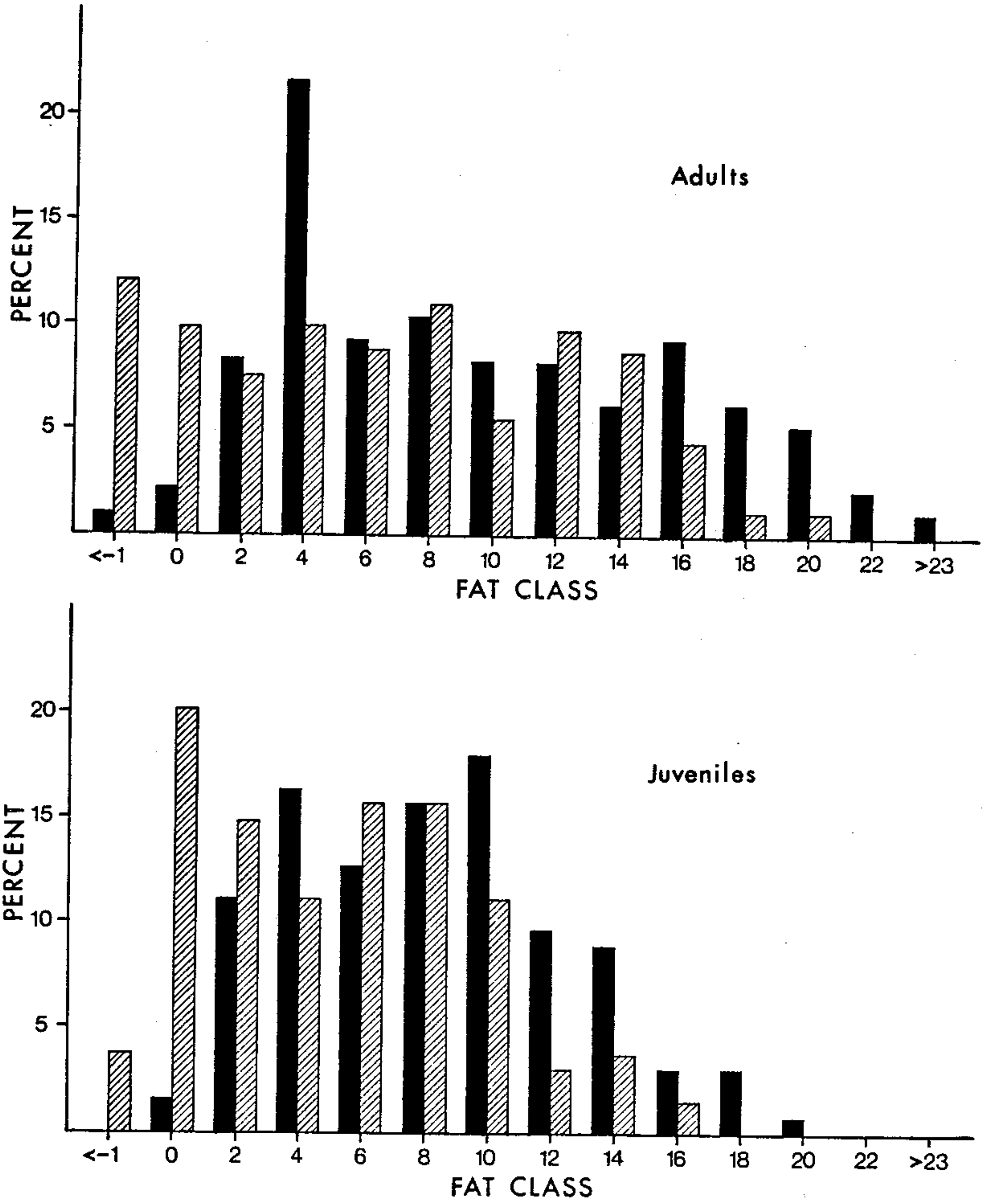
The results of the chi-square tests comparing PRE and POST fat distributions are shown in Table 12. None of the four NOGO analyses showed significant differences, which is the expected result if the populations were stable and the time of day adjustment of fat produced no artifacts. Balanced immigration and emigration, while also consistent with this outcome, seems improbable on a large scale. This result also implies that birds that may have been physiologically ready to migrate did not do so, since no significant changes occurred. On the other hand, all four of the comparisons on GO days showed significant differences between PRE and POST fat class distributions, reflecting the effects of migration. Further analyses will examine only data from GO days.

Histograms of the proportions of birds in each fat class in the PRE and POST distributions on GO days are presented in Figures 40 and 41 for adults and juveniles at Sibley Lake and Kent Island. In all cases, there were both more very fat birds and fewer very lean birds before migration. Since the analysis involves proportions of the distribution in each fat class, an increase in the proportion of one class necessarily means a decrease in others. However, the differences in the distributions cannot be accounted for simply by an influx of very light (4 g.) birds. In that case, uniform (or random) decreases in the proportions at other levels would be expected, rather than the large differences seen at the extremes of both of the distributions. Following similar logic, the patterns do not simply reflect the departure of heavy birds. The tail with the smallest difference between PRE

Table 12. Fat vs. the probability of departure analysis for GO and NOGO pairs of days.

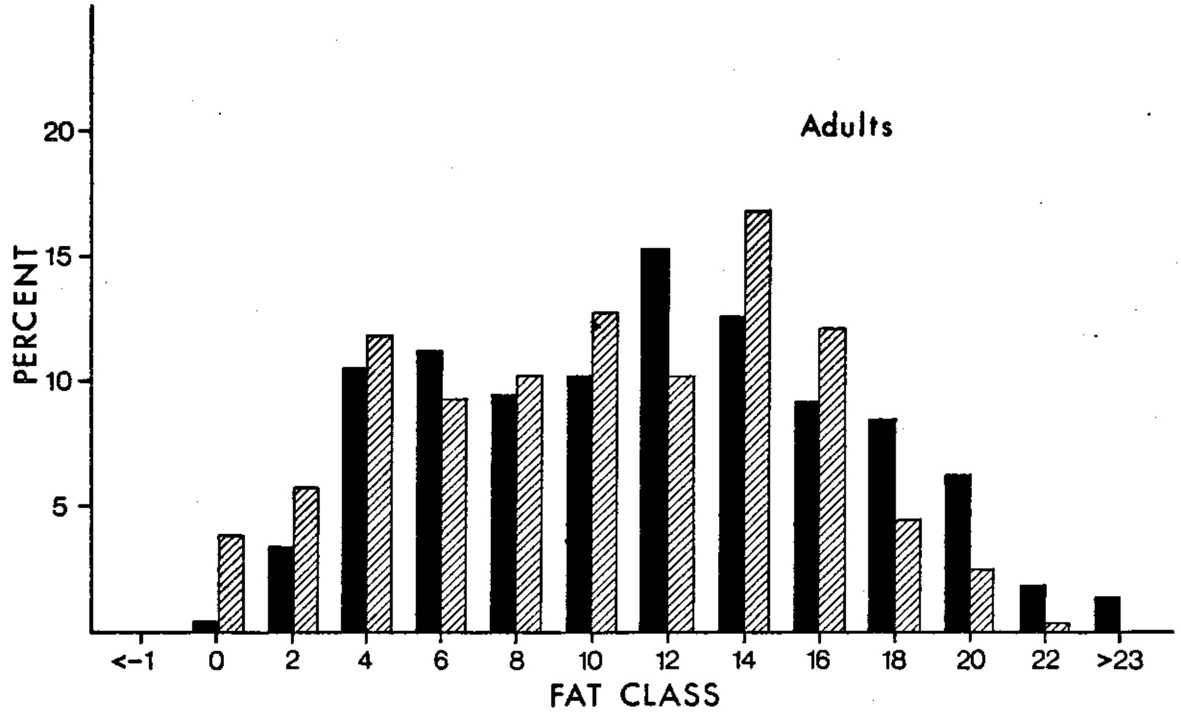
Comparison	N days	N birds	X^2	df	P
NOGOs:					
Sibley Lake					
adults	5	195	16.1	12	>.05
juveniles	13	482	8.9	11	>.05
Kent Island					
adults	13	445	19.2	12	>.05
juveniles	13	126	8.3	8	>.05
GOs:					
Sibley Lake					
adults	6	187	32.4	13	<.005
juveniles	6	270	44.4	11	<.005
Kent Island					
adults	11	608	33.9	12	<.005
juveniles	6	163	20.2	8	<.01

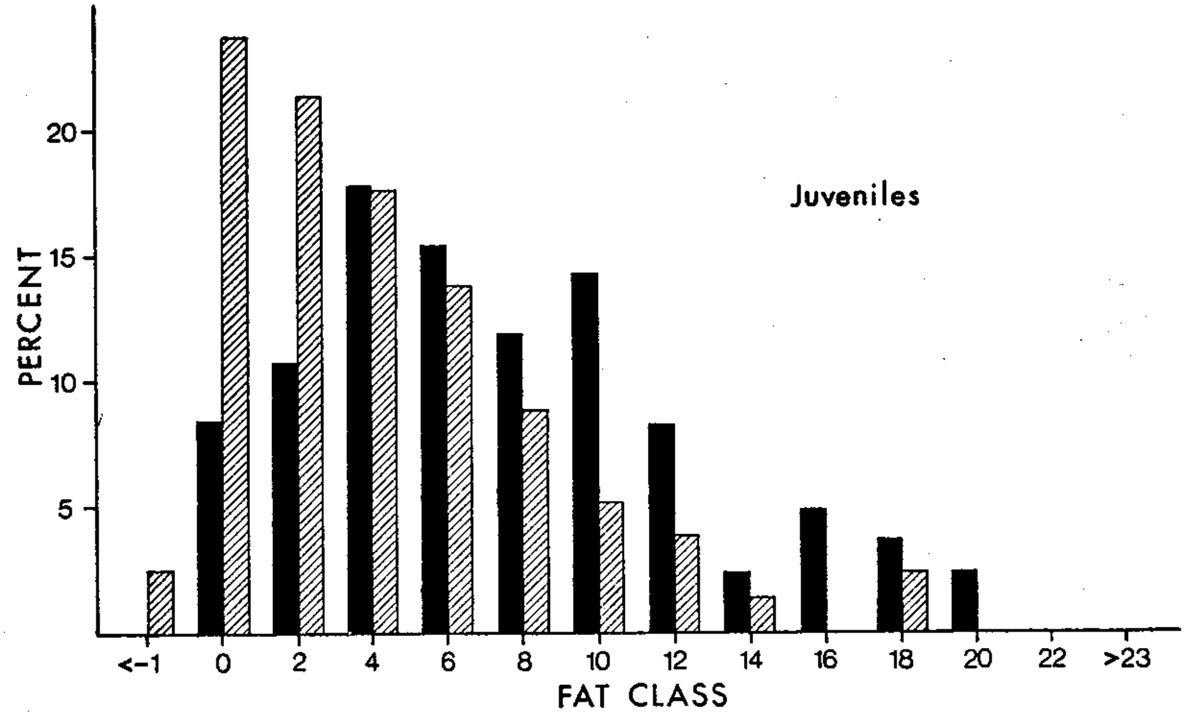
Figure 40. The proportion of birds in each fat class for PRE and POST days at Sibley Lake. Solid bars represent the frequency distributions of PRE days; shaded bars represent the POST distributions.


Adults
PERCENT
5
10
15
20
<−1
0
2
4
6
8
10
12
14
16
18
20
22
>23
FAT CLASS
Juveniles
PERCENT
5
10
15
20
<−1
0
2
4
6
8
10
12
14
16
18
20
22
>23
FAT CLASS

SIBLEY LAKE

Figure 41. The proportion of birds in each fat class for PRE and POST days at Kent Island. Solid bars represent the frequency distributions of PRE days; shaded bars represent the POST distributions.


Adults
PERCENT
20
15
10
5
<-1
0
2
4
6
8
10
12
14
16
18
20
22
>23
FAT CLASS


Juveniles
PERCENT
20
15
10
5
<-1
0
2
4
6
8
10
12
14
16
18
20
22
>23
FAT CLASS

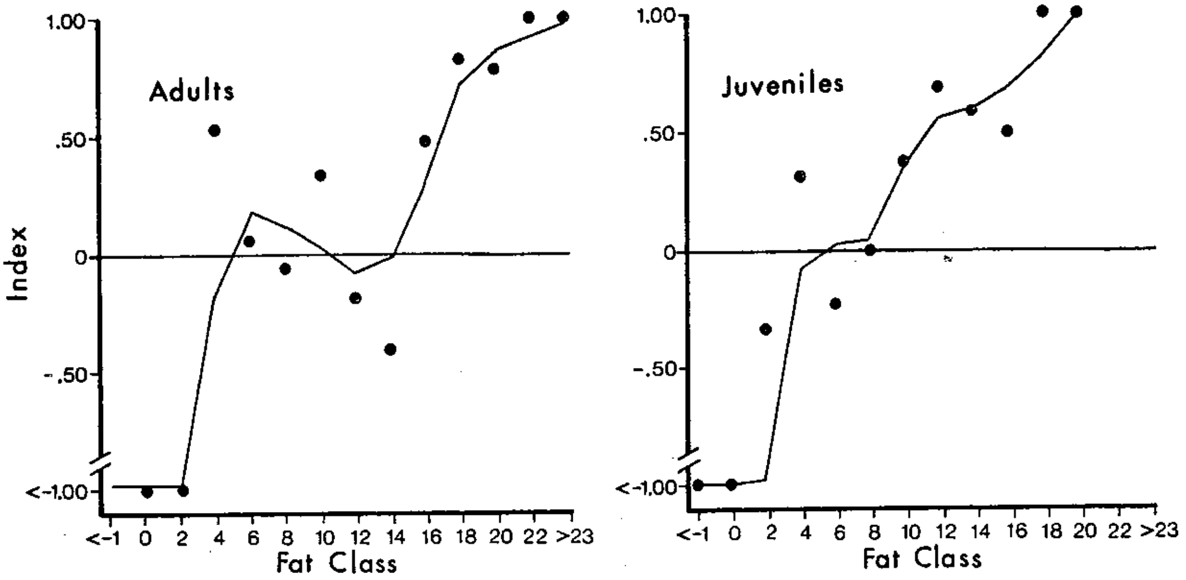
KENT ISLAND

and POST distributions is the light end of the Kent Island adults. This implies, as was concluded earlier, that adults arrived at Kent Island with some fat stores (Section 4.2.2).

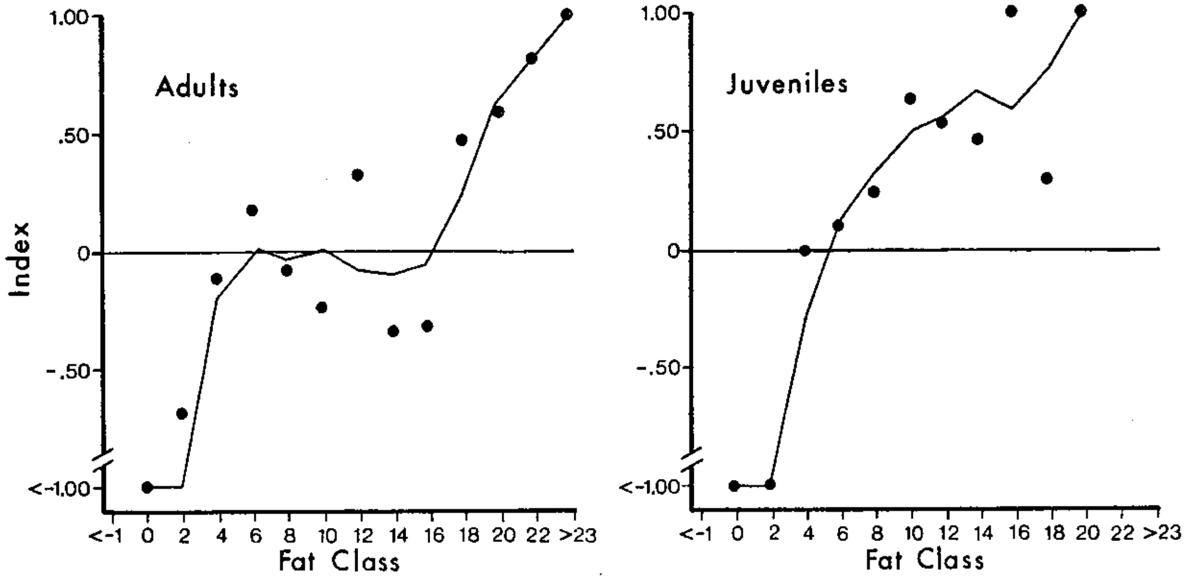
The changes in proportions of each fat class are visualized through plots of the migration indix (Figure 42, see Section 5.4.2.1). Dots indicate the value of the migration index for each fat class, and the lines are averaged values of three classes, except on the ends, where they go to the terminal points. An influx of light birds is visible in all four cases, indicated by the strongly negative values, and all higher values are strongly positive, indicating emigration.

I have established that net changes in fat distributions occurred with migration. To proceed to an estimation of how fat affects the probability of initiation or termination of migratory flight is not possible without knowledge of the magnitude of immigration or emigration. At the extremes, where all birds departed or birds appeared where there were none previously (migration indicies of 1 or "minus infinity", respectively), the effect of fat level was unambiguous. Under favorable weather conditions, for example, nearly all birds carrying 22 or more g. of fat departed at both locations. Similarly, extremely light birds at both locations were obviously new immmigrants. The situation at intermediate points is less clear. Figure 42 shows some sort of ordered relationship, albeit a noisy one, at intermediate levels. Two interrelated questions arise from this data. First, what was the relationship between amount of fat and the probability of migration in individual birds? Is there a linear relationship, or is it more of a threshold phenomen? Second, were there differences in the variability of responses among the four age/location classes?

Figure 42. Migration index versus fat class for Sibley Lake and Kent Island adults and juveniles.



SIBLEY LAKE



KENT ISLAND

To go from net population changes to behavioral statements in the absence of immigration or emigration data requires assumptions. I will assume that no bird arrived carrying more than nine g. of fat, or that no bird departed carrying less than nine g. of fat. If no bird arrived carrying more than nine g. of fat, then changes in the fat distribution for birds <u>above</u> that level would be due to emigration alone. Similarly, if no bird departed with less than nine g. of fat, changes <u>below</u> that level would be due to immigration alone. Given these assumptions, I can estimate relative rates of arrival in fat classes up to eight g., and relative departure rates for classes ten g. or higher. I calculated the proportion that each fat class represented in the truncated PRE and POST samples (excluding either birds above or below nine g.), and calculated separate immigration and emigration indices on the lighter and heavier weights, respectively. The immigration index was calculated as:

$$(\text{post}_i - \text{pre}_i / \text{post}_i)$$

with terms defined as before, and thus was positive if birds arrived. A value of 1 indicates that birds were present in that fat class only after migration. The emigration index was calculated in the same manner as the migration index in Section 5.4.2.1.

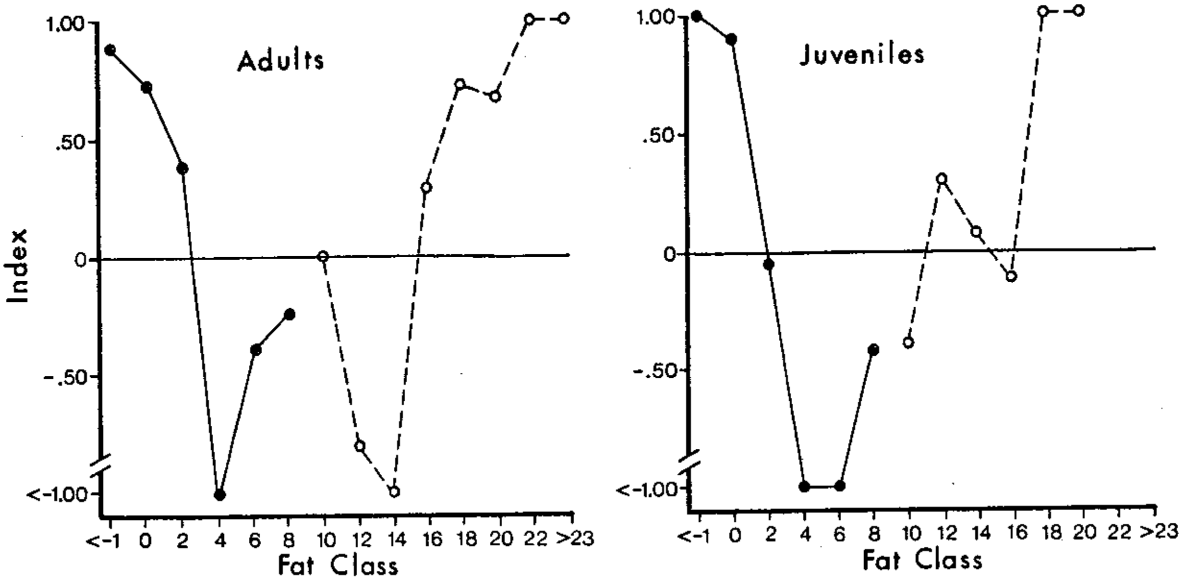
These indices have a different interpretation than in the previous analysis. The migration index showed net changes in the balance of immigration and The immigration and emigration indices refer to the relative probabilities of arrival or departure among the fat classes considered. If birds arrived in all of the lower classes, some would still show "negative arrival rates", meaning that relatively fewer birds arrived in those classes. The shapes, rather than the magnitudes, can be meaningfully interpreted, thus no smoothed 3-point averages are presented, as was done earlier.

Figure 43 plots the immigration and emigration indices for all four age/location classes. The immigration indices show that in all four cases very light birds (fat class 0 or less) arrived in far greater proportions than mid-range birds. The shapes of the curves show that among adults, incoming birds were more different from residents at Sibley Lake than at Kent Island (the points were farther from the zero line). This reinforces the conclusions made in section 4.2.2., that birds arrived at Sibley Lake with little fat stores, while adults arrived at Kent Island with some fat remaining. Juveniles at both locations appear to have arrived light, as concluded earlier.

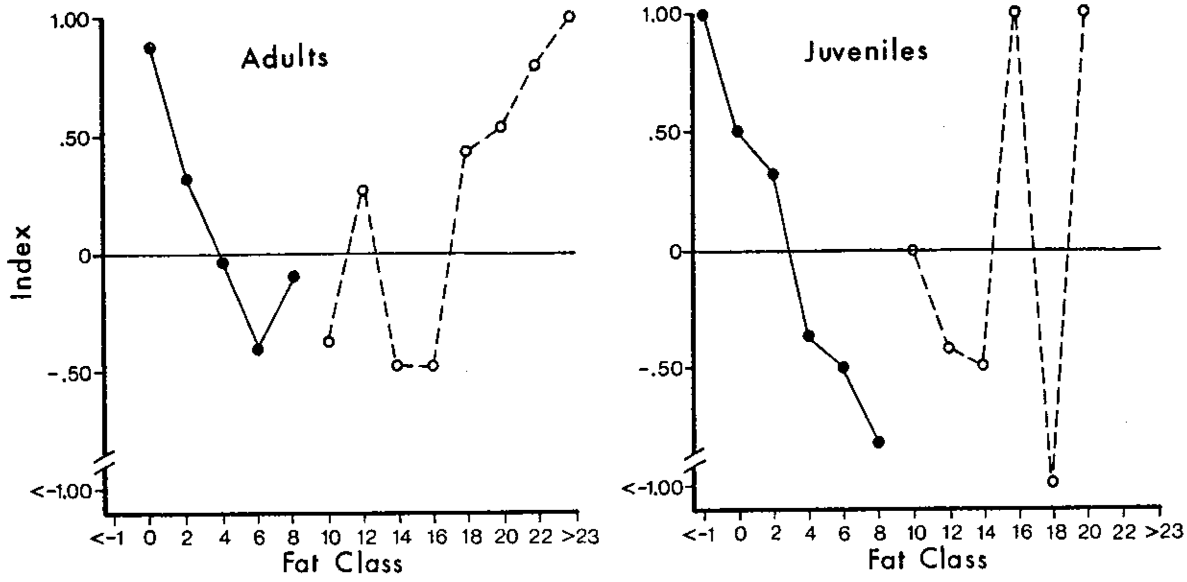
The emigration curves in Figure 43 show that a large change in the behavior of adult birds occurs between fat classes 14-18 at Sibley Lake, and classes 16-18 at Kent Island. These fat levels might be "departure thresholds" at the two sites, with smaller increases in responsiveness at higher levels, producing a flatter curve. I looked for evidence of changes in behavior at 15 and at 17 g. by comparing the PRE and POST distributions of birds above and below these two points. To look for a 15 g. threshold, I compared the PRE and POST frequencies of birds in fat classes 10-14 with those of birds in classes 16-20. Fat classes 12-16 and 18-22 comprised the lighter and heavier groups for testing for a threshold at 17.

For Sibley Lake adults, both thresholds resulted in significant differences beteen heavier and lighter birds ($\chi^2 = 4.94$, $p=.03$ for break at 15; $\chi^2 = 5.56$, $p=.02$ for break at 17). For Kent Island

Figure 43. Immigration and emigration indices versus fat class for Sibley Lake and Kent Island adults and juveniles.



SIBLEY LAKE



KENT ISLAND

adults, however, only the comparison of birds above and below 17 was significant ($\chi^2 = 1.46$, ns for break at 15; $\chi^2 = 9.26$, $p<.01$ for break at 17). The juveniles have more erratic curves. Neither group showed significant differences with a break at 15, and there was insufficient data to test for a break at 17 (see Figures 40 and 41, and Table 12).

5.4.3 Discussion

The finding that none of the NOGO days showed significant changes in fat distributions shows that the methodology used was reasonably sound. It also implies that birds that would migrate if the weather were favorable will not do so when the weather is not. In this species, motivational factors related to fattening are apparently not sufficient to produce migratory flights.

The results from GO days clearly show that fatter birds left at higher rates than less fat birds, and that many birds ended migratory flights in very lean condition, except for adults arriving at Kent Island. Several aspects of fat levels have been discussed earlier (Sections 4.2- 4.4), and this discussion will focus on interpreting the analysis presented here.

Suppose that each bird has a particular, discrete threshold level of fat at which it will depart. Under this assumption, the emigration indices plot the distributions of these thresholds in the four age/location classes. If the emigration curve were a straight line, it would indicate an even distribution of thresholds (e.g. some birds with thresholds from 10-23 g.). If it were steeply sigmoidal, or a step function, it would indicate a skewed distribution of thresholds (e.g. only 18-23 g., for example). Figure 43 shows that the four age classes did show different responses, as populations, to fat levels of nine g. or more. The curves for young birds are more linear, showing a relatively even distribution of threshold fat levels for migration. The adult bird class at Sibley Lake showed a wider range of thresholds, with large changes from 14-18 g., while Kent Island adults show dramatic changes at 16-18 g.

These results indicate greater variability in fat levels at departure in juveniles than adults, and in adults at Sibley Lake than those at Kent Island. The juvenile-adult differences might be reflections of ontogenetic changes, or might reflect the action of selection against birds with lower thresholds. Similarly, the higher, and less variable, thresholds of departure in coastal birds may be interpreted with regard to the demands of their overwater flightpath.

The class differences in variability of fat levels at departure do not depend on the existence of sharp thresholds in individual birds. If changes in fat produce more gradual changes in the probability of migration in individuals, then the slopes of the population emigration curves still reflect the average change in behavior at given fat levels. Steeper slopes show more agreement about departure fat levels within a class than shallower slopes. Behaviorally, the coastal individuals would have a more threshold-like relationship than the inland birds, and adults more of a threshold than juveniles.

There are few published data with which these results may be compared. Nisbet _et_ _al_. (1963) present a table showing the fat distributions of Blackpoll Warblers (Dendroica striata) caught on five successive days during fall migration in Massachusetts. In that study, 30 September was a GO day, and I calculated the migration indices for different fat classes using the data on weights from 30 September to 1 October. There was a steep jump in the migration index value between fat classes 11 and 13, suggesting a rather steep threshold. Blackpoll Warblers are believed to be one of the few passerine species to make an transoceanic flight similar to that of shorebirds (Drury and Keith, 1962; Nisbet, 1970; Wingate, 1973 McClintock et al., 1978; but see Murray, 1965, 1966a). It would be interesting to analyze comparable data from warbler species facing potentially shorter flights, and a great deal of such data might be available from banding stations.

Chapter VI

DISCUSSION

The final discussion is divided into three parts. First, I review the overall staging and takeoff behavior of Semipalmated Sandpipers, and compare it with general models of migratory behavior in birds. Second, I compare the behavior of inland and coastal migrant population relative to their specific flightpaths and environmental variables, and contrast their behavior with other populations of Semipalmated Sandpipers, and with the migratory behavior of the congeneric Dunlin, *Calidris alpina*. Finally, I discuss the implications of this study with regard to the evolution of the overwater migration route used by eastern migrants.

6.1 CONTROL OF MIGRATORY BEHAVIOR

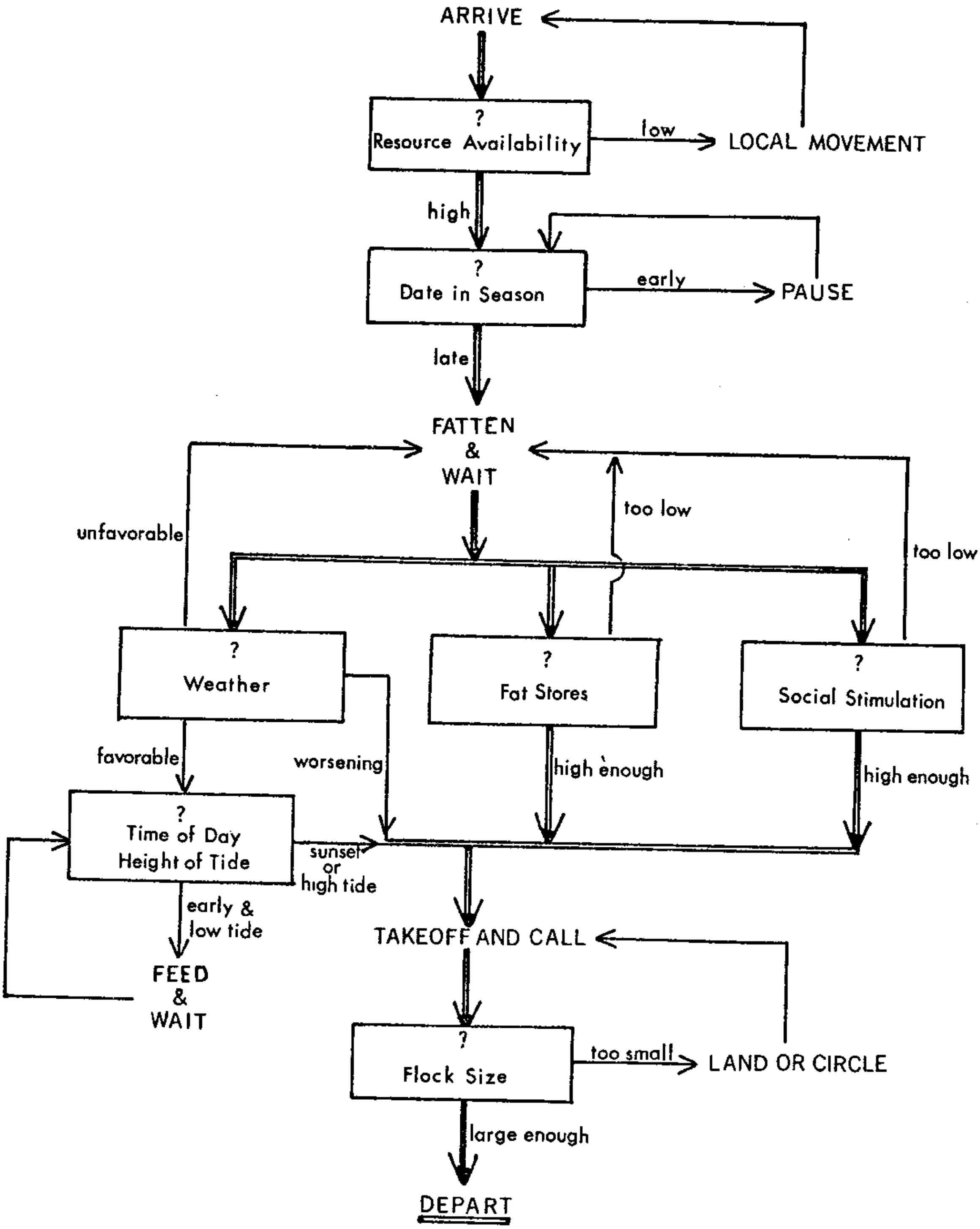
This section compares the migratory behavior of *C. pusilla* with general models of the control of migratory behavior in birds. The differences between inland and coastal populations, which are minor relative to the between-species comparisons made here, are considered in the next section.

6.1.1 Staging and Takeoff Behavior of Semipalmated Sandpipers

A flow diagram of the staging and departure behavior of Semipalmated Sandpipers is presented in Figure 44. Examination of the diagram provides a quick review of the general migratory behavior of Semipalmated Sandpipers. Behavioral states or events are in large capital letters. Variables on which behavior is contingent are in boxes, with question marks. The arrows leading out of the boxes are labeled with the state of those variables that will lead to changes in behavior and/or to other contingencies. Double arrows indicate evaluations and states of variables that are considered necessary and sufficient to cause changes in behavioral states. Thus, successful migrants must follow all double arrows. Figure 44 is basically digital (e.g. it is "early" or "late" in the season), although intermediate conditions do occur. The diagram is not concerned with the specific level at which a particular assessment of migratory conditions will be made (e.g. what date is "early" or "late"), but concentrates instead on how variables affect migratory behavior. The diagram also does not address many of the potential interactions among variables. The evaluation of weather, for example, might be affected by date in the season, the amount of fat carried, and/or the degree of social stimulation. Since I could not quantify these interactions, they are not shown.

Arrival and Local Movement: Examination of Figure 44 begins at the top of the diagram, with a bird's arrival at the study site following a migratory flight. Birds arrive with little stored fat (Sections 4.2.2 and 5.4.2.2). To be successful, a sandpiper must at some point find an area where it can accumulate sufficient resources to fuel a long flight.

Figure 44. The migratory staging and departure behavior of Semipalmated Sandpipers: a graphical model. Behavior patterns are written in capital letters. Variables on which behavior is contingent are in boxes with question marks. Arrows leading from boxes are labeled with states of the variables which lead to changes in behavior or other contingencies. Double lines indicate pathways which must be followed prior to departure. Where double lines run parallel, all conditions at the same level must be satisfied to move further down the model.


ARRIVE
? Resource Availability
low
LOCAL MOVEMENT
high
? Date in Season
early
PAUSE
late
FATTEN & WAIT
unfavorable
too low
too low
? Weather
? Fat Stores
? Social Stimulation
favorable
worsening
high enough
high enough
? Time of Day Height of Tide
sunset or high tide
early & low tide
FEED & WAIT
TAKEOFF AND CALL
? Flock Size
too small
LAND OR CIRCLE
large enough
DEPART

Upon arrival in a new area, the bird may settle as a resident, or may make local movements in search of less crowded areas. I have diagrammed local movement as contingent upon resource availability. At Kent Island, transience rates increased at high population levels, suggesting that intraspecific competition for resouces was one reason for making a local movement (Section 4.1.4). Thus, the behavior of conspecifics, as well as prey densities and distributions, will influence resource availability. If a bird continues moving, it will "Arrive" at a new site and be in a similar position to a bird at the end of a migratory flight.

Pause: Once a bird enters the local population, it might stay at the area for two weeks or longer. The length of time that birds remained at the study sites became shorter during the course of the migratory season, averaging over 20 days in early July, but only about ten days by mid-September (Section 4.3.2). I have diagrammed this effect by putting a "Pause" in the diagram, which is taken early, but not late, in the season. Early birds remained much longer than necessary for simple fattening, so I have shown this "Pause" as a separate behavioral state from "Fatten and Wait". The length of the pause may be controlled by internal circannual rhythms and/or be under photoperiodic control. I can only speculate on the adaptive significance, if any, of the pause (Section 4.4).

Fatten and Wait: If it is "late" in the season, relative to an individual's annual clock, the bird will put on fat stores and wait for appropriate departure conditions. Birds were capable of putting on fat at rates of 1.3-2.5 g./day, (Sections 4.2.3 and 5.4). Appropriate departure conditions are evaluated with regard to four factors: 1) weather, 2) total fat stores, 3) social stimulation, and 4) time of day (and, on the coast, height of tide). Favorable conditions with respect to all but diel and tidal timing are shown as necessary for migratory takeoff.

1. Favorable weather was best defined by an increase in the strength of winds from the northwest (Section 5.3.3.1). Such increases resulted in tailwinds for flight in the normal migratory direction, as documented by sightings of birds further down the migration route, departure directions from the study sites, and radar data from other studies (Sections 3.5 and 5.1.2). Surface winds at takeoff were 25°-30° counterclockwise of the mean departure direction. If birds responded to the direction of surface winds, this suggests that they compensated for the normal clockwise shift in wind direction with increased altitude.

2. The maximum fat stores carried by migrants were about equal to their fat-free body weights (Section 4.2.2). This fat could provide fuel for non-stop flights of 40 hours or longer. Fatter birds had a higher probability of departing than lean ones, and, at least among adults, there appeared to be a threshold level (14-18 g.) where a small increase in fat produced a large increase in the probability of migration (Section 5.4.2.2). Birds with high levels of fat, which were physiologically ready to migrate, did not leave during unfavorable weather (Section 5.4.2.2).

3. Departures on migratory flights were noisy, conspicuous, social events (Section 5.1). I have no data on the quantitative effects of call notes, decreased interbird distances, or increased feeding rates on the probability of migratory flight. I believe that there was always a

sufficient quantity of social stimulation present in the populations studied, but I have drawn a speculative arrow in the diagram suggesting that insufficient amounts of social stimulation might inhibit takeoff under otherwise satisfactory conditions.

4. Even when the weather was favorable for migration, birds generally did not depart until sunset, or, on the coast, until the tide was rising (Section 5.2.2). Both sunset and rising tides cause periods of decreasing food availability, which may be both a proximate and an ultimate determinant of hourly departure timing. When the weather was favorable, but worsened prior to sunset, birds sometimes departed earlier in the day, apparently "overriding" the normal schedule to take advantage of the weather (Section 5.3.1.4). I have represented this alternative in the necessary conditions of weather <u>plus</u> time of day by drawing single arrows out of these boxes.

<u>Takeoff</u> <u>and</u> <u>Call</u>, and <u>Depart</u>: If all conditions were met, birds take off, giving call notes. Flocks usually began flights in the appropriate migratory direction. Departing flocks contained at least three birds, and averaged around 15-20, with a few large flocks ranging in size up to 200. Departure bearings of flocks showed a decreased scatter with increased flock size, at least at one study site (Section 5.1.3). Although I never clearly observed it, I propose that if flock sizes were too small, birds might return to the ground or circle over the staging area in an effort to recruit additional flock members. Circling flights of this kind have been described in other shorebird whether they serve this function is unknown (e.g. Henshaw, 1910; Sauer, 1962; Johnson and McFarlane, 1967). It would be

enlightening to know whether flocks of all sizes return to the ground at the same freqencies in this situation. Finally, birds depart from the staging area, climbing into the sky and out of sight.

6.1.2 Comparison with General Models of Migratory Behavior

A number of authors have presented general models outlining the control of migratory behavior (Section 1.3). In the main, the models differ in their emphasis on particular control mechanisms, rather than presenting alternative conceptualizations of the processes involved. This discussion will concentrate on areas where the results from this study, as summarized in Figure 44, differ from the schemata of other models.

What are the behavioral responses of birds that fail to successfully compete in the local area? Rappole and Warner (1976) stressed the importance of intraspecific competition for foraging space as a component of their model. Evidence from this study supports this view, but such competition may not result in continued migration, as they suggest it does. At least some of the sandpipers in this study made local movements in search of resources, rather than continuing migratory flight. This difference in interpretation may relate to behavioral differences in the two study species. Rappole and Warner studied a small passerine, the Northern Waterthrush (Seiurus noveboracensis), which makes short flights through more continuous habitat. Whether unsuccessful competitors make local movements or continue migrating will vary with the ecological situation.

Alerstam (1978b, 1979) addressed the question of what degree of wind selectivity migrants of various flight speeds and migratory distances might be expected to show. His algebraic treatment (Alerstam, 1979) allowed simulation of energetic and temporal costs in terms of variables such as the total migration distance, the frequency of suitable departure conditions, the fraction of those conditions exploited by birds, the amount of variation in wind directions and strength, the total energy requirement of a migratory journey, the cost of transport of fat itself, the length of migratory flights, and the fraction of a bird's weight carried as fuel on flights. He pointed out that there were costs to transporting large amounts of fat for use as fuel (c.f. Pennycuick, 1975), and that migrants could minimize their total energy expenditure on migration by making many short flights, rather than a few lengthy ones. This sets up counter-selection to maximizing selectivity of winds. Since covering the total distance will require many short flights, some will have to be made under less than perfect conditions, unless the winds are constantly blowing in a favorable direction. Alerstam solves for optimum levels of wind selectivity under various wind patterns, distances, flight times, rates of fuel consumption, and sizes of birds, with the optimum being defined as the level at which the least amount of energy is expended on the entire migratory journey.

Alerstam specifically excludes from his model cases where large bodies of inhospitable habitat must be covered in a single flight, since no option is available in these cases. The model would predict that inland migrants had lower fat levels and a greater variance in meteorological conditions at departure, and, to a small degree, this was the case.

However the model would not apparently predict that inland migrants would have as strong adaptations to long-distance flight, in terms of fat stores and wind selectivity, as they do. The discrepancy between Alerstam's prediction and the behavior of inland birds might be resolved by considering most of the eastern United States as inhospitable habitat for Semipalmated Sandpipers, however I believe that a different interpretation is more plausible. Perhaps the most fundemental tool of behavioral ecology is the concept of optimization, yet chosing what quantity to optimize (other than relative lifetime fitness, which is in most cases impossible to measure) involves other intrinsic limitations (see papers in Krebs and Davies, 1978, for discussions of this problem). For migrant Semipalmated Sandpipers, the total energetic costs of travel may not be the optimized function at this stage of their migration. The flight strategy that maximizes survival probability need not be coincident with that requiring the least amount of energy accumulation, the quantity optimized in Alerstam's model. Information on the survival rates of sandpipers in different foraging habitats, geographic locations, and those making flights of different distances would be needed to resolve this issue. Alerstam's formalization of the behavioral ecology of many aspects of migratory strategies can help focus attention on essential problems in the field, and deserves more attention than it has received to date.

To what degree are internal daily rhythms important in determining the timing of migration? Able (1974:1039) explicitly includes an "Endogenous Rhythm of Zugunruhe" in his model of migratory behavior. As discussed earlier (Section 5.3.1.5), no systematic examination of daily activity patterns is available for any shorebird. The field observations of departures in this study suggest that any rhythms of *Zugunruhe* in shorebirds are not as important in determining the hourly timing of migratory flight as is the case with nocturnal passerine migrants. Tidal cycles and changes in weather conditions stimulated departures throughout the day, although most flocks did leave around sunset. It is possible that the need to feed around shifting tidal cycles has preadapted shorebirds towards more flexible daily scheduling of other behavior patterns, including the timing of migratory flights. It is even possible that endogenous tidal rhythms are present in shorebirds, as has been found for other littoral creatures (see Palmer, 1976, for review). However, an experimental study of Oystercatchers (*Haematopus ostralegus*), which feed only during a narrow tidal window, failed to demonstrate any such internal rhythms (Hulscher, 1974).

Systematic laboratory studies of daily activity patterns would be helpful in determining what role *Zugunruhe* plays in the regulation of migration timing in shorebirds. The lack of such studies may be due to the avicultural difficulty of maintaining these birds in small cages, and to the problem of measuring activity in these non-perching birds. Studies of *Zugunruhe* in shorebirds might better be conducted in a larger space on a group of birds, which would also allow for normal social behavior. Movement detectors of some kind, such as infrared beams, might be used to record activity; it also might be profitable to record the frequency of vocalizations.

To what degree can internal physiological factors alone stimulate migratory flight? Hinde (1951:336), using the ethological terminology of the time, states:

> The threshold of stimulation necessary from both internal and external factors is such that a very high internal drive may cause migration when the external factors are far from optimal ....

The notion that internal conditions will lead to migration when external conditions are not optimal is also expressed by Lack (1960:198), Mueller and Berger (1966:109), Able (1973:1039, hypothesis #4) and Alerstam (1978a). There are few data to support this widely-expressed hypothesis. This lack may be due to the difficulty of measuring the amount of drive present. An assumption in some studies is that weather-induced delays in migration will lead to an increase in "internal drive". Nisbet and Drury (1968), for example, examining spring passerine migration in New England, found no evidence of increased migration after weather-induced delays up to a week in length, but did see increased migratory activity after a full week of delay. Alerstam (1978b) points out that a determination of whether birds migrate with lower fat stores after periods of delay would be a critical test of this hypothesis. Other workers assume that fatter birds will have greater internal drive (e.g. Dolnik and Blyumenthal, 1967; Rappole and Warner, 1976).

The sandpipers in this study showed no signs of departing without substantial external stimulation. In addition, the lack of significant changes in the fat distribution on NOGO days (Section 5.4.2.2) shows that fat birds did not leave during unfavorable weather. It is possible that weather-induced delays of sufficient length to result in alternate behavior did not occur. Favorable weather was fairly frequent throughout the season (Figure 25). The longest period of continuously unfavorable migratory weather was a week at Sibley Lake, in early

September, and only four days, in late August, at Kent Island. These periods were not long compared to the average length of stay, even as length of stay shortened late in the season (Section 4.3.2).

The emphasis on external rather than internal control in my model of migratory behavior reflects both the meteorological sensitivity of shorebirds discussed earlier (Section 5.3.1.5), and ignorance about the internal mechanisms of their activity patterns. Limited data on the apparent degree of internal and external control of shorebird migration timing is available from other studies. Holmes (1966) showed that spring arrival times of Dunlin (*Calidris alpina sakhalina*) in northern Alaska varied with the timing of snow melt. Some adjustment of spring arrival times with weather also occurs in Spotted Sandpipers, *Actitus macularia* (Oring, Lank, and Maxson, unpublished data). On the other hand, Hilden (1979) reports almost no yearly variation in the spring arrival times of Spotted Redshanks (*Tringa erythropus*) in Finland, despite considerable meteorological variablity. For passerines, Gwinner (1971) suggested that the large difference in inter-individual variability of laboratory *Zugunruhe* between Chiffchaffs (*Phylloscopus collybita*) and Willow Warblers (*P. trochilus*) reflected species differences in the degree of internal and external control of migratory behavior. A similar spectrum is to be expected among shorebirds with different migration distances and pathways. This will be considered further when discussing the migrations of Dunlin (*Calidris alpina*) in Section 6.2.3.

The data on sandpipers are of interest with regard to Berthold's (1978b) proposal on the possible interaction of endogenous circannual patterns of Zugunruhe with the weather. Berthold extends the earlier model of endogenously programmed migration in several species of European warblers (e.g. Berthold, 1975a; Gwinner, 1977). The "temporal hypothesis" proposed that the total distance moved by warblers was a function of endogenously programmed periods of migratory activity that vary in duration. It arose from data showing that longer distance migrants have longer seasonal durations of Zugunruhe in the laboratory (Gwinner, 1971; Berthold, 1973).

The theory that strong internal factors control the timing of migratory flight is difficult to reconcile with observed correlations between the numbers of migrants and short term changes in weather (e.g. Bruderer, 1977). Berthold (1978b) proposed that alternating periods of activity and pauses were regular features of the patterns of Zugunruhe in individual warblers. Favorable weather caused the internal rhythms to be expressed in migratory flight, while unfavorable weather delayed their expression, thus producing the waves of migration associated with particular weather conditions. The total amount of activity, and the total distance moved, would remain constant.

How do the data from Semipalmated Sandpipers fit these hypotheses? Gwinner (1977) states that the basic temporal hypothesis outlined above cannot account for movements of birds to highly localized and remote sites, and that other mechanisms are probably involved in these cases. Birds that depart under specific environmental conditions that occur unpredictably in time also would not be expected to fit the model well. It is difficult to envision how strong internal controls could play a large role in the migratory timing of Semipalmated Sandpipers on a day-to-day basis, since they stage for such long periods and make relatively few migratory flights. On the other hand, the sandpipers in this study did change their behavior over the course of the season. The seasonal changes in the length of stay might be a function of internal rhythms. The migratory pauses seen earlier in the season are structured quite differently from the periods of activity and inactivity considered by Berthold (1978a) for warblers, but they might reflect something of a similar nature. Further research on the internal mechanisms of Semipalmated Sandpipers will be necessary to evaluate more completely the interactions of internal and external control of migratory behavior.

6.2 THE BEHAVIORAL ECOLOGY OF MIGRATION

This study was initiated to examine differences in behavior between a population that committed itself to a two-day overwater flight and one that did not. Information is also available from an intermediate population that staged at Long Point, Ontario (Page, 1970, see below). For contrast, the migratory behavior of the conspecific Dunlin (*Calidris alpina*) will be compared with that of *C. pusilla*.

6.2.1 Semipalmated Sandpipers at Sibley Lake and Kent Island

The behavior of migrants at the two study sites is compared in Table 13. I cautioned in the introduction that ecological factors, in addition to flightpath, might differ between sites, making interpretation of differences in behavior more complex, and this turned out to be true. Coastal birds, at least those that established themselves at the site, appeared to enjoy a richer and more stable feeding situation than

Table 13. Comparison of migratory flight path, environmental resources, and migratory behavior of Semipalmated Sandpipers at Sibley Lake and Kent Island.

Variable	Sibley Lake	Kent Island
Flight path	overland variable lengths	overwater long
Feeding habitat	less stable	more stable
Rate of fat deposition	lower	higher
Fidelity to local area:		
Number of transients	lower	higher
Movement of residents	greater	lesser
Length of stay:		
Adults	longer, variable	seasonally decreasing
Juveniles	seasonally decreasing	shorter, variable
Fat level at migration:		
Adults	high, more variable	high, less variable
Juveniles	wider range than adults	wider range than adults
Departure direction	southeast	southeast
Daily timing	weather-dependent	weather-dependent
Hourly timing	predictable, dependent on sunset and changing weather	predictable, dependent on sunset, tide and changing weather
Favorable weather	equal average frequency more annual variation	equal average frequency less annual variation
Meteorological specificity	high	slightly higher
Departing flock size	smaller less variable	larger more variable

midwestern migrants. Fattening rates were higher on the coast. Several lines of evidence suggested less local movement by resident coastal birds, reflecting the greater stability of the feeding resource. There also appeared to be a greater amount of competition for feeding areas on the coast, indicated by the higher levels of transience. Coastal birds stayed for shorter, and more seasonally predictable, periods than inland birds. Stronger seasonal trends suggest directional selection for more precise timing of migration, whether internally or externally controlled.

Shorter staging periods are consistent with higher rates of fattening, and perhaps also with increased local competition. Many more birds stage along the coast than inland (see Figure 9). Increasing levels of competition as more birds arrive during the season might have selected for more rapid movement of birds through coastal areas. The total migratory population in the midwest is smaller, and fewer birds are likely to be site-attached to the less stable feeding areas. There may be less selective pressure to hurry along at inland staging areas, at least early in the season.

At both sites there was a relationship between the amount of fat carried and the probability of departure on migration. Major changes in the probability of departure occurred between 14-18 g. of fat for adults, with the threshold level at Kent Island slightly higher than that at Sibley Lake. These fat levels would fuel flight for about 42 hours (McNeil and Cadieux, 1972a). The threshold fat levels are evidence that birds at both sites were preparing for long migratory flights, albeit somewhat longer ones at Kent Island.

At both locations, strong hourly patterns of departures were seen. While departures at Sibley Lake were primarily related to sunset, those at Kent Island were related to tidal cycles as well. At both sites, therefore, birds migrated during hours when food availability was decreasing.

At both sites, birds overrode their predictable daily departure pattern to take advantage of favorable migratory weather. Sandpipers were highly selective about departure weather, generally initiating flights with following winds. Kent Island birds left with stronger tailwinds and weaker sidewinds than those at Sibley Lake, and a greater 24-hour increase in the strength of tail winds occurred before Kent Island birds departed. As with the difference in fat thresholds, however, this quantitative difference was small, showing that coastal populations were only slightly more selective about departure conditions than inland birds.

Frequent periods of favorable weather were an environmental necessity for the evolution of the migratory systems seen at both sites. The mean number of days with favorable weather per season was about one in five at both locations, but the annual variation was greater in the midwest. This makes favorable weather a somewhat less stable resource on which selection can operate. Nonetheless, the migratory behavior of midwestern birds was not substantially less weather-dependent than that of coastal migrants.

Perhaps the most striking difference in the departure behavior of birds at the two sites related to departing flock sizes. Few departing flocks had seven or fewer birds on the coast, while this flock size was the modal class inland. Analysis of the relationship between flock size and departure bearings at Sibley Lake showed a central tendency in the orientation of larger flocks; regrettably, this relationship could not be examined at Kent Island. A number of hypotheses on the adaptive significance of flock size were presented, but none could be unequivocally rejected. I believe that navigational and/or aerodynamic advantages may well be involved. This is an area where future work may be fruitful.

Evidence of high fat threshold levels, and a high selectivity of weather conditions for flight, indicate adaptations for lengthy flights by birds at both study sites. While the recovery of tagged individuals at relatively short distances from Sibley Lake showed that some overland migrants did make short flights (Figure 12), the basic adaptation appears to be for long flights from both locations. On the other hand, the behavior of coastal birds did indicate a slightly less variable response to weather conditions, and slightly higher threshold fat levels for flight. The more stable food and meteorological situation may have been necessary ecological preconditions for the increased specialization on the coast. Nevertheless, the differences may be attributed to stronger directional selection on these behavioral contingencies for birds flying over the ocean than for those flying over the land.

6.2.2 Semipalmated Sandpipers at Long Point, Ontario

The results from this study may be compared with those found by Page and co-workers, working with *C. pusilla* at Long Point, Ontario, 1966-1969 (Page and Bradstreet, 1968; Page and Salvadori, 1969; Page

1970; Page and Middleton, 1972; Bradstreet et al., 1977). Long Point is a 32 km. long peninsula, running parallel to the north shore of Lake Erie, that attracts fall migrant Semipalmated Sandpipers along its sandy southern shore. Daily censuses showed up to 90 individuals present at one time, so the number of birds at Long Point was considerably lower than that at either Sibley Lake or Kent Island (c.f. Figures 13 and 14). The bill of birds moving through Long Point were intermediate in length between those at Sibley Lake and Kent Island (see Figure 8). The seasonal occurrence of adults and juveniles was similar to that seen at Sibley Lake.

Page determined the length of stay of Semipalmated Sandpipers by color-marking cohorts of birds caught on different days and regularly censusing thereafter. As in this study, a large proportion of the birds marked were transients (50%, see section 4.1.4), never seen after the day of marking. Page believed that there was a relationship between transience rate and incoming "waves of sandpipers associated with rain and strong southerly winds" (Page, 1970:25). This might be comparable to the density-dependence of transience rates proposed in section 4.1.4, in that more birds left when waves of immigrants increased the local population size. However, Page interpreted his data somewhat differently, implying that these transient birds were headed elsewhere, and stopped at Long Point only temporarily because of adverse winds. Overall, birds averaged staging periods of seven to ten days, with variation between age classes and years of the study. Some individuals stayed for up to 25 days. In a simple comparison of early and late adult migrants, Page found no seasonal differences in staging periods.

This suggests similarities with Sibley Lake in terms of seasonal schedules of adult staging periods, in contrast to the behavior on the coast.

Page estimated rates of fat deposition during stopovers from the weights of recaptured individuals. For three days after capture, birds showed small declines or no change in weight. Thereafter, recapture weights showed a fairly even gain from day to day. Adults gained about 0.5 and 0.7 g./day in two different years, which is considerably lower than my estimates (Section 4.2.3). Some individuals showed higher rates, gaining 11-12 g. in nine to ten days. If these individuals showed the 3-day no-change period, their subsequent rates would be 1.7 g./day, comparable to my data.

Page and Middleton (1972) examined the question of whether the amount of fat carried by a bird was related to the probability of its remaining in the local area. Captured birds were classified as light or heavy, and distinctively marked prior to release. As with my attempt to relate fat levels and staging periods (Section 4.3.3), they found no difference in the length of stay of the two groups. Page (1970:40) concluded that there was "no evidence that the departure of Semipalmated Sandpipers from Long Point ..... was related to the fat levels of the sandpiper". I was able to uncover such a relationship by utilizing an approach that controlled for meteorological events (Section 5.4.2). The failure of fat level as a predictor of length of stay in both studies, and its demonstrated importance in determining departure probabilities in this study, reinforce the idea that sandpipers do not simply fatten and leave the staging areas as fast as possible.

6.2.3 Autumn Migrations of Dunlin

The most intensively studied migrant shorebird is the Northern European Dunlin, *Calidris a. alpina*. *C. a alpina* are larger than *C. pusilla*, with fat-free body weights of about 41 g. (Mascher and Marcstrom, 1976) to *pusilla*'s 21 g. (McNeil, 1970; Page and Middleton, 1972). *Calidris a. alpina* breed on the northern coasts of Europe and Asia, from the west coast of Norway around northern Scandinavia and eastward along the Arctic Ocean to Siberia (Soikkeli, 1966). They winter on the coasts of Britain, in western Europe south of Denmark, and in smaller numbers in the western Mediterranean and on the Atlantic coast of North Africa (Jansen, 1979). Their migration has been documented by marking, morphometric, radar, visual and physiological studies at breeding, staging, and wintering areas (Svardson, 1953; Norrevang, 1955; Ogilvie, 1963; Evans, 1964, 1966a; Soikkeli, 1966; Mascher, 1966, 1971; Pienkowski and Dick, 1975; Masher and Marcstrom, 1976; Meltofte and Rabøl, 1977; Leslie and Lessells, 1978; Dick and Pienkowski, 1979; Jansen, 1979; Noer, 1979). The migratory route documented in these studies involves comparatively short, primarily coastal flights along the Barents and White Seas, the Gulf of Bothina and Finland, the Baltic and North Seas, and the Atlantic coasts from Norway to Africa. The birds may fly overland 500-600 km. when leaving the arctic coast, and some pass a similar distance from the Gulf of Bothina over Sweden to the North Sea, but there are no greater distances of inhospitable habitat. The coastal migrations of this species are a sharp contrast to the lengthy flights made by both populations of Semipalmated Sandpipers in this study.

Mascher (1966) and Mascher and Markstrom (1976) captured, measured and collected C. a. alpina at staging areas along the coasts of Sweden. As with C. pusilla, adults preceded juveniles. The investigators used walk-in traps, and obtained many recaptures. Few adults were recaptured more than three days after initial capture. The juveniles, which migrated later, remained for longer periods, with about 20% of the capture-recapture intervals longer than a week. These staging periods are much shorter than those of pusilla, and they show a reversal of the seasonal trend of shorter lengths of stay later in the season found in this study.

Dunlin carried an average of 12% of their fresh body weight as fat. The maximum found in lipid extractions from collected specimens was 29% of total body weight (Masher and Markstrom, 1976). The estimated fat levels at Sibley Lake and Kent Island show averages of 17% and 25%, respectively, with maximum levels of around 50% of fresh body weight at both sites. Mascher (1966) found a significant inverse relationship between the percentage of Dunlin recaptured and their weight at initial capture. This suggests a positive relationship between fat and the probability of departing, as was the case for Semipalmated Sandpipers, although the comparable analysis (fat versus staging period) failed to reveal it.

Studies of Dunlin migration and weather present quite a different picture from that shown for Semipalmated Sandpipers. From radar studies, it appears that Dunlin move nocturnally at moderate altitudes in favorable wind conditions (Evans, 1966b, 1968). In addition, however, visual observations along the coasts of Sweden, Denmark, and the Netherlands show large numbers of low, diurnally migrating flocks, often flying parallel to the coast. They are seen in the largest numbers when the wind direction is opposite to the direction of migratory flight (Svardson, 1953; Meltofte and Rabøl, 1977; Jansen, 1979). Alerstam (1978b) and Jansen (1979) proposed that when winds oppose movement in the migratory direction, birds would encounter the weakest winds by flying low over the water. I saw nothing resembling such flights in *C. pusilla*, and know of no reports of such migratory movements in this species.

How would a figure showing the staging and migratory behavior of C *a. alpina* differ from that constructed for *C. pusilla* in Figure 44? First, there is no indication of a migratory pause, since the staging periods are relatively short. If there is a seasonal trend in staging periods, it is the opposite to that seen in *pusilla*, since the later-migrating juvenile Dunlin appear to stay longer than the earlier adults. Young *pusilla*, on the other hand, tend to arrive late and leave early. Both species move in flocks, and both appear to have positive relationships between fat levels and the probability of migration. However, the levels of fat needed for flight are proportionally higher in *C. pusilla*.

The most intriguing difference in the migratory behavior of the two species is in their responses to weather conditions. While Semipalmated Sandpipers wait for favorable winds, Dunlin are less selective, and have two modes of migratory flight, flying at high altitudes with tailwinds, and low altitudes with headwinds. This behavior pattern is probably related to two aspects of their migration route: 1) it is mainly coastal, which means that long flights over inhospitable habitat are not necessary, and 2) the migration route of *C. a. alpina* does not include especially favorable wind conditions. The birds are moving eastward against an underlying westward circulation. Favorable migratory weather is not, in this case, a reliable resource.

The shorter staging periods, lower fat levels, and lesser weather selectivity of Dunlin suggest the possiblity of a greater degree of internal than external control of migratory flight in *C. a. alpina* than is the case for *C. pusilla*. Alerstam (1979) argued that for many birds that did not cross large areas of inhospitable habitat, a series of shorter flights in more variable weather would be less costly energetically than fewer flights carrying more fat in favorable winds. Essentially, the increased cost of flight as a heavy bird, plus the time spent waiting for favorable weather, might outweigh the energetic advantages of flying with tail winds. Where this situation occurred, the timing of migration would be less influenced by external factors and under greater internal control. The migration of *C. a. alpina* might profitably be further examined in this light.

Not all populations of Dunlin migrate in the manner described above. *C. alpina* has a circumpolar distribution, with well-defined subspecies, and the separate populations make very different migratory flights. Populations breeding in eastern Greenland (*C. a. artica*) make substantial transoceanic flights to Europe. At least some birds breeding in western Alaska (*C. a. pacifica*) move to coastal staging areas on the south side of the Alaska peninsula, and then make a weather-dependent, transoceanic flight directly to the California coast (Gill and Jorgenson, 1979; Gill, 1979, personal communication). Interestingly, birds breeding in northern Alaska and Siberia (*C. a. sakhalina*) winter along the northeast coast of Asia and Japan. Thus, birds breeding on the Seward Peninsula (*C. a. pacifica*) migrate southeastward, while Dunlin breeding a few hundred kilometers north at Cape Thompson (*C. a. sakahlina*) move westward and winter on the opposite side of the Pacific.

Migratory patterns such as those seen in abutting populations of Dunlin are often interpreted as an historical retracing of expanding breeding ranges of populations (e.g. Welty, 1982:562-564). Alternatively, one could try to establish that the energetically optimal migratory pathways for Dunlin change between Cape Thompson and the Seward Peninsula. I believe that the former explaination is the more likely, assuming that the survival probabilities of birds moving in both directions are nearly equal. Cases such as this demonstrate the importance of history in the development of migration routes. The final section of this discussion will consider the history of Semipalmated Sandpiper migration routes.

6.3 THE EVOLUTION OF TRANSOCEANIC FLIGHT

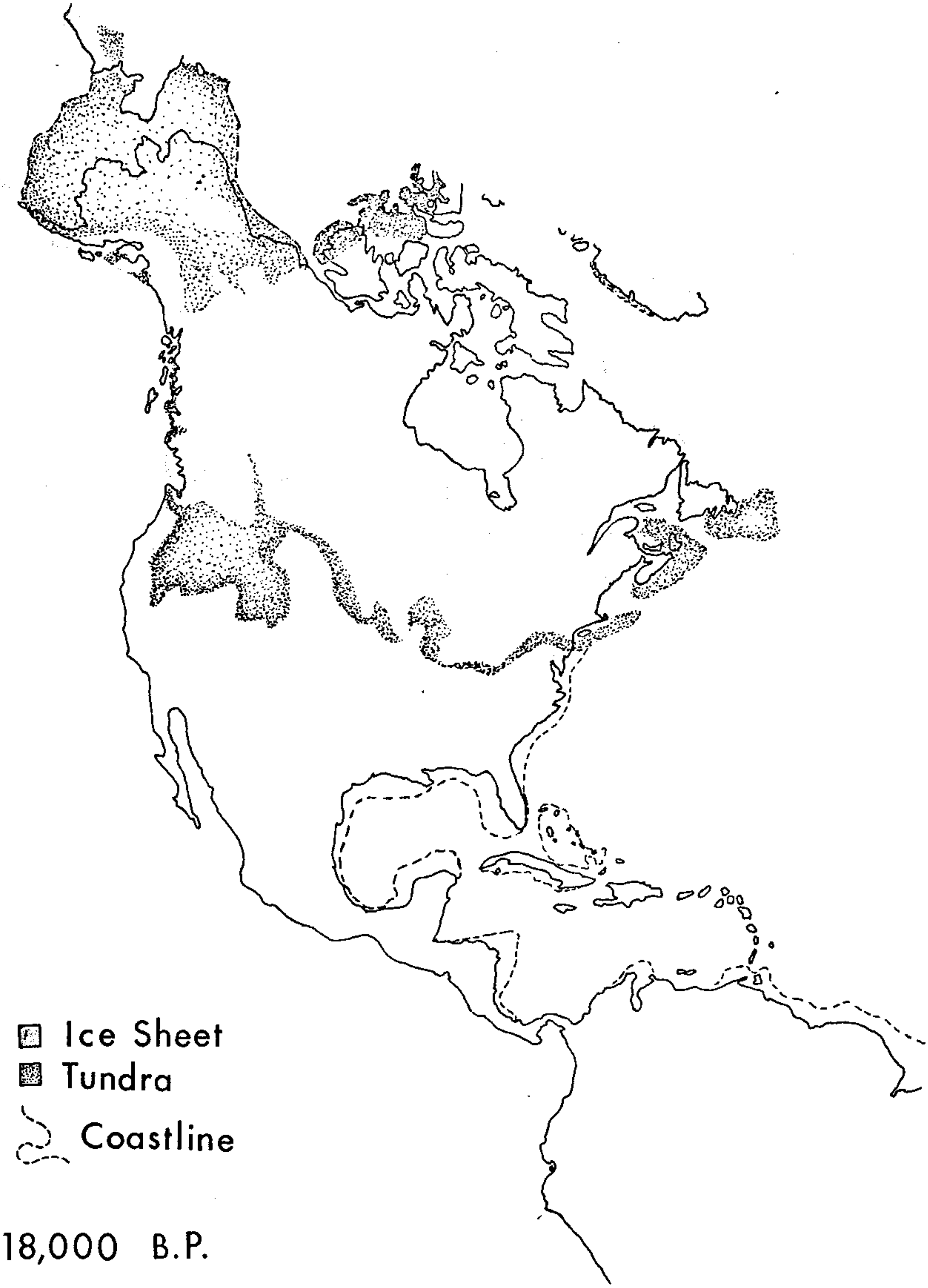
We have seen that long flights are a feature of the migrations of both populations of Semipalmated Sandpipers in this study. The case of the Dunlin showed that other shorebirds may differ substantially from Semipalmated Sandpipers in their migratory behavior due to differences in ecological and geographical conditions. While ecological factors will ultimately determine whether migrants following different migratory routes are successful or not, natural selection does not act instantaneously. Population geneticists have shown that the rate of evolutionary change is a function of the amount of variability in a trait (Fisher, 1930), and historical factors also play a role in explaining the present conditions. This final discussion considers the probable evolution of migratory routes of *C. pusilla* since the last glacial maximum about 18,000 years ago.

6.3.1 Post-Pleistocene Migration Patterns

Current patterns of migration in north temperate and arctic regions may be viewed against the background of the recent geologic past. At the end of the Pleistocene era, the antecedents of today's *C. pusilla* were probably breeding in the areas of tundra shown in Figure 45. Hare (1976) suggests that much of this tundra may in fact have been closer to boreal forest in character, and thus may not have been suitable breeding habitat for Semipalmated Sandpipers. As the glacier receded, however, open tundra-like conditions would have formed over the freshly exposed rock, creating a transcontinental band of suitable habitat that would still be far south of current breeding grounds.

Semipalmated Sandpipers may have bred in three major areas, and followed three different migration routes as the glacier receded. First, *C. pusilla* may have breed in the unglaciated Beringa refuge in Alaska and eastern Asia. These populations might have have migrated to the southeast in a lengthy flight to the southern edge of the ice sheet. This would indeed have been a flight over inhospitable habitat! Second, populations breeding on the exposed continental shelf off present-day Newfoundland might have made overwater flights basically similar to those of today's coastal migrants. The atmospheric circulation in the

Figure 45. The location of tundra in North America at the height of the most recent glaciation, approximately 18,000 years ago.



18,000 B.P.

western Atlantic was probably not drastically different from that seen today (Lamb and Woodroffe, 1970; Lamb, 1977). The "Bermuda High" would have been compressed and/or shifted further south. Birds flying out over the Atlantic from Newfoundland would have had a greater chance of being swept westward than is the case at present. If they began flights with northerly winds, however, they should have been able to enter the trade wind belt and complete the flight. In contrast to the present situation, however, they would have been leaving directly from the breeding grounds. This migratory route might have developed during an earlier interglacial period by a process similar to that outlined below for birds breeding south of the glacier.

Third, I would like to consider the migrations of populations of sandpipers breeding along the line of tundra due south of the retreating glacier. The changes in migratory routes of these birds hypothesized below provide a scenario for the evolution of current migratory patterns. I am assuming that the basic flight direction of post-Pleistocene sandpipers from temperate latitudes was southeasterly, since the location of suitable coastal wintering areas probably has not changed substantially.

The migrations of western and midwestern breeders would have been similar to those made by birds staging at Sibley Lake today. As with Newfoundland populations, however, they would have been departing directly from the breeding grounds. Eastern populations would have left the coast no further north than present-day New Jersey. Such departures would have been far enough north to catch the clockwise circulation of the Bermuda High pressure system. Much of the West Indies was exposed at this time, and eastern migrants could have made a relatively short transoceanic flight from the mid-Atlantic coast. On the other hand, it is possible that birds leaving the coast might have flown directly to the northern coast of South America, rather than arriving in the West Indies, as appears to be the case for many migrants today.

As the glacier retreated, both suitable breeding habitat and large-scale pressure systems also gradually shifted northwards. Let us assume that shorebirds maintained the direction of their migratory flights. As the total distance between breeding and wintering grounds increased, a multi-stage migration would have been established in populations that previously flew directly to the sub-tropics. As departure points shifted northward, the minimum length of successful overwater flight would have increased, creating strong selection for increased fat stores at departure and precision in choosing departure weather. The situation as it stands today would have gradually developed. Alternatively, birds might have changed the direction of their flights, and moved southwestwardly down the Atlantic coast to avoid such long, overwater flights. For shorebirds, this does not appear to have happened.

6.3.2 Factors Maintaining Transoceanic Flight in Shorebirds

Drury and Keith (1962) outlined the possible ecological rationale for autumn flights of birds over the western Atlantic, which was reviewed in Section 3.5.2.2. Essentially, they pointed out that birds leaving New England with northwesterly winds would avoid headwind flights, and, in fact, obtain a significant northerly wind component over the course of the entire transoceanic flight. This interpretation gains credence from the observation that shorebirds do not attempt to fight the trade winds by reversing this flight in the spring. Spring radar studies in the West Indies show northwesterly movements in the trade wind zone, rather than the north to northeasterly flights that would be a reversal of the autumn route (Richardson, 1974b). While Semipalmated Sandpipers marked along the northeast coast of North America in autumn were recovered in northern South America and the West Indies (see Section 3.5.2.2), Semipalmated Sandpipers marked in Suriname have been recaptured in spring almost exclusively in central North America (Spaans, 1979). Thus, the birds have an eliptical migration route that is readily interpreted in terms of prevailing large-scale wind patterns (e.g. Bellrose and Graber, 1963; Drury and Keith, 1962; Gauthreaux, In Press).

I agree in general with Drury and Keith's interpretation. However, this route is not necessarily the optimal one available, in terms of time, total energy consumption, or the chance of survival of the birds during migration. Obviously, strong selection against overseas flight would quickly eliminate populations of transoceanic migrants, and this has not happened. However, the preponderance of oversea flights cannot be taken simply as direct evidence that it is the best route theoretically available to these populations.

Gauthreaux (In Press) reviewed the standard migratory directions of spring and fall passerine migration in North America as seen in moon-watching, ceilometer, and radar studies. While he could identify a single mean direction in nearly all of these studies, there were a string of bimodal distributions along the northeast coast in fall, from northern Virginia to the Canadian Maritimes. These represent areas where some passerines are heading out over the ocean, while others move parallel to the coast. There is some evidence that different species of passerines are involved in southeasterly versus southwesterly movements (e.g. Drury and Keith, 1962; Nisbet, 1970; McClintock et al., 1978; Larkin et al., 1979), and that the route taken by a species may relate to the location of its wintering grounds (Drury and Keith, 1962). The bimodality seen along the coast shows that a southwesterly coastal route is a viable alternative to transoceanic flight, and this should be true for shorebirds as well as passerines. Unfortunately, it is not possible to determine what proportion of shorebird movement is southwesterly along the coast, because such movements are usually swamped on radar by dense passerine migrations (Richardson, 1979). The evidence presented earlier with regard to transoceanic flight (Section 3.5.2.2), and the departure bearings seen at Kent Island (Section 5.1.2) argue against substantial coastal movements by Semipalmated Sandpipers.

I propose that two features of shorebird migrations might have acted as conservative forces in maintaining overwater flights. The first relates to the central tendency in flock bearings shown by Semipalmated Sandpipers (Section 5.1.3). Second, I propose that a gradual shift in migratory direction from southeast to southwest is opposed by the general pattern of atmospheric circulation in the western Atlantic.

Semipalmated Sandpipers migrate in anonymous flocks, and the departure bearing of a flock seems to be determined by some process similar to statistical averaging of individual preferences (Section 5.1.3). The actual migratory directions of populations of sandpipers will be less variable than if they migrated singly. Thus, selection will operate more slowly on shorebird migration bearings than it would, for example, on passerines. A quantitative assessment of the possible importance of this smaller variance is not possible without some knowledge of the selection pressures involved.

The second conservative factor relates to the position of the Bermuda High pressure system. It is clear that under present conditions, few birds attempt to fly on the southwestern side of this system. Hundreds of thousands of shorebirds leave the New England and Maritime coasts on tracks that take them north and east of the system, where they encounter favorable winds in the counterclockwise circulation, or pass through light and variable winds towards the center of the system. However, relatively few birds leave the coast south of Virginia (Figure 9, Section 3.3), due to the southeasterly winds prevailing on the western side of the system. I propose that a gradual shift in migratory direction from southeasterly to southwesterly might not occur due to selection against the intermediate condition of southerly flights through or to the west side of the Bermuda anticyclone.

By drawing attention to these two potentially conservative forces, I am not suggesting that a southeasterly course is in fact a poorer route than southwesterly, coastal movements. For birds headed to northeastern South America, coastal movements would necessitate subsequent eastward flights against the trade winds, which would be costly indeed (e.g. Richardson, 1976b). We will probably never be able to measure the survival rates of transoceanic migrants, or to estimate what they might be via a coastal route. This makes it difficult to determine whether the transoceanic flightpath is a local optimum perpetuated by historical developments, or is truly a global solution to the problem of moving shorebirds from North to South America.

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APPENDIX

The appendix lists sources consulted for distributional information on Semipalmated Sandpiper migration, as presented in Figure 9. Sources are listed in alphabetical order by political subdivision. Abundance categories were taken from the texts of each source. An asterisk indicates that the source was omitted, due to possible confusion between wintering Semipalmated and Western Sandpipers.

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