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# **Radar observations of bird movements in east-central Alberta**

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# Introduction

Since the discovery that modern surveillance radar routinely detects bird movements (Harper, 1957; Sutter, 1957; Houghton and Coultas, 1958; Tedd and Lack, 1958), there have been many radar studies of migration in Europe and North America (see Myres, 1964b, and Eastwood, 1967, for bibliographies). These studies have provided much new information about migration routes, the height of migration, the relationships between visible and actual migration, and correlations between the amount of migration and weather. Radar has also provided information of relevance to theories of migrational orientation (reviewed by Eastwood, 1967; also Bellrose, 1967; Evans, 1968a,b; Graber, 1968; Steidinger, 1968; Lack, 1969; Parslow, 1969). In spite of the extensive use of radar by ornithologists in the last decade, the major published studies of migration in North America are confined to coastal New England (Drury and Keith, 1962; Nisbet, 1963a,b; Drury and Nisbet, 1964; Nisbet and Drury, 1967a,b, 1968) and the northern Mississippi Basin (Bellrose and Graber, 1963; Hassler *et al.*, 1963; Bellrose, 1964, 1966, 1967; Graber, 1968).

In 1963 a radar study of bird movements was begun by the Canadian Wildlife Service in association with the National Research Council's Associate Committee on Bird Hazards to Aircraft. Since then, time-lapse films have been taken at various times of 24 different radar displays in eight provinces of Canada, at two radar sites in France, and at seven sites in the United States. The major purpose of this study has been to find means of reducing the number of bird-aircraft strikes (Gunn and Solman, 1968; Blokpoel, 1970); hence the methods of recording and analysing data have not always been those most suitable for some ornithological purposes, especially studies of orientational ability. However, many data of scientific interest have been accumulated. Reports on a number of radar studies of specialized types of bird activity are currently in preparation or in press. However, this is the

first paper dealing with migration in general and based on our standard film-assessment procedures. We will describe the radar view of migration from one site in east-central Alberta and include an analysis of correlations between migration volume and weather and the effects of wind direction on migration direction.

# Methods

## Radar and filming

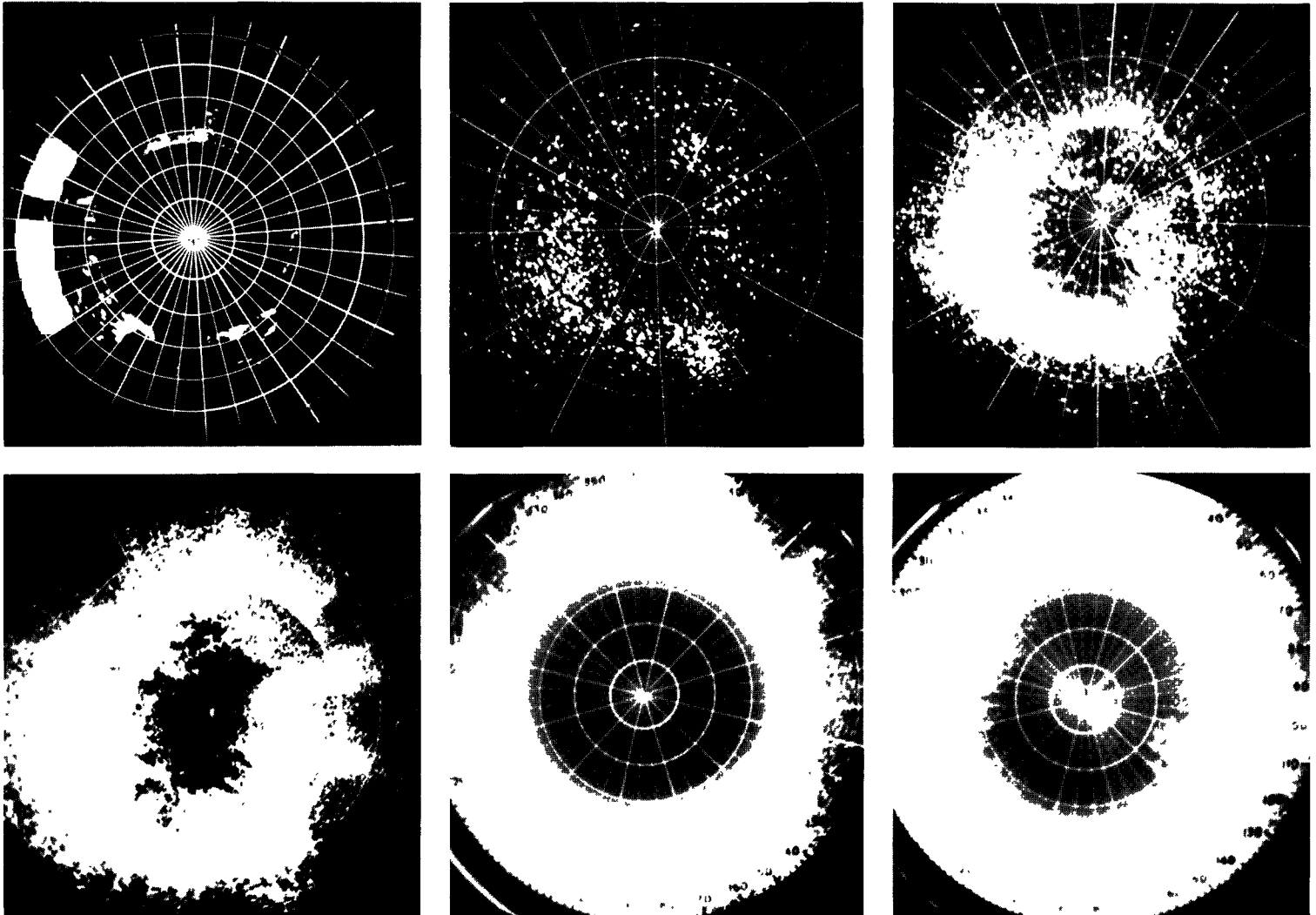
This paper is based on time-lapse filming of a radar display at Cold Lake, Alberta (54°24'N; 110°17'W) from April 1 to June 10, 1965, and from September 10, 1965, to November 30, 1966. Film was available for 11,077 of a possible 12,216 hours (90.7 per cent) in these periods. The radar was a high-powered L-band surveillance installation with a Plan Position Indicator (PPI) display showing an area with 70 nautical miles radius. Moving Target Indicator (MTI) circuitry was always used in the central part of the display (out to about 30 miles range). Beyond that range normal video was used.

Radar adjustments sometimes made very few birds visible in the central MTI area of the display (e.g., in Fig. 1, intensity levels 7 and 8). Also, an irregularly shaped area containing few bird echoes is visible near the centre of intensity levels 2, 4 and 6 in Figure 1. This occurred because the echoes from some of the birds flying above areas of intense ground clutter tend to be suppressed with the ground clutter by MTI systems. We have observed this phenomenon on a number of different types of radar. Besides the suppression of some echoes near the centre of the display by various radar adjustments and over areas of ground clutter, echoes from most birds within a few miles of the radar site were suppressed by Sensitivity Time Control (STC) circuitry.

The radar operated at five sweeps per minute. Initially, five frames of 16-mm film were exposed per minute, with one frame per sweep. Later, five frames were exposed every 2 minutes, with successive sweeps being recorded and skipped in sequence. A clock and a date card situated beside the PPI were included in every frame.

Some directional data from radars at Edmonton and Calgary, Alberta, Regina and Yorkton, Saskatchewan, and Beau-sejour, Manitoba, are presented for comparison. The last two sites (numbered 47 and 6 respectively on Fig. 7) had radars comparable to that at Cold Lake. The first

Figure 1. Intensity scale used to record the amount of migration at Cold Lake, Alberta. Reading from left to right and top to bottom, intensity levels 0, 2, 4, 6, 7, and 8 are shown. Range rings are at 10-n.m. intervals. Birds are not seen near the centre of the display because of performance characteristics of the radar.



three sites (numbered 18, 103, and 29 in Fig. 7) had 550-kw, 23-cm Air Traffic Control radars similar to those described by Richardson and Haight (1970).

#### Data recorded

In order to analyse the large amount of filmed radar data obtained at Cold Lake and at the many other sites studied, we had to develop a standard numerical recording system. We recorded bird activity visible with radar in terms of units which we called events. An event consists of a

continuous flow of bird-echoes showing similar characteristics and behaviour over a period of time. Events may range from a few echoes making a local movement a few miles long to thousands of echoes in broad-front migration across the whole radar coverage area. Gradual changes over time in the intensity, direction, and echo size of a flight were not considered grounds for dividing the activity into separate events, but discontinuous changes in these parameters (indicating separate types of birds or types of movements) caused us to

divide the flight into separate events. While there was unavoidably some degree of arbitrariness in this procedure, most activity fell naturally into separate events. Occasional arbitrary decisions about how to divide the activity into events had no resultant effect on the analysis of weather correlations with migration volume, because this analysis was based on the total amount of activity each night rather than on events (see below). The terms "event" and "movement" have equivalent meaning in this paper.

For each event, a wide variety of information was abstracted from the time-lapse film. General data included the date, the start, peak (greatest intensity), and end times, and indications of how precisely the start and end times could be determined. At each of the start, peak, and end times, the following were recorded: (i) the three most common echo sizes (measured on a more or less arbitrarily defined 7-grade ordinal scale), (ii) the position of the event on the radar display (either in certain octants or over the whole display), (iii) the proportion of the display containing bird echoes, and (iv) the type of movement, e.g. a local flight (defined here as beginning and ending on the display); a flight beginning on the display and moving out of range; a flight entering one side of the display and leaving the other; a roosting flight; a disoriented flight. Two other parameters, the mean direction of flight (estimated by eye to the nearest  $10^\circ$ ) and the intensity of flight (see below), were recorded every hour throughout the duration of the event. All these data were placed on punch cards for machine analysis.

The intensity of each event was estimated each hour by eye in terms of the 9-level arbitrarily defined ordinal scale illustrated in Figure 1. The scale is based on the number of echoes per unit area at various distances from the centre of the display. At low intensities, the scale takes into account the progressive "thinning" phenomenon (Nisbet, 1963a) and the suppression by the radar of echoes close to the antenna. ("Thinning" is the progressive decline in number of echoes per unit area on the display as one moves from the centre to the periphery.) At moderate and high intensities, the display is saturated (completely covered with bird echoes) out to some distance from the centre. Hence, this distance is the basic density criterion for moderate and heavy movement. A slightly changed intensity scale was in use when the October and November 1966 films were assessed. These data have been omitted from the analysis whenever this

change would require a different interpretation of the results. We are aware of the difficulties involved in obtaining quantitative radar observations (Nisbet, 1963a). We claim only that our data provide a rough estimate of migration volume measured on an ordinal scale. The accuracy of our density estimates is considered in the Discussion.

### Data analysed

The Cold Lake radar data were subjected to various types of analysis using computers whenever appropriate. While all types of movements detected by the radar were recorded, the analyses considered here deal only with long-distance "migratory" movements, which were defined as those events that either entered the radar coverage area from out of range, or moved out of range, or both. Unless otherwise stated, we did not consider local movements (defined above). Totals of 873 long-distance and 309 local movements were recorded (exclusive of local roosting flights similar to those described by Eastwood *et al.*, 1962).

### Basic data units

We used different basic units for different parts of the analysis.

(i) The description of migration is based on events.

(ii) The analysis of correlations between volume of nocturnal migration and weather is based on the total amount of activity each night rather than on individual events. To determine this total, all the migratory events (usually none, or one, but occasionally two) occurring on a given night within a given  $90^\circ$ -wide range of directions were allocated a single number representing the peak intensity of movement in that range of directions during the night. On those few occasions when there was more than one movement during one night in a single range of directions, the following procedure was used. When the events were of unequal intensity, the overall peak intensity was taken as that of the peak intensity of the

strongest event. This procedure was followed because the relation of the lower intensity levels is such that, for example, simultaneous intensity-2 and intensity-3 events looked at together do not appear to show as many birds as a single intensity-4 movement. On nights when two movements did occur in the same direction range, both movements were usually of low intensity. When there were two events with the same peak intensity, the total intensity was taken as the peak intensity of each single event plus one (i.e. two intensity-3 events in a single directional category were assigned an overall intensity of 4). This reflects the general appearance of the display when two events of equal intensity occur simultaneously. On most nights there was no more than one movement in each of the direction ranges, and hence this summation procedure was not needed.

(iii) The analysis of the effects of wind direction on direction of nocturnal migration is based on "event-nights". An event-night is that portion of any migratory event occurring between sunset and sunrise. While an event reaching its peak intensity at night forms an event-night, the few events lasting more than 24 hours may include two event-nights.

### Methods of analysing relationships between migration volume and weather

The statistical analyses of correlations between intensity and various weather parameters are based on the peak intensity of movement in the normal and the reverse directions of flight each night. Since we have not yet accurately determined the number of birds represented by each of the values in our intensity scale, procedures based on interval scales of measurement (such as calculating mean intensities or using multiple regression techniques) could not be used. Furthermore, because the normal intensity of nocturnal movement changes from one part of a migration season to another and from year to year, we considered it advisable to develop a modified intensity scale wherein each night's

Figure 2. Peak nocturnal intensities of NW (range W to N) migratory movement. The curves are smoothed 15-day moving quartiles representing the intensities reached on 25 (---), 50 (—), and 75 (---) per cent of the nights. (See Methods section.)

intensity was compared to the normal intensity at that time of year. The computer determined the intensity levels reached or exceeded on 25, 50, and 75 per cent of the nights in 15-day periods centred on each day. This was done separately for NW (range W to N) and SE (range S to E) movements. We drew smoothed "15-day moving quartile" curves through these values (Fig. 2 and 3) and recorded the intensities of NW and SE movement each night as being in the first, second, third, or fourth quartile. Our "moving quartiles" are analogous to a moving average, but are appropriate to an ordinal scale. Thus, a night whose intensity was in the first quartile had very little migration relative to the normal for that time of year, while a night in the fourth quartile had an intensity reached on less than one-quarter of the nights at that time of year. Points lying on a quartile curve were alternately (by date) assigned the quartile intensity values above and below the curve.

The analysis procedures applied to the normal migration situations (W to N movement in spring and E to S in autumn) differed from those applied to reverse migration (SE in spring and NW in autumn) and to winter movements. In the normal situations there were relatively few nights with no movement in the relevant direction and there were large shifts over a period of weeks in the normal intensity (Fig. 2 and 3). Hence the modified 4-level (quartile) scale was used, and the distributions of weather parameters at each of these 4 levels of migration were compared by non-parametric procedures (Siegel, 1956). In the reverse migration and winter situations, only a few nights had any movement. Hence the fourth quartile was usually the only one containing nights of non-zero intensity. Rather than use the quartile scale for these types of movement, we compared the distributions of weather parameters on nights having no movement with those on nights having some movement using the Mann and Whitney U-test (Siegel, 1956).

Relationships between intensity and the synoptic weather situation were examined

Figure 2

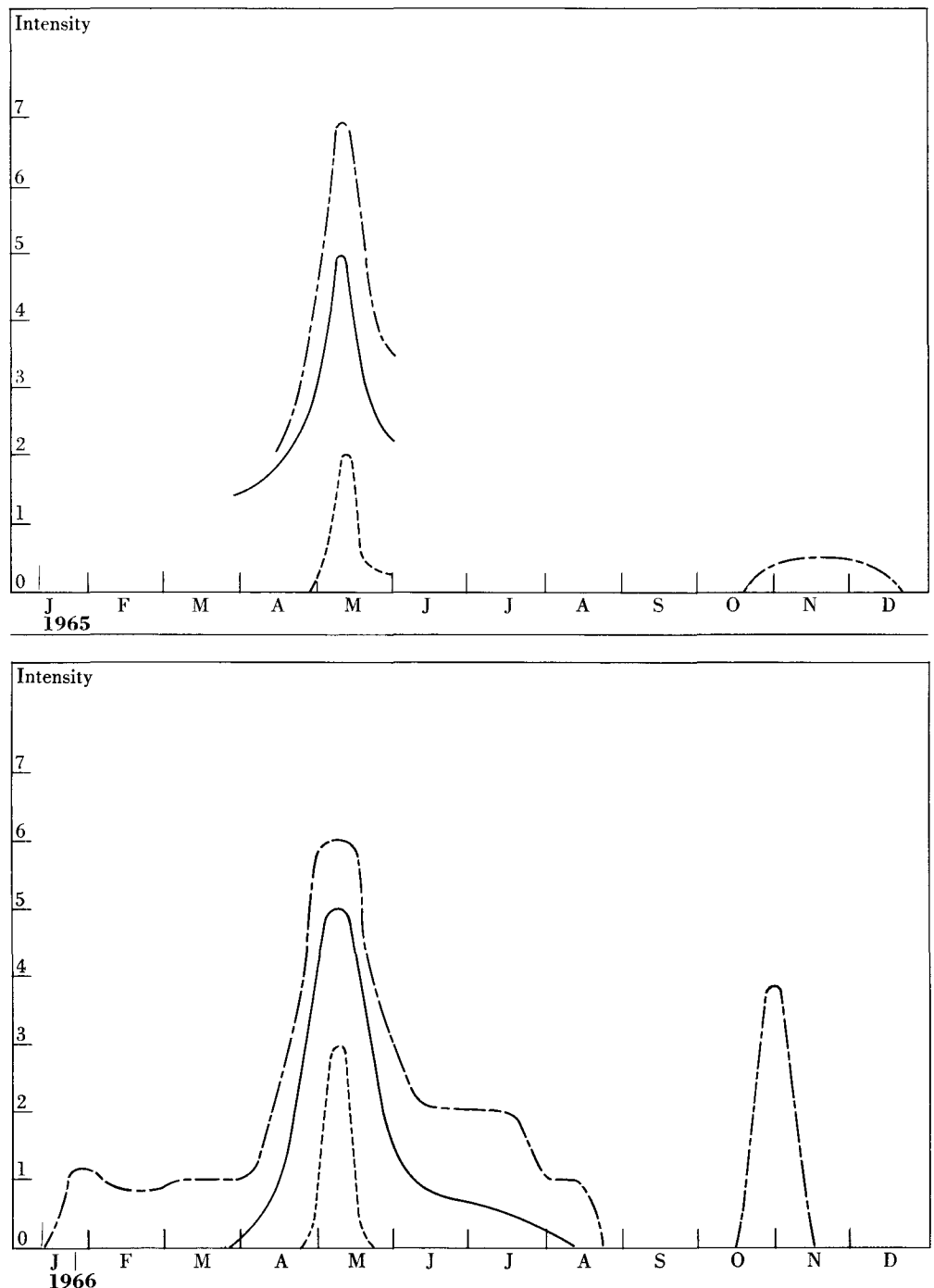
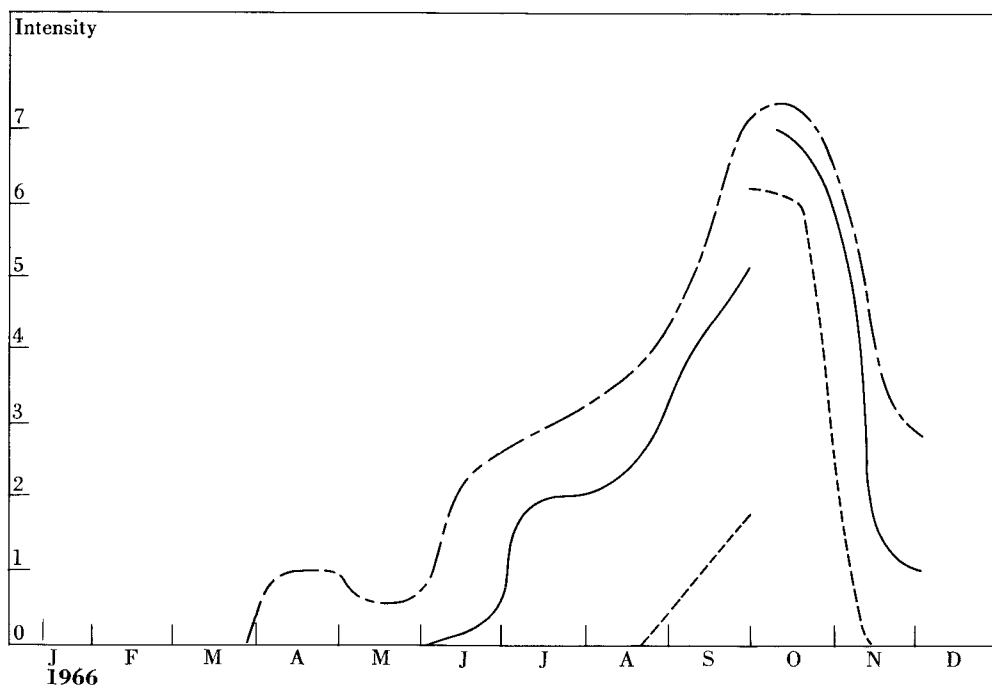
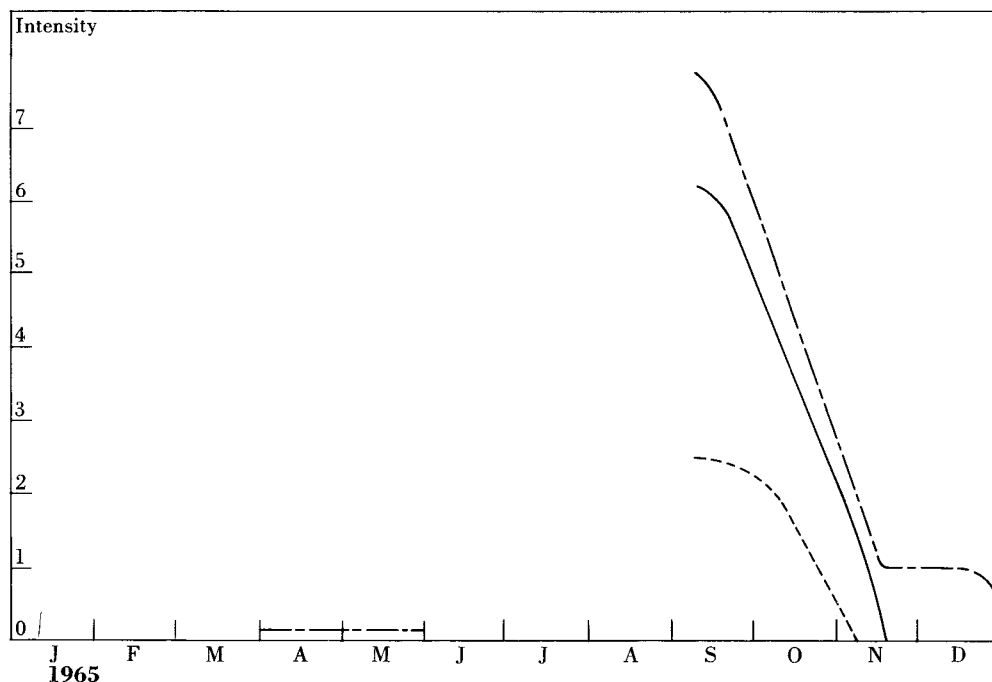


Figure 3. Peak nocturnal intensities of SE (range E to S) migratory movement. The curves are smoothed 15-day moving quartiles representing the intensities reached on 25 (---), 50 (—), and 75 (- - -) per cent of the nights. The sudden increase in the apparent intensities at October 1, 1966, is an artifact of a changed intensity scale. (See Methods section.)

Figure 3



using the U.S. Weather Bureau Daily Weather Maps. In the analyses of correlations between intensity and individual weather parameters we used punch-card records of hourly observations of surface weather at CFB Cold Lake. Figure 10 indicates that most nocturnal movements began near sunset. Hence we chose weather conditions at sunset for use in the analysis. A preliminary examination of the data revealed that sunset temperature relative to normal and relative to that 24 hours earlier was better correlated with intensity than maximum or minimum temperatures relative to their respective normal values for the date in question. Hence the first two temperature parameters were used in the main analysis. The weather data were examined relative to nocturnal intensity of NW (range W to N) and SE (range E to S) movement in spring (April 15 to June 15), autumn (August 1 to October 31), and winter (December 1 to March 15).

# Results

## General description of activity

The Cold Lake radar detects bird activity routinely out to 50 nautical miles from the antenna site and occasionally 70 n.m. away. This activity consists of local (beginning and ending within radar range) and long-distance (appearing from out of range, moving out of range, or both) movements. Both local and long-distance movements occurred throughout the year, although with varying frequency and intensity. Local movements were more common by day than by night in all seasons except winter (181 with hour of highest intensity by day vs 75 by night in spring, summer, and autumn; 14 by day vs 35 by night in winter). Long-distance movements were roughly as common by day as by night except in fall, when they were more common at night. However, the peak intensity of long-distance movements was on average higher at night than in the day except in winter, when they were nearly equal. This paper deals only with long-distance movements unless otherwise noted.

Virtually all long-distance movements visible on the Cold Lake radar are "broad-front movements". While there are several lakes in the area, the terrain is relatively flat and is devoid of pronounced valleys or rows of hills that might concentrate the birds. Although the predominant flight direction by both day and night is SE in fall and NW in spring, low-intensity movements in other directions are common in both seasons. In winter and summer both NW and SE movement occurs. Because there is long-distance movement throughout the year, migration seasons are hard to define. Figures 2 and 3 indicate the peak migration periods.

## Direction of flight

Distributions of mean directions of long-distance nocturnal and diurnal movements at various times of the year are shown in Figures 4 and 5 respectively. In January and February the low-intensity movements (peak intensity 1 to 4) usually moved either north or south. Northward movements were more common than southward ones,

Figure 4. Mean directions of nocturnal long-distance movements through the year. Events with their hour of highest intensity during the night are included; the mean direction of each of these at the hour of peak intensity is presented. The left and right diagrams of each pair indicate low-intensity (1-4) and high-intensity (5-8) events, respectively. The relative lengths of lines show the number of movements in each direction proportional to the number in the most-used direction. The total number of events included is given below and to the right of each diagram.

Figure 4

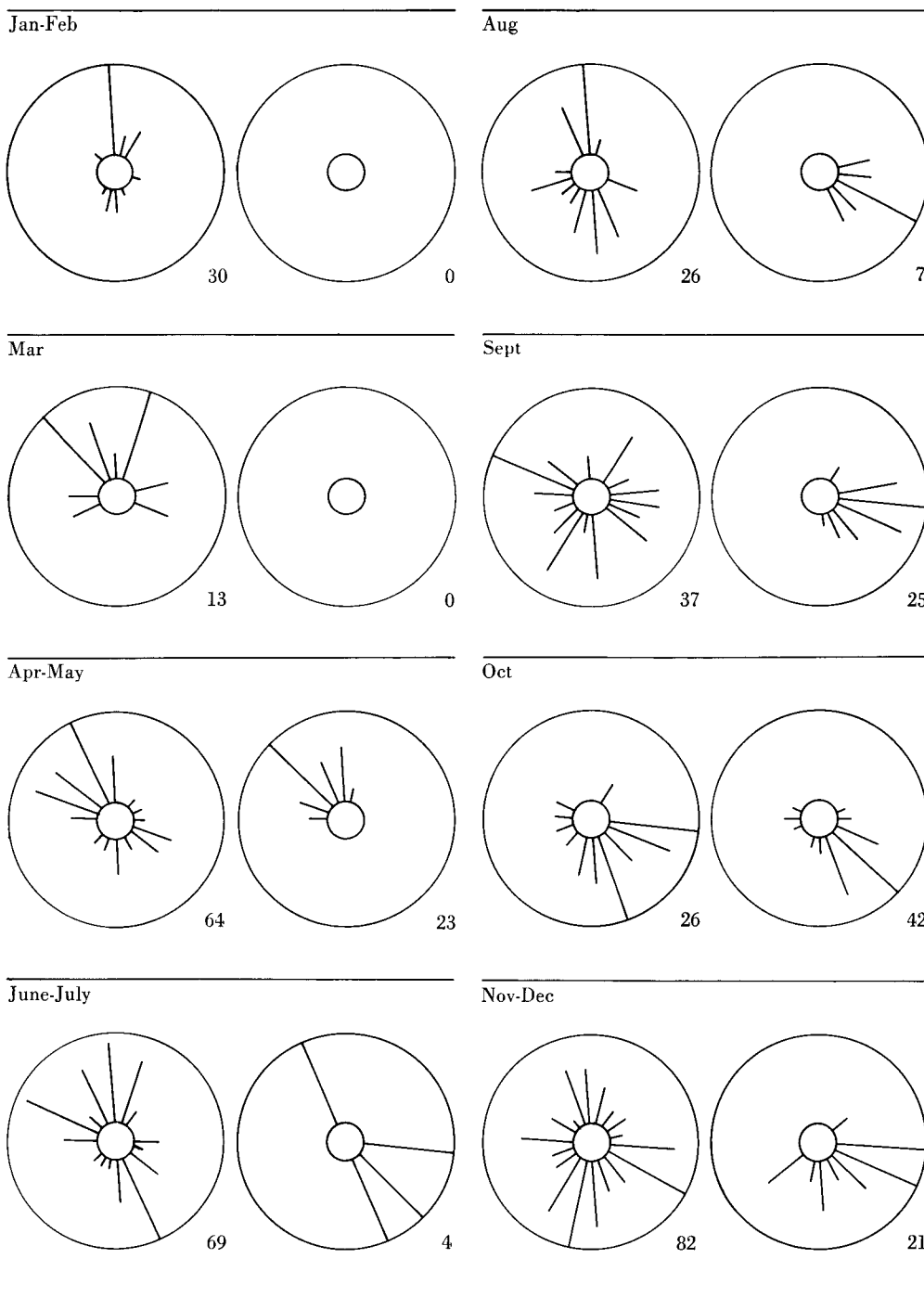
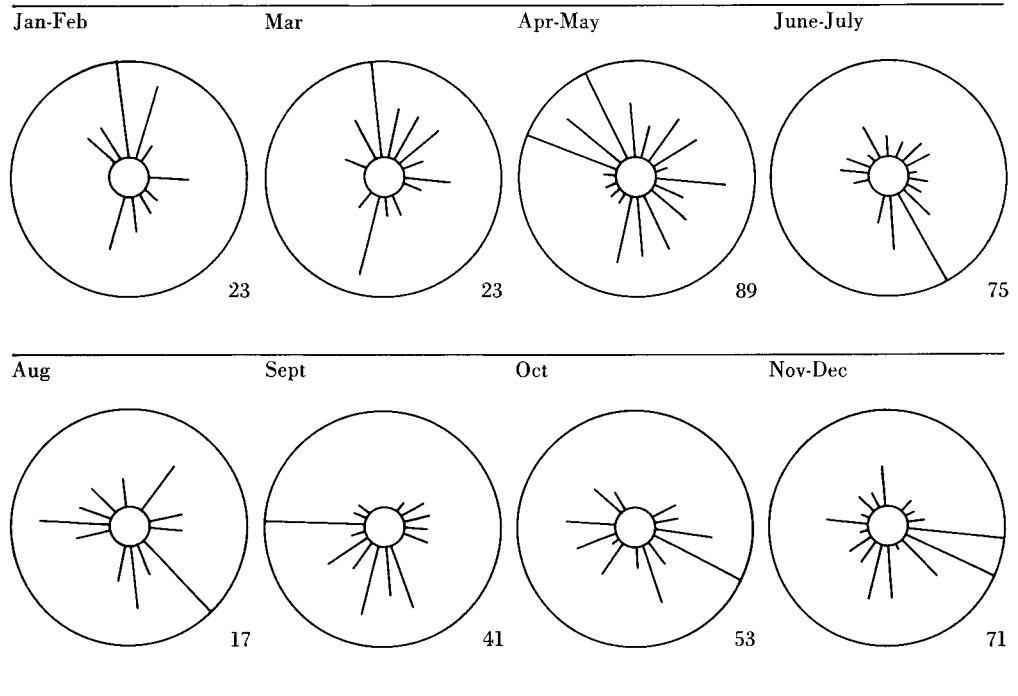


Figure 5. Mean directions of diurnal long-distance movements through the year. Events with their hour of highest intensity during the day are included. Before October and November 1966 (when the intensity scale was modified), 98 per cent of the events were of intensity less than 5. Hence, low- and high-intensity events are not distinguished. The relative lengths of lines show the number of movements in each direction proportional to the number in the most-used direction. The total number of events included is given below and to the right of each diagram.

Figure 5



especially at night. In March most (69 per cent) of the nocturnal movements were in the range of directions WNW–NNE, while the diurnal events were scattered over a wide range of directions. In April and May, many (66 per cent) of the low-intensity and virtually all (96 per cent) of the high-intensity (5 to 8) nocturnal events were in the range west to north; most of the remainder (70 per cent) were in the range east to south. The diurnal events were again more scattered. In particular, there was considerable movement in the NE as well as the NW and SE directions. In June and July, most of the movements were directed in either the range west to north or the range east to south. While diurnal activity was predominantly to the SSE, nocturnal activity was roughly equally split between NW and SE.

By August, the predominant direction was clearly SE. Although many low-intensity nocturnal events moved NNW, most of the high-density and about half of the low-

intensity nocturnal events were in the autumn E to SSW range of directions. The low-intensity movements tended to go SSE, while the stronger events went E and ESE. A similar situation occurred in September. In October both low- and high-intensity nocturnal events usually went SE. The E and ESE to SE shift in the predominant direction of high-intensity events from August and September to October occurred in both 1965 and 1966 and was statistically significant ( $P < .01$  for the hypothesis that the distributions are the same; Kolmogorov-Smirnov test modified for circular distributions — Batschelet, 1965). Diurnal events from August to October had a wide scatter of mean directions. In November and December there was a wide range of directions by both day and night, but movements in the range east to south were especially common.

Figures 6 and 7 show the mean directions of long-distance nocturnally peaking high-



Figure 6. Distributions of mean directions of high-intensity (5–8), nocturnally peaking, long-distance movements in spring (April–June) at five prairie radar sites. The relative lengths of lines show the number of movements in each direction proportional to the number in the most-used direction. The total number of events included is given on the figure.

Figure 7. Distributions of mean directions of high-intensity (5–8), nocturnally peaking, long-distance movements in autumn (August–October) at six prairie radar sites. The relative lengths of lines show the number of movements in each direction proportional to the number in the most-used direction. The total number of events included is given on the figure.

Figure 6

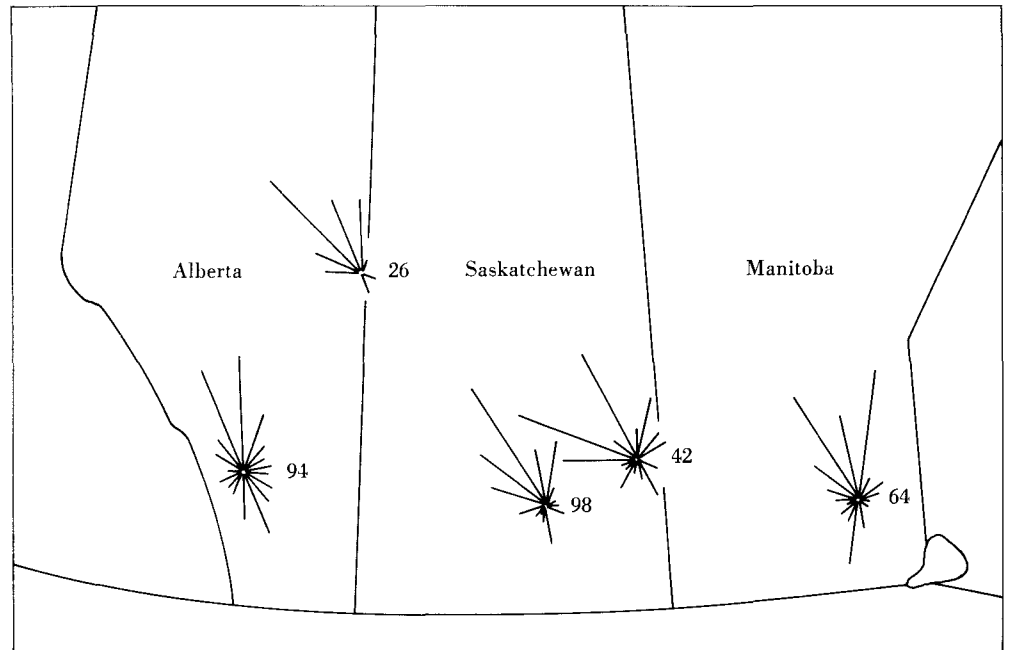


Figure 7

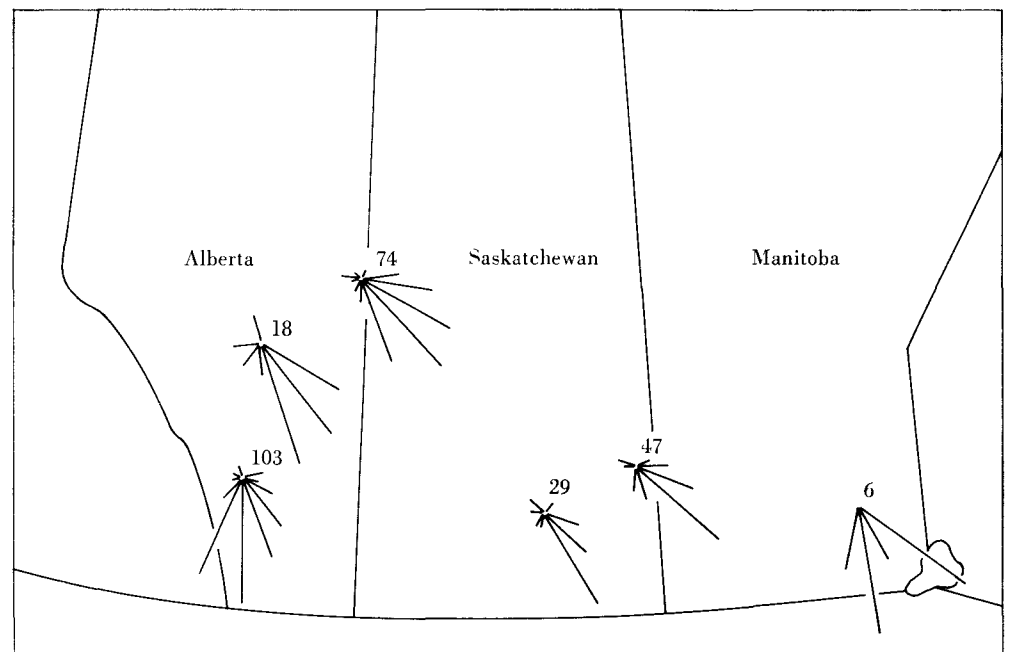


Figure 8. Mean directions at hour of peak intensity of nocturnal light (1-4) and heavy (5-8) long-distance movements in spring (April 1 to June 15) and autumn (July 16 to October 31) with various wind directions. The radial line outside each circle indicates the overall vector mean direction. The relative lengths of lines show the number of movements in each direction proportional to the number in the most-used direction. The total number of events included is given below and to the right of each diagram.

intensity events at Cold Lake and several other prairie sites in spring and autumn respectively. It is apparent that the NW-SE axis of migration observed at Cold Lake is typical of sites in central Alberta and in Saskatchewan. In SE Manitoba, spring migration is more typically to the N than the NW. Data are too sparse to show whether autumn migration in SE Manitoba is more to the south than at sites farther west. At Calgary, Alberta, 300 miles sw of Cold Lake, migration seems to be predominantly on a N-S axis.

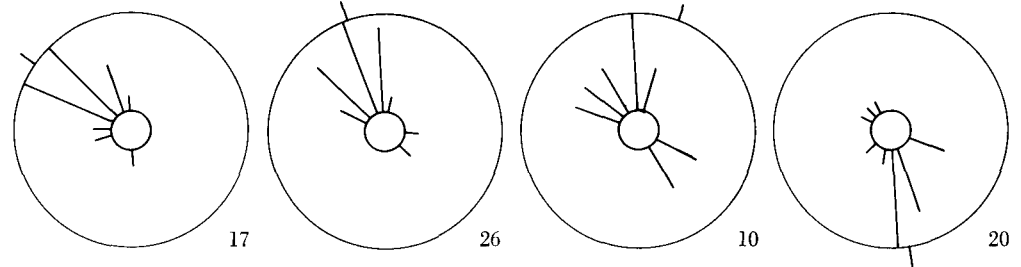
Figure 8 and Table 1 show the influence of wind direction on the direction of nocturnal migration by seasons. *Low-intensity movements* tended to be directed downwind. In autumn, small movements with NW winds were nearly always downwind (expected direction), while with SE winds both forward and reverse movements occurred. *High-intensity movements*, on the contrary, were nearly always NW in spring and SE in autumn. Hence, the direction and the amount of variability in direction were less dependent on wind direction in high-intensity movements than in low-intensity movements. There was, nevertheless, some indication that wind direction affected the direction of autumn high-intensity movements. The vector mean direction of the 14 autumn movements occurring with winds in the range NNW to NE was  $159^\circ$ , while that of the 17 movements with SSE to SW winds was  $114^\circ$ . However, there was wide variability among the mean flight directions and among directions of individual echoes within movements.

#### Changes in direction during a movement

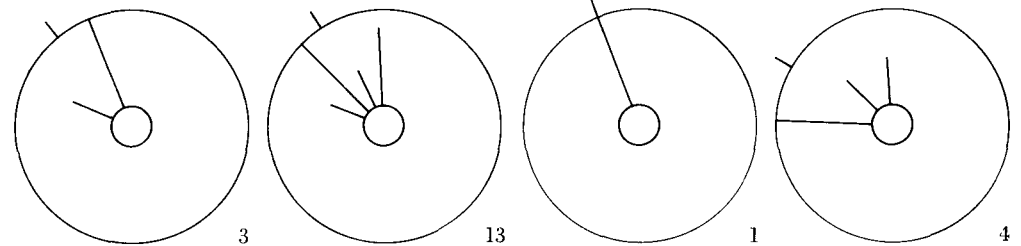
The data presented above refer to the direction of each event at its hour of greatest intensity. However, there are often shifts in mean direction from the start to the end of a movement. Figure 9 shows that by both day and night and throughout the year, the direction of an event rarely shifted by more than  $30^\circ$ . Examination of Figure 9 suggests that with the possible exception of autumn

Figure 8

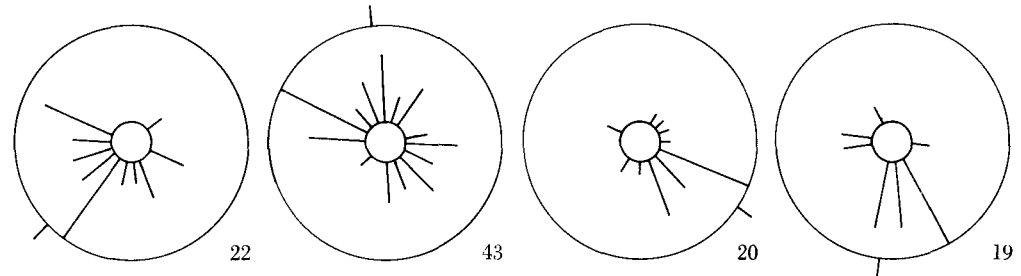
Light movement in spring



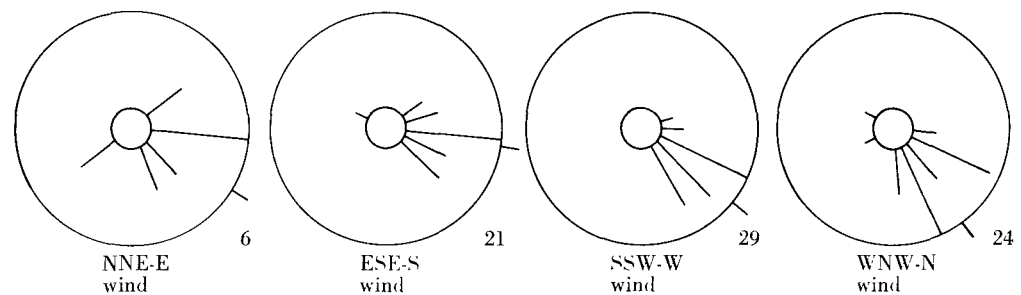
Heavy movement in spring



Light movement in autumn



Heavy movement in autumn



**Table 1**  
Directions of nocturnal long-distance movements  
in spring and autumn

Wind direction	Time*	Spring						Autumn					
		Intensity 1-4			Intensity 5-8			Intensity 1-4			Intensity 5-8		
		Mean, °	AD, °	N	Mean, °	AD, °	N	Mean, °	AD, °	N	Mean, °	AD, °	N
NNE to E	1	300	41	18	325	16	4	223	51	21	143	50	4
	2	306	34	17	322	18	3	228	55	22	120	51	6
	3	324	23	7	327	20	5	199	58	17	115	—	1
ESE to S	1	339	35	26	323	23	12	358	71	46	97	46	19
	2	337	35	26	327	56	13	353	72	43	100	34	21
	3	334	34	18	337	20	10	31	66	23	104	33	20
SSW to W	1	20	61	8	335	—	1	136	44	19	126	21	29
	2	21	64	10	335	—	1	126	45	20	128	20	29
	3	97	69	12	345	—	2	131	44	18	137	23	29
WNW to N	1	170	56	21	307	29	5	176	51	22	142	41	28
	2	169	50	20	304	32	4	189	49	19	142	37	24
	3	179	69	17	255	—	2	156	40	13	145	40	15

Wind directions are surface wind direction at CFB Cold Lake at the time of the start, peak, and end of the event night.

Spring and autumn are April 1 to June 15 and July 16 to October 31.

Mean is the vector mean of the movement means. AD is the mean angular deviation ( $=\sqrt{2(1-r)}$ ), where  $r$  is the ratio of the mean vector length to

the maximum possible mean vector length—Batschelet, 1965). This measure is comparable to the standard deviation of a normal distribution, e.g. the mean  $\pm 1$  AD includes about 67 per cent of the values. N is number of event-nights.

\* Time:

- 1 Starting time of event-night or sunset, whichever was later. Events beginning after midnight were not included.
- 2 Peak intensity hour.
- 3 Ending time of event-night or sunrise, whichever was earlier. Events ending before midnight were not included.

**Table 2**  
Change in mean direction between start and end  
of nocturnal long-distance migration-season events

Season	Intensity	Shift (Mean $\pm$ St. Dev.)*	N	Significance†
April–May	1-4	+17.1 $\pm$ 24.6°	55	$P < .001$
	5-8	+30.0 $\pm$ 31.6	9	$P \approx .02$
August–November	1-4	+9.0 $\pm$ 22.7	67	$P \approx .002$
	5-8	+16.2 $\pm$ 35.4	39	$P < .01$

\* Positive shifts clockwise; negative counter-clockwise.

† Testing hypothesis that mean shift is zero using 2-tailed t-test.

nocturnal events, shifts clockwise are more frequent and larger than shifts counter-clockwise. This possibility was clearly confirmed (in autumn also) by the analysis of migration season events presented in Table 2. The table indicates that for both low- and high-intensity events in both spring and fall, the mean shift between starting and ending times is significantly different from zero and in the clockwise direction. Because high-intensity movements tended to last longer than those of low intensity (see below), one might expect greater directional shifts on the average with high-

intensity events. This appears to be the case in both spring and autumn, but only the autumn difference is significant ( $P \approx .8$  and  $P < .01$  respectively for hypothesis that the shifts are equal; Kolmogorov-Smirnov 2-sample 1-tail tests — Siegel, 1956).

The data in Table 1 permit us to examine the mean directions of movements early and late in the night when only those occasions within certain wind-direction ranges are considered. With various combinations of season, surface wind direction, and intensity of migration, both clockwise and counter-clockwise shifts are seen.

Heavy spring movements with SE (following) winds show a clear clockwise shift from early to late in the night, but heavy autumn movements with NW wind do not. Of the eight situations with side winds (NNE to E and SSW to W) relative to the normal NW–SE axis of movement, three show some degree of shift of their direction of movement *into* the wind. These three cases are light spring movement with NNE to E winds and heavy autumn movement with both NE and SW winds. The other five cases show no change, have very few data, or are not directed on the NW–SE axis of movement and so are not being subjected to side winds. While the three cases of shift in mean direction into the wind might be taken as evidence of overcompensation for lateral wind drift, the shifts are small and inconsistent. Furthermore, differences between wind direction at the surface and at the level of flight are frequent enough that serious biases may result from the use of surface data. Unfortunately, upper wind data were not available at frequent inter-

Figure 9. Distributions of change in direction from first to last hour of long-distance movements, plotted as number of events with a given change in direction relative to number of events with no change. Movements with diurnal and nocturnal peak intensity hours plotted with broken and solid lines, respectively.

Figure 9

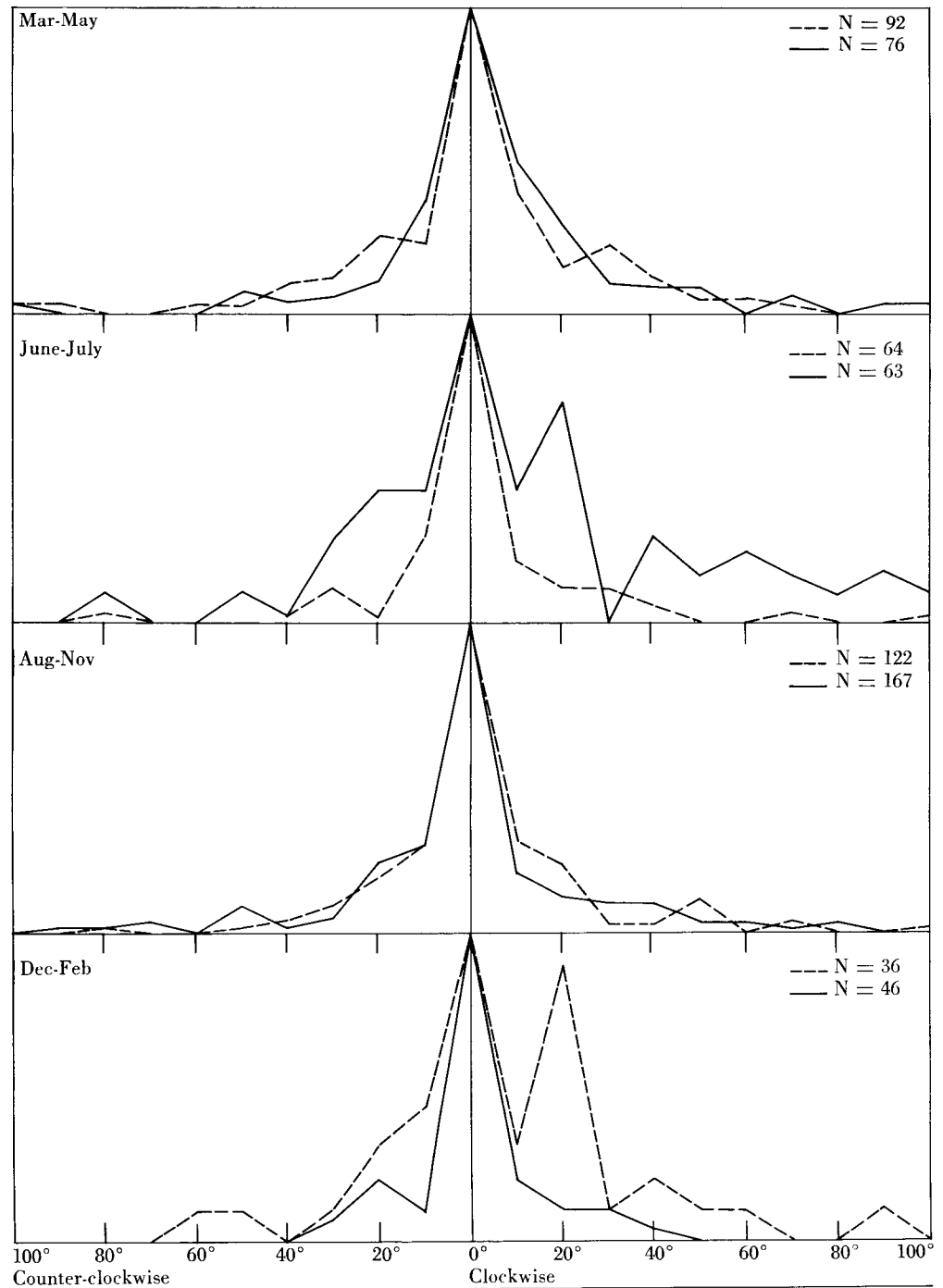
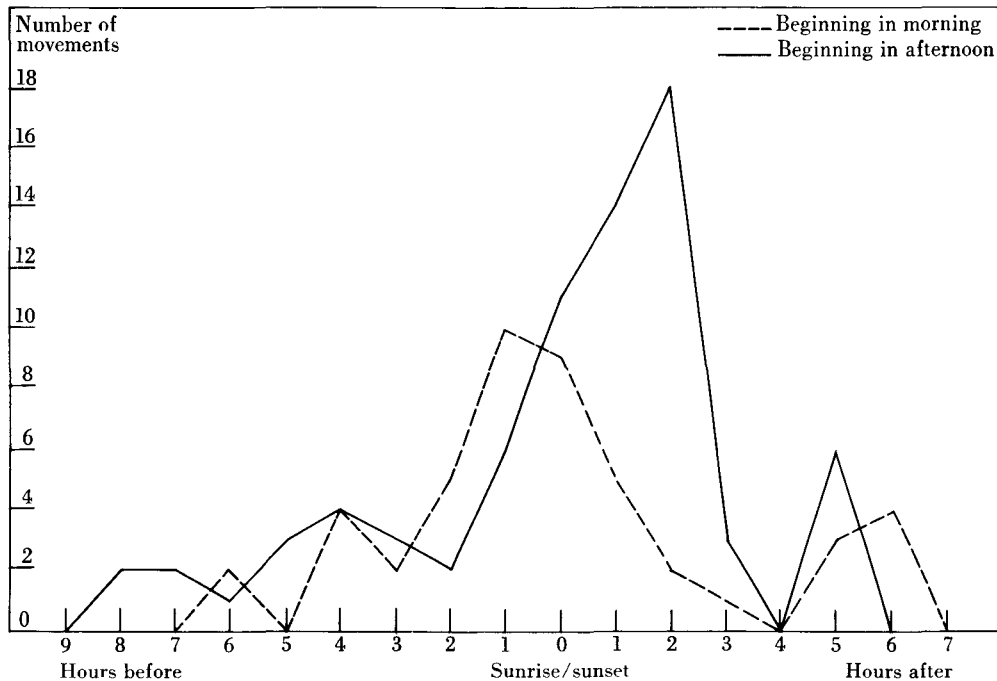


Figure 10. Distributions of starting times of migratory movements in April to November beginning within radar range. Starting times of movements beginning in the morning and afternoon are plotted relative to sunrise and sunset, respectively.

Figure 10



vals, and so could not be used to evaluate the effects of wind shifts during the course of bird movements.

#### Intensity of long-distance movements

The amount of diurnal migratory activity at Cold Lake was usually low, and it varied much less through the year than did the amount of nocturnal movement (Richardson, 1970). Excluding the data for October and November 1966 (when the interpretation of the intensity scale was changed), 73 per cent of the 330 diurnally peaking events had a peak intensity of 1 and only 1.5 per cent had a peak intensity above 4. In contrast, 42 per cent of the 388 nocturnally peaking events had a peak intensity of 1 while 19 per cent had a peak intensity above 4. The amount of nocturnal activity varied markedly through the year. From November to April, the median intensity of nocturnal events was little or no greater than that of diurnal events. In June, July, and November the median noc-

turnal event was only slightly stronger than the median diurnal one. However, in May and in August through October, the median intensity of nocturnal events was much greater than that of diurnal events. The heaviest migration of the year occurred in September, followed by May, October, and August in that order.

Figures 2 and 3 indicate the yearly variation in peak nightly intensities in the two main directions of movement. The prevalence of NW over SE movement in winter is obvious. A progressive decline in the amount of NW movement from May to October contrasts with a progressive increase in the amount of SE movement from March to September. The frequency of moderate-intensity movement in both directions during the summer is noteworthy.

During the migration seasons, the intensity of movement was usually relatively low in the early afternoon. It increased sharply from just before sunset until about 2 or 3 hours after sunset and then more

Figure 11. Proportion of the diurnally (---) and nocturnally (—) peaking migratory events having each echo size as the most frequent size. The number of events having a given echo size as the most frequent size is plotted relative to the

number of events recorded with the seasonally most common size. Total number of movements and the probability that the diurnal and nocturnal distributions are identical (2-tailed Kolmogorov-Smirnov test) are given.

gradually to reach a peak usually before or near midnight. There was a parallel seasonal variation in sunset time and peak time. On the average (but not on all nights), the intensity was maintained at or near its peak until well after midnight, especially in autumn. A gradual decline in intensity until dawn then occurred. During the migration seasons, little or no increase in the typical intensity was apparent at dawn.

During the winter and to a lesser extent during the summer, an increase in intensity on the average did occur at dawn. This was followed by a gradual decline through the day. Particularly in summer but also in winter, an increase in intensity occurred again at sunset.

Further details of hour-to-hour changes in intensity are given in Richardson, 1970.

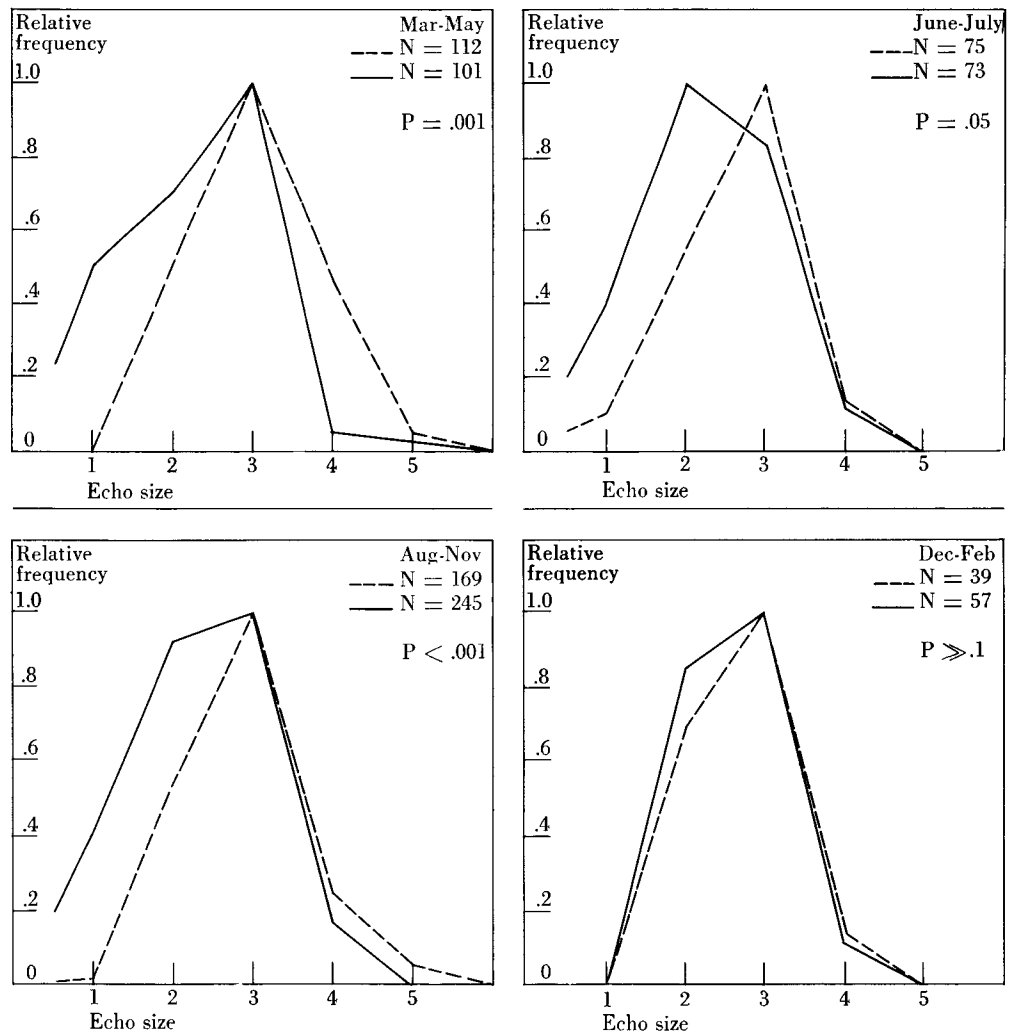
### Timing of long-distance movements

Most events which reached their peak intensity during the day began within a few hours of sunrise, but some began in the afternoon. In contrast, nocturnally peaking events usually began between 4 hours before sunset and 2 hours after sunset. Most heavy (intensity 5–8) nocturnally peaking events began before sunset (42 of 59); 11 began between sunset and midnight; and only 6 began between midnight and sunrise.

The above analysis of starting times is based on all long-distance events; that is, it includes those which entered the radar coverage area from out of range as well as those movements which began within range. When only the latter are examined, the close relation of the starting times of diurnal and nocturnal movements to sunrise and sunset respectively can more clearly be seen (Fig. 10). These nocturnal movements tended to begin at or after sunset while diurnal ones usually began at or before sunrise.

Almost all (73 of 78) the heavy-intensity (5–8) events peaked at night. Most peaked between 1 hour after sunset and 3 hours before sunrise. Low-intensity (1–4) events reached their peak intensities at all hours,

Figure 11



but with concentration at and just after sunrise and sunset.

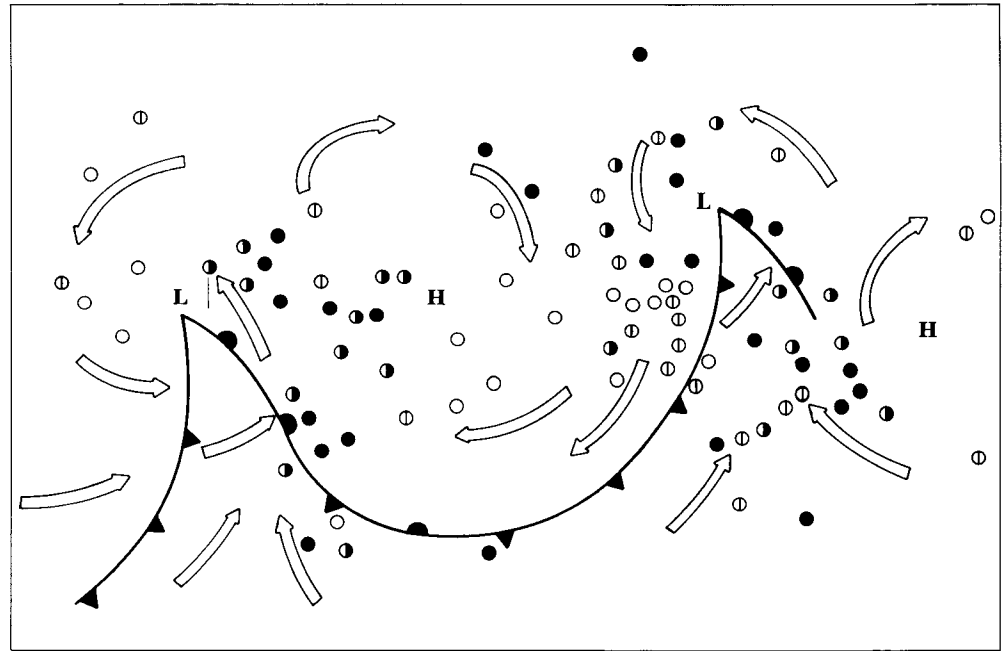
Nearly all (96 per cent) diurnally peaking events ended by 3 hours after sunset. Most (76 per cent) of the low-intensity events peaking at night ended by sunrise. High-intensity nocturnally peaking events almost never ended before midnight (1 of 47 compared to 86 of 276 low-intensity nocturnal events), and most ended near sunrise or during the day. Thus, heavy nocturnal events tended to end later than smaller ones.

In all months, high-intensity events had longer intervals between their start and their peak times and had longer durations than low-intensity movements ( $P \ll .001$  in each case for hypothesis that interval was independent of intensity; Kolmogorov-Smirnov 2-tail tests on intensity 1–4 vs 5–8 events). Median intervals from start to peak for low- and high-intensity events were 2 and 5 hours respectively; median intervals from start to end were 5 and 18 hours. Winter events reached their peaks

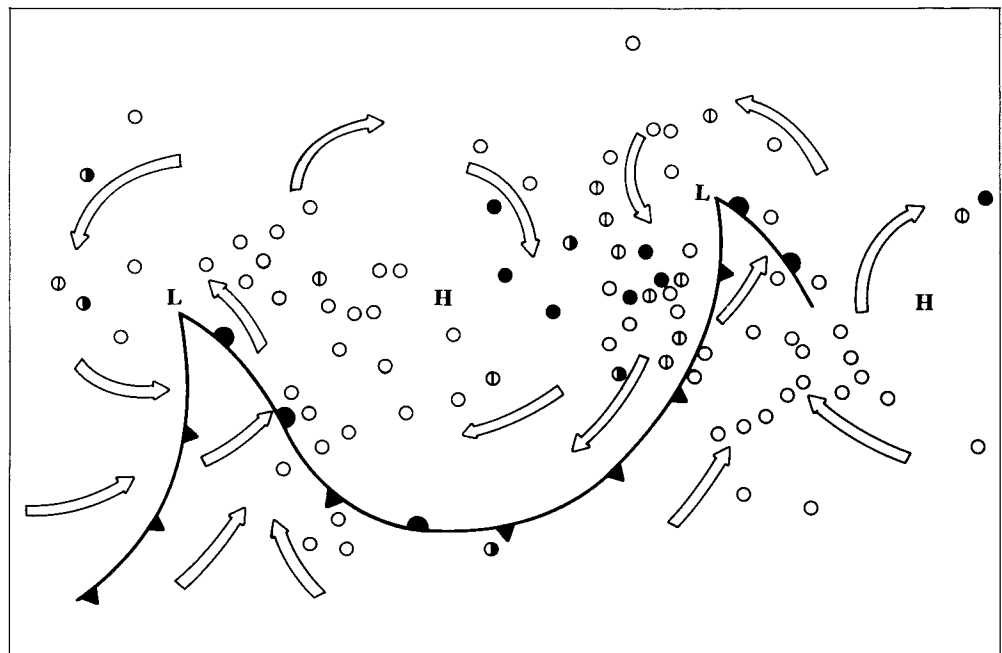
Figure 12. Intensity of nocturnal movement in spring (April 15 to June 15) at Cold Lake, Alberta, with different synoptic weather situations. Each circle represents the peak intensity of movement on one night. The circles are plotted on a generalized weather map in the position most representative of the radar site relative to the prevailing synoptic situation on that night (see text).

Low and high pressure systems, warm (semi-circles) and cold (triangles) fronts, and wind direction are indicated. Intensity of migration is indicated on a 4-level scale by increasing darkness of the circles. For forward movement, the quartile scale is used; for reverse movement, the original 0 to 8 scale with intensities 3 to 8 combined is used.

Figure 12



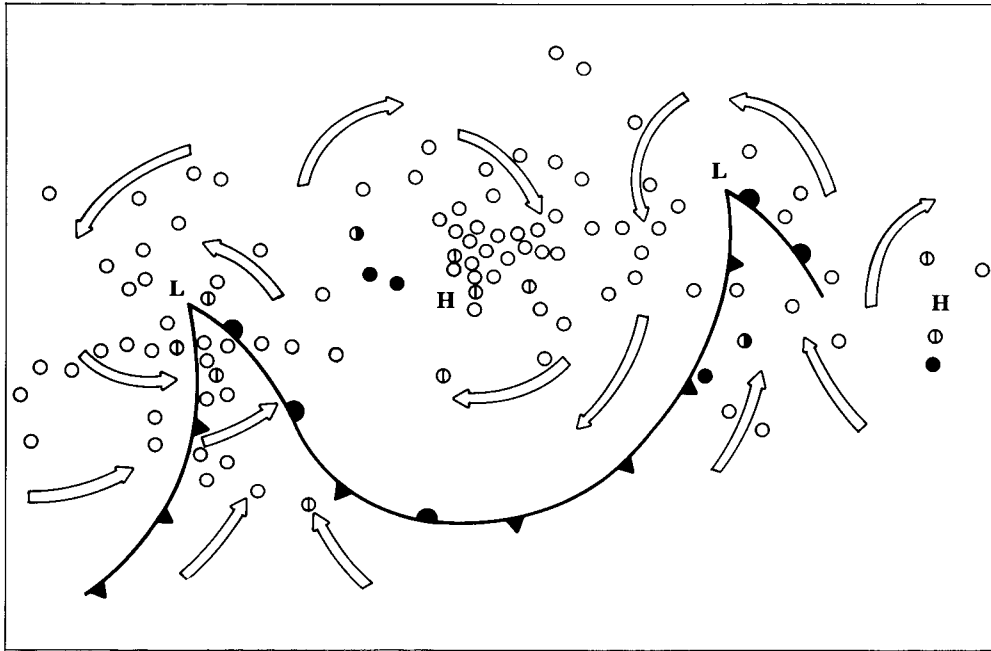
Spring NW movement



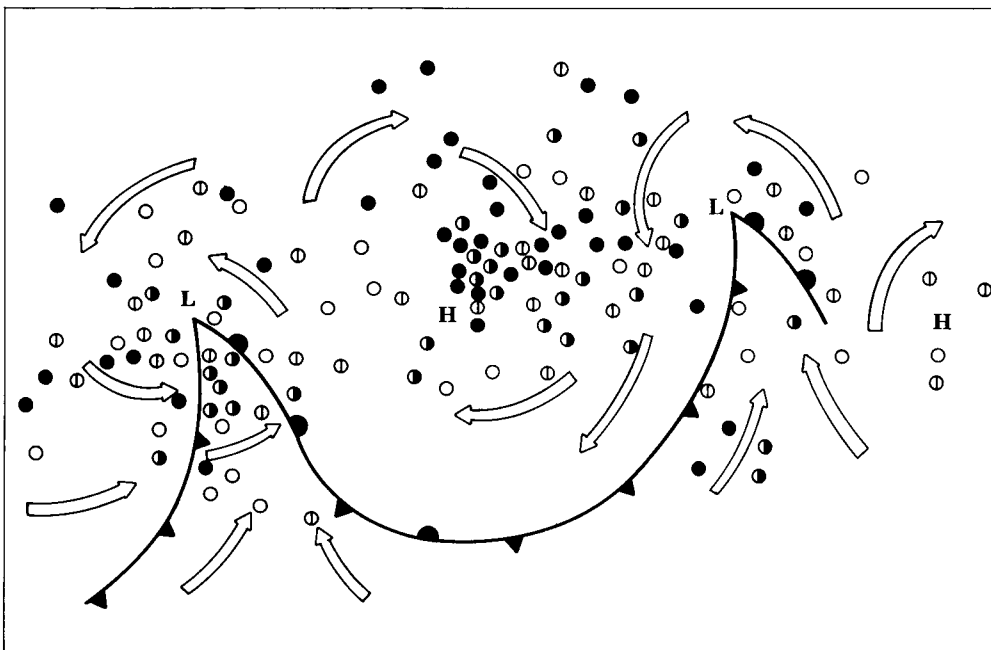
Spring SE movement

Figure 13. Intensity of nocturnal movement in autumn (August 1 to October 31) at Cold Lake, Alberta, with different synoptic weather situations. Symbols as in Figure 12. Four nights were excluded because their synoptic situation could not be classified into any situation found on the generalized map. Data for October 1966 were not used on the NW direction figure because of the change in intensity scale mentioned in the text.

Figure 13



Autumn NW movement



Autumn SE movement

sooner and had shorter durations than low-intensity events in other seasons ( $P < .025$  and  $P < .001$  respectively).

#### Temporal changes in intensity within long-distance movements

The intensity of a movement usually (84 per cent of 718 events) rose gradually from zero to a single peak and then decreased again to zero. On rare occasions the rise was very sharp (when many echoes appeared simultaneously on the radar screen). Sometimes a prolonged period of peak intensity (11 per cent of the events) or a bimodal intensity curve (5 per cent) was found. The latter was particularly common in movements which continued through a day and a night. Since high-intensity movements usually lasted longer than low-intensity ones, it is not surprising that high-intensity nocturnal events had flat or bimodal peaks more frequently than low-intensity nocturnal events ( $P < .001$ ;  $\chi^2$  test).

#### Echo sizes

Figure 11 shows that, except in winter, the most prevalent size of echo in diurnal movements was on the average larger than that in nocturnal movements. The second-most frequent echo size was also notably larger by day than by night in the migration seasons. The day-night difference is readily apparent from an examination of the time-lapse films of migration in any area of Canada that we have studied. Echo sizes become notably smaller as the activity increases near sunset and notably larger as diurnal movements begin near sunrise. While there are many difficulties in interpreting the relationship between bird and flock size and sizes of individual radar echoes (Nisbet, 1963a; Eastwood, 1967; Schaefer, 1968), our results indicate that, on the average, diurnal echoes come from more birds per "flock", larger birds, or both, than do nocturnal echoes. This is not surprising in view of the evidence that most types of birds fly either individually or in very loose flocks at night (Lowery, 1951; Nisbet, 1963a; Eastwood and Rider, 1966).



Radars have signal amplitude limiters that would tend to prevent spot size from increasing with target echoing area. The fact that many bird echoes are barely visible and hence below the limiting amplitude probably causes the variability in spot size. Lunar observations of migration at Cold Lake by Mr. Hans Blokpoel have verified that tight flocks are very rare there at night. Of 609 birds seen on 6 nights in September 1967, all except nine pairs and one flock of about 10 waterfowl passed the moon individually (Blokpoel, 1971b).

In late autumn one would expect a larger proportion of the migratory flow to be comprised of waterfowl than in early autumn. Since waterfowl probably fly in flocks at night as well as by day, one would therefore expect that the difference in echo sizes between day and night would be larger and more significant early than late in the autumn. This was indeed the case. The maximum difference between the cumulative distribution of echo sizes by day and that by night ( $D_{\max}$  in the Kolmogorov-Smirnov test procedure) was 0.401 in August and September but only 0.162 in October and November. These values correspond to respective 1-tailed significance levels of  $P \ll .001$  and  $.05 > P > .02$  for the hypothesis that day and night sizes are identical.

### General relationship between migration intensity and weather

We examined the relationship between the peak intensity of nocturnal migration and the synoptic weather situation as shown on the 2300 MST U.S. Weather Bureau Daily Weather Map. The data are shown diagrammatically in Figures 12 and 13, which are described below. First, we drew a generalized weather map which shows most of the common relationships among pressure systems, fronts, and wind direction at some point on the map. Next, we examined the actual weather map at 2300 on one night in a migration season and noted the locations of these synoptic features relative to Cold Lake (e.g., a high pressure area to

**Table 3**  
Percentage of nights with non-zero intensity of movement

	Winter		Spring		Autumn	
	SE*	NW†	SE*	NW†	SE*	NW†
Following wind‡	23	54	55	91	97	40
Side or opposing wind	11	10	12	54	72	8

\*Direction of movement range E to S.

†Direction of movement range W to N.

‡E to S for NW movement; W to N for SE movement.

the W, a low to the E, a cold front to the SE, and NW winds). Then, we found the location on our generalized map which had a similar position relative to the synoptic features as Cold Lake had relative to the actual synoptic features. At this location a symbol representing the peak intensity of migration on that night was placed. The procedure was then repeated for each night from which we had radar data. Northwest and southeast movements were treated separately on different generalized maps. On most nights, the appropriate position on the generalized map was obvious. On others no position was completely appropriate, and hence we chose the position most closely approximating the true spatial relationships. On 4 autumn nights, we could not locate even an approximately appropriate position; these nights were not plotted. To minimize bias, the appropriate map location was determined in each case without knowledge of the intensity of migration on that night. When examining the resulting figures, it is important to compare the proportions of low-intensity and high-intensity nights under different synoptic conditions and not to look only for concentrations of points (which indicate those synoptic situations which were most common, not necessarily that migration was intense in those situations).

In spring (Fig. 12), NW migration with intensity above normal was proportionately very common with the SE or S winds on the SW and W sides of highs and the SE, E, and NE sides of lows. Heavy NW migra-

**Table 4**  
Correlations between intensity of migration and wind direction in 10°F-temperature categories<sup>1</sup>

Temperature at sunset hour, °F		Winter		Spring		Autumn	
		SE	NW	SE	NW	SE	NW
With respect to normal							
-30 to -21		NS	NS	—	—	—	—
-20	-11	—	—	—	—	—	—
-10	-1	—	—	*	*	***	***
0	9	NS	*	NS	NS	*	**
10	19	—	—	—	—	—	—
20	29	—	—	—	—	—	—
With respect to previous day							
-30 to -21		—	—	—	—	—	—
20	-11	—	—	—	—	—	—
-10	-1	—	—	**	**	**	***
0	9	NS	**	NS	*	**	*
10	19	—	—	—	—	—	—
20	29	—	—	—	—	—	—

NS (no significance)  $P > .05$ . \*  $.05 \geq P > .01$ .

\*\*  $.01 \geq P > .001$ . \*\*\*  $P \leq .001$ . — Insufficient data for test.

<sup>1</sup>Each test examines the null hypothesis that intensity is greater with following than with opposing winds. The one-tailed Mann and Whitney U-test was used.

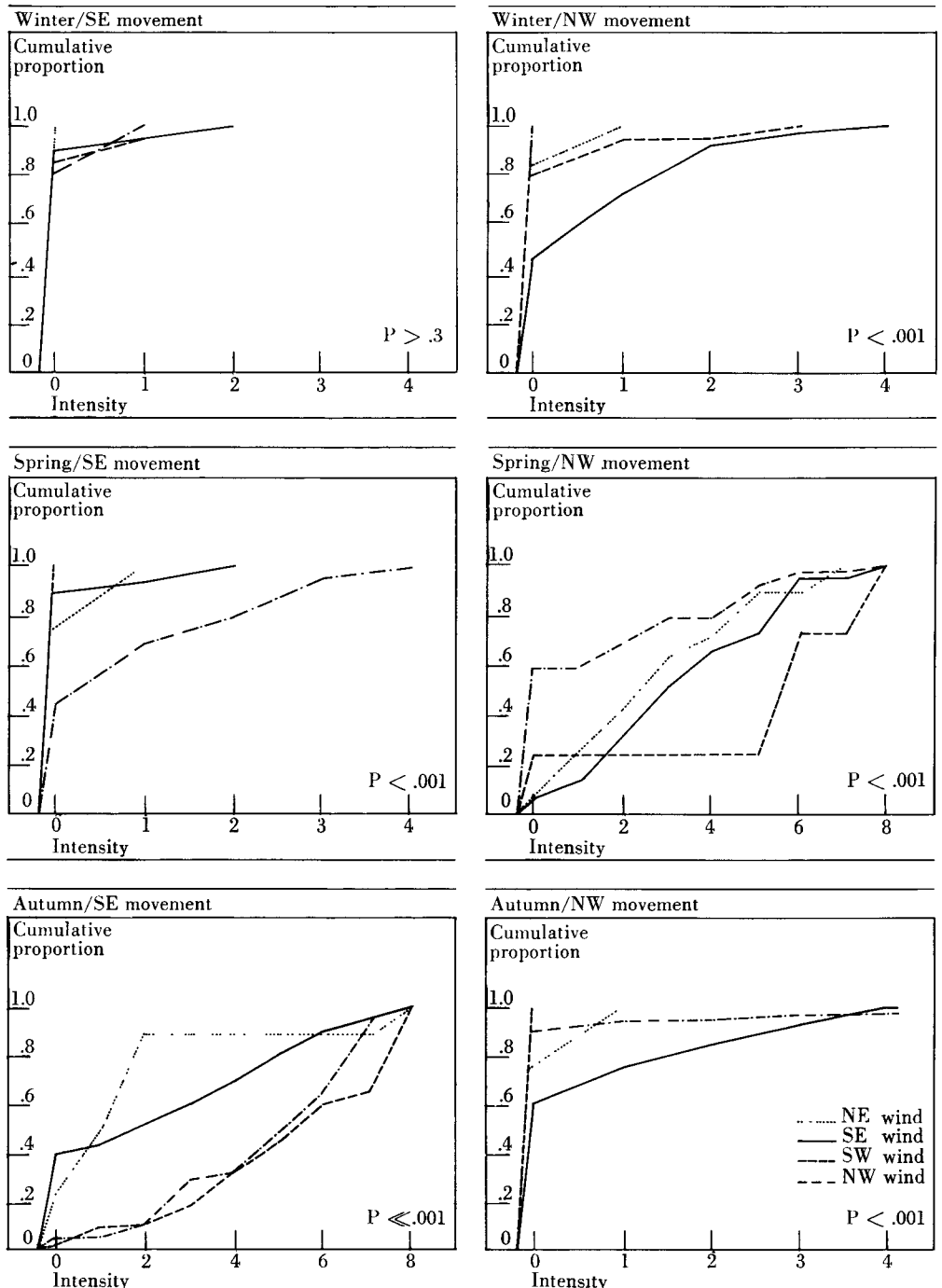
**Table 5**  
Correlations between intensity of migration and wind direction in 10 per cent humidity categories<sup>1</sup>

Humidity, %		Winter		Spring		Autumn	
		SE	NW	SE	NW	SE	NW
With respect to normal							
... to -21		—	—	—	—	—	—
20	-11	—	—	*	NS	NS	NS
10	-1	NS	**	—	—	NS	*
0	9	NS	*	—	—	**	NS
10	19	—	—	—	—	*	NS
20	...	—	—	NS	NS	NS	*
With respect to previous day							
... to -21		—	—	—	—	—	—
20	-11	—	—	—	—	**	NS
-10	-1	NS	*	NS	*	**	NS
0	9	NS	*	NS	*	NS	NS
10	19	—	—	—	—	*	NS
20	...	—	—	—	—	—	—

<sup>1</sup>Legend as in Table 4.

Figure 14. Cumulative frequency distributions of number of nights with each peak intensity under different wind conditions. Southeast movement is shown on the left, and northwest movement on the right. The farther a line is to the right, the higher are the intensities with that wind direction. Probabilities are for hypothesis that distributions under different wind directions are alike.

Figure 14



**Table 6**  
Temperature with respect to normal with different combinations of intensity of migration<sup>1</sup> and wind direction

Bird direction	Wind direction	Intensity	Spring			Autumn			Intensity	Winter		
			Mean	SD	N	Mean	SD	N		Mean	SD	N
Forward	All	1	-4.39	12.28	18	-0.79	6.06	29	None Some	-12.80	15.37	69
		2	-4.67	9.16	24	-0.29	7.76	35		-6.07	14.99	31
		3	0.04	8.15	23	-1.88	10.87	32		*		
		4	0.78	7.39	23	-0.32	9.80	41				
			NS			NS						
Forward	W-N	1	-7.23	12.52	11	-1.00	4.24	4	None Some			
		2	-6.00	8.69	12	-1.00	8.04	13				
		3	-1.00	6.22	10	-4.58	10.49	19				
		4				-0.83	10.13	23				
			NS			NS						
Forward	E-S	1	-1.55	10.85	11	-1.39	5.87	18	None Some	-11.50	13.74	20
		2				0.46	7.91	13		-7.61	16.07	23
		3	-0.43	8.86	14	1.40	5.13	5		NS		
		4	0.10	8.54	10	-2.00	7.07	9				
			NS			NS						
Reverse	All	None	0.16	8.12	64	-0.04	9.15	111	None Some	-12.31	15.08	87
		Some	-7.58	10.43	24	-3.92	6.66	26		0.00	14.42	13
			**			(*)					**	
Reverse	W-N	None	-2.80	7.23	15	-1.22	9.23	54	None Some			
		Some	-6.94	11.18	18	-11.40	8.05	5		*		
			NS			*						
Reverse	E-S	None				0.26	7.31	27	None Some			
		Some				-2.06	5.20	18		NS		

NS  $P > .1$  (\*)  $.1 \geq P > .05$  \*  $.05 \geq P > .01$  \*\*  $.01 \geq P > .001$  \*\*\*  $P \leq .001$

<sup>1</sup>The quartile scale is used for spring NW and autumn SE movement. Weather with some movement is compared to weather with no movement in reverse migration and winter situations. The Kruskal-Wallis test was applied to the spring NW and autumn SE situations while the 2-tailed Mann

and Whitney U-test was applied to the reverse and winter movements. The "Forward" bird direction sections refer to movements NW in spring and winter and SE in autumn; the "Reverse" sections refer to movements SE in spring and winter and NW in autumn (NW = W to N; SE = E to S).

tion frequently occurred prior to the passage of a nearby warm front, and it also was not uncommon in the westward air-flow N of a low. The intensity of migration was very frequently below normal on the E side of a high and the SW side of a low. Somewhat more nights of high-intensity NW migration occurred on the W side of a low than might have been anticipated.

Reverse migration in spring occurred almost exclusively with more or less NW winds and a high pressure area to the W, a low to the E, or both. It was very infrequent in the synoptic situations which commonly had strong spring NW movement.

The intensity of autumn SE movement (Fig. 13) was related to the synoptic features in a manner similar to that of spring SE movement. Above-normal intensities were especially common with the W, NW, and N winds on the N, NE, and E sides of highs and the NW, W, and SW sides of lows. Heavy SE migration was more common than expected on the S side of lows, including ahead of the cold front and inside a warm sector. However, on these occasions the winds were usually westerly and the birds were not far ahead of the cold front.

Reverse migration in autumn usually occurred in the same conditions as strong

**Table 7**  
Temperature change from previous day with different combinations of intensity<sup>1</sup> of migration and wind direction

Bird direction	Wind direction	Intensity	Spring			Autumn			Intensity	Winter		
			Mean	SD	N	Mean	SD	N		Mean	SD	N
Forward	All	1	-3.06	10.44	17	0.00	7.71	27	None	-1.09	9.12	65
		2	0.71	6.50	24	-1.67	6.51	33	Some	1.27	6.55	30
		3	2.43	7.16	21	-0.16	8.28	31			NS	
		4	0.35	5.75	20	1.33	7.64	40				
Forward	W-N	1	-7.40	9.78	10	0.75	5.12	4	None			
		2	1.25	6.66	12	-3.58	5.47	12	Some			
		3	0.44	7.75	9	-1.58	6.58	19				
		4				-0.39	8.81	23				
Forward	E-S	1	0.18	7.31	11	0.25	8.90	16	None	3.25	9.32	20
		2				1.25	5.80	12	Some	1.70	6.62	23
		3	2.92	6.87	13	2.60	4.16	5			NS	
		4	0.33	5.72	9	1.88	4.36	8				
Reverse	All	None	2.10	6.77	58	0.27	7.81	108	None	-0.55	8.38	85
		Some	-4.13	7.77	24	-1.57	6.04	23	Some	1.40	9.12	10
Reverse	W-N	None	2.39	7.02	13	-0.98	7.15	53	None			
		Some	-4.78	8.82	18	-5.40	7.89	5	Some			
Reverse	E-S	None				1.54	7.56	26	None			
		Some				-0.07	5.02	15	Some			

<sup>1</sup>Legend as in Table 6.

spring NW migration. It virtually never occurred in the conditions typically associated with autumn SE migration.

It should be emphasized that in Figures 12 and 13, the weather at 2300 MST is considered. While the peak intensity usually occurred about that time, it occasionally was not reached until several hours later. Especially when fronts or lows are nearby, the conditions may change considerably in a few hours.

#### Winter movements

Both northerly and southerly movements occurred throughout the winter. This might not be expected in an area where in mid-January the normal daily maximum and minimum temperatures are +6° and -12°F. There was movement W, NW, or (most commonly) N on 31 nights between December 1, 1965, and March 15, 1966.

Only 9 of these 31 movements occurred on nights when the surface temperature rose above freezing at any time during the two preceding or one following days, and 5 of these 9 nights were in March. During the period January 19 to 28, 1966, the temperature never rose above -12°F, and reached a minimum of -50. Nevertheless, on 4 of these 10 nights small, long-distance movements to the N or NW occurred. The surface wind was easterly on each of these 4 nights. The movements persisted for periods of 3 to 19 hours, although individual birds did not necessarily fly that long.

Nearly all the winter movements were very light. In the Discussion we will indicate that these small movements involve very few birds compared to the large spring and autumn movements. However, on one occasion (January 17/18, 1966) medium-intensity north and later south flights oc-

curred. A movement to the N and NNE began at 1400 (about 2 hours before sunset) and reached its peak intensity around sunset. This flight began with a low pressure area to the west and with southerly geostrophic winds. At sunset the surface wind was SE, the temperature was 25°F (15° above the normal sunset hour value for that date and 12° above the sunset temperature the previous day), the pressure had dropped 7 millibars in the previous 6 hours, and the sky was 9/10 overcast. The low and an associated cold front moved through about 2100, some 5 hours after sunset. At that time, the northerly flight ended and a new southerly flight began. Thereafter the winds were northerly. It is not known whether the same birds were involved in the northerly and southerly flights. The light southerly flight ended at 0100, but began again at 0600, reached medium intensity briefly at 0800, and continued at low intensity until sunset. At sunset on the 18th, the wind was NNW at 16 mph, the temperature was -8°F, and the pressure had risen 3.5 millibars in the preceding 6 hours as the low moved away to the east. This sequence of movements, the heaviest of the winter, thus occurred in the typical conditions for north and south migration-season flights.

#### Correlations between wind direction and intensity of migration

Intensity of nocturnal flights was strongly correlated with wind direction in five of the six types of movement examined (NW in spring, autumn, and winter; SE in spring and autumn but apparently not winter). In each of these five types of movement, the intensity distributions with NE, SE, SW, and NW winds differed significantly ( $P < .001$  in each case; Kruskal-Wallis tests), and in each case the intensities with following winds were markedly higher than the intensities with opposing winds (Fig. 14). With side winds, the intensity distributions were lower than with following winds for reverse and winter movements, but not always for migration in the

**Table 8**

Barometric pressure change from 6 hours before sunset to sunset with different combinations of intensity<sup>1</sup> of migration and wind direction

Bird direction	Wind direction	Intensity	Spring			Autumn			Winter			
			Mean	SD	N	Mean	SD	N	Intensity	Mean	SD	N
Forward	All	1	10.61	29.62	18	-21.31	26.35	29	None	-1.64	32.38	69
		2	-6.04	26.00	24	-6.94	31.64	35	Some	-21.74	25.46	31
		3	-8.74	24.72	23	1.56	30.88	32		**		
		4	-7.39	21.38	23	-4.73	27.13	41				
		NS			**							
Forward	W-N	1	23.00	27.50	11	11.00	22.32	4	None Some			
		2	2.00	27.69	12	16.39	30.08	13				
		3 } 4 }	13.20	20.29	10	16.58 10.48	21.99 24.15	19 23				
		NS			NS							
		Forward	E-S	1 } 2 }	-17.73	19.64	11	-30.28 -30.15	20.53 24.63	18 13	None Some	-20.20 -30.91
3	-15.50			26.38	14	-36.80	36.78	5	NS			
4	-10.60			21.65	10	-30.89	20.53	9				
NS				NS								
Reverse	All			None	-10.72	24.57	64	-4.45	29.19	111	None	-9.23
		Some	15.04	19.87	24	-19.65	29.90	26	Some	1.23	47.97	13
		***			*			NS				
Reverse	W-N	None	5.40	32.76	15	13.72	25.26	54	None			
		Some	18.22	18.57	18	14.40	12.12	5	Some			
		(*)			NS							
Reverse	E-S	None				-29.63	22.34	27	None			
		Some				-33.28	24.61	18	Some			
					NS							

<sup>1</sup>Legend as in Table 6. Pressure change is measured in tenths of millibars.

normal direction. While intensities of spring NW movement appeared to be higher with SW side winds than with SE following winds, SW winds occurred on only 4 days and hence the difference is not statistically significant. Figure 14 and Table 3 indicate that reverse and winter movements occurred on only about 10 per cent of the nights without following winds, while the forward-direction spring and autumn movements occurred with any but directly opposing winds (although little autumn SE movement occurred with NE side winds). While the analysis summarized in Figure 14 showed no significant relationship, Table 3 shows that SE movement in winter was twice as frequent with following wind as without. The absence of significant correlation using the Kruskal-Wallis test resulted from the small range of intensities which occurred in this type of activity.

The above analysis is based on the original 0 to 8 intensity scale. When the intensity distributions based on quartile curves were examined with the four different wind directions, we again found a significant effect of wind on intensity ( $P < .02$  for spring NW movement and  $P \ll .001$  for autumn SE movement; Kruskal-Wallis tests). As before, intensities were markedly higher with following than with opposing winds and intensities with side winds were similar to those with following winds.

Because (i) there are previous reports that both temperature and wind direction are correlated with intensity, (ii) temperature and wind direction are strongly inter-related, and (iii) there is inconclusive and conflicting evidence about the relative magnitude of the partial correlations of intensity with wind direction and temperature

**Table 9**Wind speed with different combinations of intensity<sup>1</sup> of migration and wind direction

Bird direction	Wind direction	Intensity	Spring			Autumn			Winter			
			Mean	SD	N	Mean	SD	N	Intensity	Mean	SD	N
Forward	All	1	10.67	6.21	18	8.45	4.41	29	None	9.41	5.21	69
		2	9.13	4.43	24	9.89	7.55	35	Some	8.26	5.73	31
		3	8.74	5.54	23	7.94	5.11	32			NS	
		4	8.74	4.94	23	9.63	4.18	41				
Forward	W-N			NS			NS					
		1	12.91	5.38	11	11.00	6.48	4	None			
		2	12.00	3.79	12	14.46	10.24	13	Some			
		3 } 4 }	10.30	5.38	10	9.42 10.74	5.19 4.38	19 23				
Forward	E-S			NS			NS					
		1 } 2 }	8.64	3.59	11	9.00 7.92	2.95 3.69	18 13	None Some	8.55 9.30	3.40 5.31	20 23
		3	10.00	5.86	14	8.00	3.24	5			NS	
		4	10.00	3.94	10	9.78	4.30	9				
Reverse	All			NS			NS					
		None	8.64	5.17	64	9.11	5.83	111	None	8.83	5.33	87
Reverse	W-N	Some	10.83	5.10	24	8.81	3.69	26	Some	10.54	5.64	13
				(*)			NS				NS	
Reverse	E-S	None	10.93	5.11	15	11.44	6.66	54	None			
		Some	12.50	4.59	18	8.00	4.80	5	Some			
Reverse	E-S			NS			NS					
		None				8.04	3.67	27	None			
Reverse	E-S	Some				9.78	2.86	18	Some			
							(*)					

<sup>1</sup>Legend as in Table 6. Wind speed measured in miles per hour.

(Richardson, 1966; Nisbet and Drury, 1968; Richardson and Haight, 1970), we looked for relationships between intensity of migration and wind direction when only days with temperatures in various 10°F-ranges were considered. The temperature at sunset relative to normal and relative to the previous day were both used (Table 4).

Considering *temperature relative to normal*, 12 combinations of movement type (e.g., NW in spring) and temperature category (e.g., 0 to 9°F above normal) had sufficient data to be used. Here, sufficient data means 5 or more nights with each of following and opposing wind. Of the 12 situations with sufficient data, 7 showed significantly ( $P < .05$ ) greater intensity with following than with opposing winds. If there is no actual correlation within 10°-temperature ranges, the probability of obtaining significant differences in 7 of 12

tests (using the  $P = .05$  criterion of significance in each test) is less than 0.0001. Hence, we conclude that the intensity of migration is correlated with wind direction within 10°-ranges of temperature relative to normal.

Considering *temperature change* from the previous day, of 10 situations with sufficient data, 3 showed significantly ( $P < .05$ ) greater intensity with following than with opposing winds. The probability of obtaining 8 or more significant ( $P < .05$ ) differences in 10 tests if there is no actual relationship is again less than 0.0001, so we conclude that intensity is also correlated with wind direction within 10°-ranges of temperature change.

In contrast to the results of our Ontario radar study (Richardson and Haight, 1970), humidity is here at least as strongly correlated with intensity as is temperature.

Hence we examined the data to see if the correlation between wind direction and intensity was also maintained when only days within certain ranges of humidity were considered. In examining the relationship between intensity and wind direction within 10 per cent ranges of *humidity relative to normal*, we found 18 situations with sufficient data (Table 5). Of these, 7 showed significantly ( $P < .05$ ) greater intensity with following than with opposing winds. Also, 7 of 16 situations had significantly more migration with following than with opposing winds within 10 per cent *humidity change* categories. The probabilities of obtaining at least 7 of 18 and 7 of 16 significant differences if there are no actual correlations are both less than 0.0001. Hence, we conclude that intensity is correlated with wind direction within 10 per cent ranges of humidity relative to normal or relative to the previous day.

### Correlation between temperature and intensity of migration

It was expected that temperature would be high and/or increasing with NW movements and low and/or decreasing with SE movements, since temperatures are correlated with wind direction and wind direction is correlated with intensity of migration. Spring NW movement showed the expected direction of correlation with temperature both relative to normal and relative to the previous day (low and decreasing mean temperature with little movement; higher and relatively stable mean temperature with stronger movement). However, these differences were not statistically significant (Tables 6 and 7). Autumn SE movement showed no evidence of correlation with temperature. Spring SE reverse movement was significantly correlated with low and decreasing temperature as expected. The correlation with decreasing temperature remained significant when only days with following winds were considered; that with low temperature dropped below the significance level. Autumn NW reverse movement was almost significantly correlated with low

(but not decreasing) temperature when all days were considered. This is the opposite direction to that expected. In winter there were no obvious correlations with temperature change, but the mean temperature was significantly higher with both NW and SE movement than without such movement. This is the expected direction of correlation for NW but not for SE movement.

When examining the results of many statistical tests, one must remember that using  $P=.05$  as a significance criterion, a Type I error (Johnson and Leone, 1964:197) will be made on the average in 5 per cent of the tests. There is only a small (0.004) probability of obtaining 4 significant ( $P<.05$ ) correlations out of 14 tests purely on the basis of Type I errors, suggesting a genuine correlation between temperature relative to normal and intensity. However, this is not the case for the temperature change situation (Table 7), where only 2 of 14 differences are significant (and these are not independent).

### Correlation between barometric pressure trend and intensity

In view of the relationships between pressure pattern positions and direction and intensity of wind (Fig. 12 and 13), one would expect days with strong SE and NW movement to have higher and lower pressure trends respectively than days with little SE or NW movement. Table 8 shows this to be the case, although the differences were not all significant. When only days with following or opposing winds were considered, none of the differences was significant at the  $P=.05$  level.

### Wind speed and cloud extent vs intensity

No clear differences in wind speed or cloud extent were found when the values of these parameters on days with much migration were compared with those on days with little movement (Tables 9 and 10). From the results of others (e.g., Lack, 1963 a,b; Parslow, 1969) and from energetic considerations, we expected the mean wind

**Table 10**

Cloud extent with different combinations of intensity<sup>1</sup> of migration and wind direction

Bird direction	Wind direction	Intensity	Spring			Autumn			Winter			
			Mean	SD	N	Mean	SD	N	Intensity	Mean	SD	N
Forward	All	1	7.17	3.09	18	6.03	3.45	29	None	6.31	3.46	69
		2	6.50	3.40	24	6.63	2.83	35	Some	6.48	4.02	31
		3	6.22	3.57	23	6.66	3.32	32		NS		
		4	5.48	3.09	23	5.56	3.41	41				
Forward	W-N			NS			NS					
		1	7.09	2.59	11	5.25	3.59	4	None			
		2	6.58	3.53	12	7.00	2.58	13				
		3 } 4 }	6.80	2.04	10	5.79 6.30	3.87 3.20	19 23				
Forward	E-S			NS			NS					
		1 } 2 }	6.91	3.70	11	6.28 6.23	3.71 3.11	18 13	None	7.70	2.36	20
		3	5.71	3.87	14	8.00	1.87	5				
		4	4.90	3.78	10	3.67	4.09	9				
Reverse	All	None	5.95	3.42	64	6.27	3.25	111	None	6.39	3.62	87
		Some	7.21	2.83 (*)	24	5.85	3.33	26	Some	6.23	3.79	13
Reverse	W-N	None	6.47	2.83	15	6.28	3.29	54	None			
		Some	7.11	2.74	18	5.60	3.58	5				
Reverse	E-S	None		NS			NS					
		Some				6.04 5.78	3.71 3.52	27 18	None			

<sup>1</sup>Legend as in Table 6. Cloud extent in tenths of the sky covered.

speed to be lower with strong than with light migration when only days with opposing winds were considered. This was not the case.

If view of the sky is necessary for orientation, one might expect the mean cloud extent would be less with strong than with light migration. Except with strong autumn migration against opposing wind, there was little indication of such an effect (Table 10). Cloud extent refers here to the fraction of the sky over Cold Lake covered by cloud of any type at sunset. Because cloud conditions frequently vary considerably over short intervals of space or time, this is probably not a very good measure of the ability of the birds to see the sky.

### Correlations between humidity and intensity

Because strong spring NW migration tends

to occur in the west sides of high pressure areas (Fig. 12), lower humidity was expected with strong than with light NW movement. This was the case (Table 11). The direction of this correlation persisted when only days with following wind were considered, but it was no longer significant. Table 12 suggests that humidity tended to be relatively stable as well as low when strong NW movement occurred, while it tended to be rising with light movement. However this difference was not significant. Intensity of autumn SE movement was significantly correlated with humidity, but not in a linear fashion. The correlation of high mean humidity with slightly above-normal intensity persisted when days with either following wind or opposing wind were considered. Spring SE reverse movement tended to occur with higher humidity than when no SE movement was occurring, but this

**Table 11**

Relative humidity with respect to normal with different combinations of intensity<sup>1</sup> of migration and wind direction

Bird direction	Wind direction	Intensity	Spring			Autumn			Winter			
			Mean	SD	N	Mean	SD	N	Intensity	Mean	SD	N
Forward	All	1	9.56	19.14	18	1.48	12.30	29	None	3.32	8.90	69
		2	13.00	19.12	24	1.29	14.66	35	Some	1.61	10.49	31
		3	1.70	16.62	23	9.69	17.03	32		NS		
		4	-3.00	13.65	23	1.15	13.19	41		*		
Forward	W-N	1	9.82	18.84	11	1.00	10.23	4	None			
		2	15.42	20.00	12	-0.08	17.69	13	Some			
		3 } 4 }	5.70	16.53	10	9.63	15.81	19				
						3.26	13.13	23		NS		
Forward	E-S	1 } 2 }	8.55	17.27	11	4.44	12.35	18	None	6.05	9.18	20
						1.69	11.38	13	Some	2.87	10.98	23
		3	2.14	16.63	14	12.60	18.69	5		*		
		4	-5.50	10.90	10	-4.22	15.03	9		NS		
Reverse	All	None	2.25	17.42	64	2.49	14.64	111	None	2.01	9.30	87
		Some	12.92	17.86	24	6.50	14.56	26	Some	8.00	8.65	13
Reverse	W-N	None	9.53	18.94	15	4.00	15.18	54	None			
		Some	11.50	18.60	18	9.00	14.98	5	Some			
Reverse	E-S	None				0.78	12.14	27	None			
		Some				5.89	15.77	18	Some	NS		

<sup>1</sup>Legend as in Table 6. Relative humidity in per cent relative to normal.

difference disappeared when only nights with following winds were considered. Autumn NW movement showed no obvious correlation with humidity. Winter days with SE movement had higher humidity than those without SE movement, while winter days with NW movement tended to have lower humidity than those without NW movement, at least when only following wind situations were considered.

We were interested in the possibility that the correlation of spring NW intensity with humidity might be the result of autocorrelation of humidity with other weather parameters to which the birds might be responding. A rigorous analysis was not possible because of the ordinal nature of the data (see Discussion). However, application of the non-parametric Kendall partial rank correlation procedure (Siegel,

1956) to various pairings of likely parameters suggested that autocorrelation neither of humidity and temperature nor of humidity and pressure gradient was responsible for the apparent intensity-humidity correlation (Table 13). This result might have been anticipated from the absence of strong temperature or pressure correlation with intensity of spring NW movement on days with SE winds.

The situations under which the various types of movement usually occurred will be summarized and discussed below.



**Table 12**  
Relative humidity change from the previous day  
with different combinations of intensity<sup>1</sup> of  
migration and wind direction

Bird direction	Wind direction	Intensity	Spring			Autumn			Intensity	Winter		
			Mean	SD	N	Mean	SD	N		Mean	SD	N
Forward	All	1	4.94	26.97	17	-1.82	11.23	27	None	1.11	11.58	65
		2	3.50	19.97	24	-0.12	16.83	33	Some	0.00	10.97	30
		3	-1.57	13.27	21	4.03	20.01	31			NS	
		4	-2.85	12.31	20	-2.70	17.33	40				
			NS			NS						
Forward	W-N	1	10.40	27.10	10	1.00	5.72	4	None			
		2	3.67	17.69	12	-0.42	16.40	12	Some			
		3 } 4 }	1.11	13.15	9	1.26	21.59	19				
			NS			NS						
Forward	E-S	1 } 2 }	8.64	17.04	11	-0.06	10.00	16	None	1.20	10.78	20
						-5.67	17.94	12	Some	1.35	10.12	23
		3	1.15	11.93	13	9.40	14.52	5			NS	
		4	-1.56	6.97	9	0.00	8.19	8				
			NS			NS						
Reverse	All	None	-1.48	16.51	58	-0.38	17.36	108	None	0.59	11.51	85
		Some	6.83	22.21	24	0.22	14.63	23	Some	2.20	10.19	10
			NS			NS					NS	
Reverse	W-N	None	0.39	11.15	13	0.98	19.60	53	None			
		Some	8.50	24.13	18	-6.20	19.97	5	Some			
			NS			NS						
Reverse	E-S	None				-1.81	13.42	26	None			
		Some				1.67	13.49	15	Some			
						NS						

<sup>1</sup>Legend as in Table 6. Relative humidity change  
in per cent.

**Table 13**  
Correlation of intensity of spring northwest  
movement with weather\* on days with following  
winds†

Factors examined for correlation	Factor whose effect held constant	Kendall correlation coefficient
Intensity and humidity	—	-.35‡
	Temperature	-.35
	Pressure	-.36
Intensity and temperature	—	.06
	Humidity	-.09
	Pressure	.07
Intensity and pressure	—	.08
	Temperature	.09
	Humidity	.13

\*Humidity and temperature are humidity and  
temperature relative to normal for that day and  
hour and are measured at sunset. Pressure is  
pressure trend from 6 hours before sunset to  
sunset.

†Winds in the range E to S were considered to  
be following.

‡This coefficient is significantly different from  
zero ( $P < .01$ ) while the comparable test in Table  
11 showed only marginal significance. The differ-  
ence results from either the differing properties  
of the two tests, the fact that quartile intensities  
were used in Table 11 and actual intensities here,  
or both.

# Discussion

## Direction of movement in different parts of North America

We have found that the heavier movements in Alberta and Saskatchewan tend to go NW in spring and SE in autumn. In SE Manitoba, they more commonly go N than NW in spring. The results of other workers, moving from east to west across the continent, are as follows: Lowery (1951:455) showed that in the E and SE United States, spring migration is more to the NE than to the N. Moon-watching studies in southern Ontario (Richardson, unpubl.) reveal that this is also the case there. The predominant directions of migration in E Massachusetts and in Nova Scotia and New Brunswick are NE or ENE in spring and SW in autumn (Drury and Nisbet, 1964; Nisbet and Drury, 1967a; Richardson, unpubl.). In central Illinois, the mean directions of the general flow of migrants are slightly E of N in spring (but not NE) and slightly E of S in autumn (Bellrose and Graber, 1963). At Havana, Illinois, and at St. Louis, Missouri, the mean directions of autumn duck migration are SSW and S respectively, while farther west at Des Moines, Iowa, and Kansas City they are both SSE (Bellrose, 1964). Mallard ducks (*Anas platyrhynchos*) banded in Illinois are recovered to the NW rather than to the N (Bellrose, 1966). The mean directions of spring migration in 1948 at Stillwater, Oklahoma, Columbia, Missouri, and Ottumwa, Iowa, were all approximately NNW, although that at Lawrence, Kansas, was slightly E of N (Lowery, 1951). The Ottumwa results are based on 10 nights of observations; only 3 or 4 nights of data are available from each of the other three sites.

In summary, the above results suggest a gradual shift in the predominant axis of migration from NE-SW in the east through N-S in the eastern plains area to NW-SE in the central and western plains of the United States and Canada. This is doubtless in large part explained by the geography of North America: the distance between the mountains to the west and the ocean to the east progressively increases as one moves

north from the Gulf of Mexico to Canada. In Alberta, the NW-SE migration axis is parallel to the eastern edge of the mountains, which are only about 300 miles SW of Cold Lake and much closer to the Edmonton and (especially) Calgary radar sites. The apparent exception to the general pattern found at Calgary may reflect the proximity of that site to the mountains. The wintering areas of most Anseriform, Charadriiform, and passerine species migrating through Alberta are largely east of the longitude of Cold Lake.

## Changes in direction over the course of a movement

When all spring or autumn small or large long-distance nocturnal events are examined as groups, slight but statistically significant clockwise shifts in direction from early to late in the night are apparent (Table 2; Fig. 9). Clockwise shifts during the night have also been found by Drury and Nisbet (1964), Nisbet and Drury (1967a), Graber (1968), and Steidinger (1968). Gehring (1963) found a clockwise shift during the day in Switzerland. While it is possible that birds passing early in the day or night have different "preferred" directions from those passing later, especially in coastal New England, it is also possible that individual birds characteristically change their direction to the right while in flight. If the latter possibility actually occurs and if the birds start to fly each night in the direction they were flying at the end of the last flight, the elliptical migration routes discussed by Bellrose and Graber (1963:383), Evans (1966a:352), Graber (1968:63), and Parslow (1969:67) would result. Such routes may have evolved to take advantage of prevailing wind directions. Gehring (1963), Graber (1968), and Steidinger (1968) all found that the clockwise shift could not be explained by wind change. Likewise, the clockwise shift at Cold Lake is still seen in heavy spring nocturnal movements when only nights with surface winds in the range east to south are considered (Table 1). How-

ever, the shift in heavy autumn movements disappears when only nights with west to north winds are considered.

## Variations in direction between movements

Smaller movements were found to occur in virtually all directions at all times of the year; generally they were directed downwind. In contrast, high-intensity movements were nearly always directed NW in spring and SE in autumn regardless of wind direction, but most frequently occurred with following winds. These results seem reasonable if one accepts the postulate that it is energetically advantageous for birds to fly with following winds. Presumably (i) certain proportions of the migratory birds in the Alberta area possess orientation systems directing them in each of several different ranges of direction, (ii) a larger proportion of these birds are oriented along the NW-SE axis than in other directions, (iii) each of these birds has a mechanism determining whether or not to fly at a given time, (iv) one of the inputs to the timing mechanism is wind direction or related factors, and (v) following wind situations (relative to the "preferred" direction for that bird) are more likely to result in migration than opposing wind situations. Such a system has been proposed by Evans (1966a) and Nisbet and Drury (1967a). This system would result in predominantly downwind flight each day, with the largest flights always directed NW in spring and SE in autumn and occurring with following winds.

The possible occurrence of lateral drift caused by the wind has been extensively debated because of its importance to theories of orientation (see Nisbet and Drury, 1967a for references; also Bellrose, 1967; Evans, 1968a,b; Steidinger, 1968; Lack, 1969; Parslow, 1969). We have found that the wind direction on a given day has a pronounced effect on the direction of any small movements which may occur on that day and, at least in autumn, a smaller effect on strong movements. Much of this effect

is probably explained by the selection of following wind situations for migration as discussed above. Whether or not there is any residual lateral drift cannot be determined from our data.

### Reverse movements

It is difficult to believe that the normal migration direction of many birds past Cold Lake is NW in autumn or SE in spring. Nevertheless, considerable numbers of movements are so directed (Fig. 4–8). This suggests that in at least some birds, the orientation systems referred to above direct individual birds in different directions at different times within the same season. Possible reasons for these changes in direction have been suggested for specific cases: (i) following of “diversion lines” along the edge of geographic or habitat barriers (e.g., Wallraff and Kiepenheuer, 1962; Bergman and Donner, 1964; Mueller and Berger, 1967), (ii) adaptive response to being over water at dawn (Baird and Nisbet, 1960; Myres, 1964a), (iii) confusion of a celestial orientation system (Lee, 1963), (iv) inaccuracy in the mechanism of the orientational system (Gehring, 1963; Steidinger, 1968), (v) overshooting of the goal area (Bellrose, 1966; Mueller and Berger, 1969), and (vi) “redetermined” orientation after lateral drift caused by the wind (e.g., Evans, 1968b). With the possible exception of overshooting, it is unlikely that these suggested reasons apply to the “reverse” flights in Alberta. Possibilities iii, iv, and vi may occasionally occur, but these would probably produce shifted but not totally reversed directions.

Reverse migration seems to occur in more restricted synoptic weather situations than forward migration (Fig. 12 and 13; Richardson and Haight, 1970). Southward flight in spring in response to a return of cold weather would seem to have some selective advantage, but northward autumn flights cannot be explained in this manner. For some reason, a few NW autumn movements began with the opposing winds found with a high pressure area close to the west

(see Fig. 13 and below). The significance of reverse movements to theories of orientation has yet to be explored.

Most radar and moon-watching studies, including this one, have found that reverse migration is frequent, but usually involves smaller movements than the large forward-direction flights (e.g., Lowery, 1951; Lowery and Newman, 1955, 1966; Drury and Keith, 1962; Gehring, 1963; Lack, 1963a,b; Lee, 1963; Drury and Nisbet, 1964; Parslow, 1969). Richardson and Haight (1970) found that reverse starling migration in Ontario is not only rather common but also frequently quite intense. In contrast to these studies, Hassler *et al.* (1963:70) found that reverse autumn migration is very uncommon in Illinois. Furthermore, moon-watching in Ontario for a total of 164 hours on 31 spring and 24 autumn nights has shown that only about 5 per cent of the migrants are directed towards the southern half of the compass in spring and the northern half in autumn (Richardson, unpubl.). Nevertheless, reverse movements are frequently seen on radar. This apparent contradiction results from the different techniques employed. Moon-watching and the narrow-beam short-range radar used by Hassler *et al.* (1963) can detect individual birds and so give a fair indication of the actual number of birds moving in each direction. Moderate and high-power surveillance radars with PPI displays (used in all the radar studies mentioned above except that of Hassler *et al.*) have lower resolution and, to oversimplify, indicate whether or not there is a threshold amount of echoing-area in a given volume of space. Whether there is 5 or 50 times the threshold echoing-area per pulse volume has little effect on the appearance of the display in that area. Hence, high-power radars tend to underemphasize the volume of large movements and overemphasize small reverse flights, unless detailed analyses (involving echo counts and examination of “thinning”) are made. Furthermore, moon-watching and narrow-beam radars sample a larger volume of space

at high than at low altitude. If reverse migrants tend to fly lower than forward migrants, a smaller proportion of the reverse than of the forward migrants might be detected with these techniques. However, we have evidence that the high-power surveillance radars we use are quite capable of detecting very low-flying migrants.

While we therefore conclude that reverse migration constitutes only a small proportion of the total migration past a given area during a season and that reverse movements usually involve comparatively few birds, both moon-watching and radar indicate that at many times more birds are involved in reverse than in forward movement. The phenomenon is certainly worth further study.

### Intensity of movement

As noted above, there are many difficulties in estimating numbers of birds from radar displays. These problems are of two types.

(i) The amount of echo on the screen is not necessarily linearly related to the number of birds or groups of birds in the air. We are just now developing the capability of calibrating the surveillance radar using moon-watching and a narrow-beam radar (Blokpoel, 1971a,b). In the meantime, we have had to use an arbitrary ordinal intensity scale and statistical methods appropriate to ordinal data rather than a more desirable interval scale and parametric statistical procedures.

(ii) There are various possible sources of error in the application of the ordinal intensity scale to the data. In the first place, adjustments of the radar over which we had no control may change the apparent intensity. Secondly, the presence of anomalous propagation (AP — described by Eastwood, 1967:51) occasionally makes assessment of the film especially difficult. Although AP and bird echoes can almost always be distinguished on the time-lapse film, AP sometimes tends to obscure bird echoes at long range and at other times increases the range to which birds are visible. The use of the quartile scale for NW spring and SE autumn movements and

of the "some vs none" analysis for reverse and winter flights minimized these two sources of error. A third possible problem is that birds flying high are more likely to be detected by radar than those flying low, especially at greater distances from the antenna. Wilcock (1964) has found that large low-altitude visible movements may not be detected by radar, and Evans (1966b) has presented evidence that visible (i.e., low-altitude diurnal) migration may constitute a significant fraction of the total migration in some areas. We must therefore qualify all our results by stating that they may be biased in favour of birds flying at medium and high altitudes. However, we believe that most birds are flying high enough to be detected, since (i) the modal height of those migrating birds flying above 1200 feet a.g.l. at Cold Lake is usually well above 1200 feet (Blokpoel, 1971b), (ii) we have detected low-altitude starling roosting and gull flights in Ontario using surveillance radars with much lower power (550 kw) than the Cold Lake radar, and (iii) we have used a height finder radar to measure the heights of many bird echoes visible on a high-power surveillance radar PPI and have found that very low migrants are visible on the PPI. A fourth source of error is the assigning of intensity values by eye rather than by any procedure involving echo counts. This source of error is minimal — repeated assessment of the same film gives very similar results (within 1 intensity scale value in nearly all cases). A fifth possible source of error is that, on the average, birds flying upwind will have lower groundspeeds than those flying downwind (although Bellrose, 1967, has provided evidence that the difference may not be as great as expected). The MTI system will therefore reduce the signal strength of echoes moving upwind more than it does of echoes moving downwind. This in turn will reduce the maximum detectable range of birds moving upwind, and so on the average will lead to a reduced apparent density at each distance from the centre of the display compared to what would be

seen if the same birds were flying downwind. This source of error is minimized in our case because Normal Video rather than MTI was used beyond about 30 n.m. range.

Considering all these possible sources of error, one might suspect that our estimates of migration density are so crude as to be useless for analyses of the effects of weather on migration. Fortunately, this does not seem to be the case. Preliminary results suggest that errors of more than 1 or at most 2 scale values (on our 0 to 8 scale) are unusual (Blokpoel, 1971b). However, many more data will be needed to confirm this. The reason for the apparent relative accuracy of our estimates in spite of the many possible sources of error is probably that migration density frequently varies by two and occasionally by three orders of magnitude from night to night (Newman and Lowery, 1964; Nisbet and Drury, 1968:502; Blokpoel, 1971b; Richardson, unpubl.). In contrast, most of the sources of error are by factors considerably less than ten.

### Weather and migration

Many authors have looked for correlations between weather and day-to-day variations in the volume of bird migration (see Lack, 1960 for review). More recent papers are cited by Nisbet and Drury (1968). It has been believed for many years that "waves" of spring migrants in eastern North America most commonly move north with falling pressure and a southerly flow of warm air associated with a high pressure area moving away to the east, a low approaching from the west, or both (e.g., Bagg *et al.*, 1950). This was confirmed statistically by Richardson (1966). Curtis (1969) has recently published an analysis of the relative amounts of departure and arrival in spring with various synoptic situations. It is believed that heavy autumn migration occurs with rising pressure and a northerly flow of cold air as a low pressure area moves away to the east, a high approaches from the west, or both (e.g., Bennett, 1952; Mueller and Berger, 1961).

Recent studies have attempted to determine (i) whether conclusions based on radar and moon-watching data are similar to the original conclusions based on diurnal visual observations, (ii) how well these generalizations apply to different species and different geographic areas, and (iii) what specific proximate factors are involved in determining whether or not a bird will migrate at a given time (Richardson and Haight, 1970). We shall discuss each of these questions in the light of the Alberta data.

### (i) Direct observations of migration vs ground censuses

In general, the Alberta data support the original ideas about relationships between pressure patterns and intensity of migration (Fig. 12 and 13). However, strong migration did not occur on all the nights with supposedly favourable conditions. More surprisingly, considerable migration occurred on some nights with supposedly unfavourable conditions. Lowery and Newman (1966) obtained similar results by examining different sites on the same nights rather than the same site on different nights. The pressure trend was indeed more negative in spring and more positive in autumn with heavy than with light migration, but only the autumn difference was significant (Table 8). Also as expected, spring intensities were greatest with S winds and autumn intensities with NW winds (Fig. 14). On the other hand, there was little difference in temperature and temperature change between days with high- and low-intensity migration.

### (ii) Differences in the responses to weather

Different birds in different areas sometimes migrate with different weather conditions. For example, Nisbet and Drury (1968:520) found more NE migration in spring when they were near the centre of a high pressure area, than a day or two later when they were in the warm sector of an approaching low. They believed that earlier authors had reported more migration in

the warm sector because "most of the previous studies were of grounded or diurnal migrants, and were biased by the fact that such birds tend to be concentrated or forced down by the disturbed weather associated with troughs". However, Richardson and Haight (1970) have found that starlings, which also migrate NE in spring, depart proportionately more frequently in the warm sectors of lows than near the centres of highs. That study was based on direct radar observations of starling migration departures, and so was not biased, although the migration was diurnal.

Spring and autumn forward and reverse starling migration appeared to be more closely related to a NW-SE than to a W-E pressure gradient; this is perpendicular to their NE-SW axis of flight. In contrast, Figures 12 and 13 suggest that migration in Alberta is strongest with a NE-SW pressure gradient (perpendicular to the predominant NW-SE axis of migration). This difference is especially apparent if these figures are compared with the corresponding ones for starling migration (Richardson and Haight, 1970: Fig. 3 and 4). Heavy autumn SE migration in Alberta is proportionately most frequent on the NE or even N sides of highs and the W and SW sides of lows; autumn SW (and spring SW reverse) starling migration in Ontario is most frequent on the E and SE sides of highs and the NW and W sides of lows. Heavy spring NW migration in Alberta is most frequent on the SW and W sides of highs and SE, E, NE, and even N of lows; spring NE starling migration is most frequent SE or S of lows. When these pressure-gradient directions are combined with the data on pressure-trend correlations (Table 8), one finds that both forward and reverse movements in both spring and autumn of both starlings in Ontario and all birds in Alberta are all strongest and most frequent when the pressure gradient is falling from the birds' right to their left. Such situations give following geostrophic winds.

However, as noted above, Nisbet and Drury (1968) found more NE migration

along the East Coast with SE winds and near the centre of a high than with SW winds in the warm sector of a low. Perhaps it is adaptively more advantageous for birds along the coast to select conditions with onshore SE side winds and little chance of a rapid change to offshore winds than to select conditions with following SW winds but an appreciable chance of a shift to offshore winds should the cold front behind the warm sector suddenly arrive.

### (iii) Responses to individual weather parameters

Many authors have attempted to determine which individual weather parameters are used in the mechanism determining whether or not a bird will fly at a given time. Some studies have examined only the simple correlations between intensity and various parameters one at a time. Since different weather variables are highly interrelated, this method is of little assistance in determining causal relationships. However, it is useful in providing a description of the conditions under which much and little migration occur. Other studies, notably Lack (1963a,b), Gruys-Casimir (1965), and Nisbet and Drury (1968), have applied multiple linear regression procedures to study the amount of correlation between each weather variable and intensity, other parameters being equal. This method could not be used here because our intensity scale is ordinal rather than interval. Other difficulties with the multiple regression model are discussed by Richardson and Haight (1970). A third approach, that used here, is to examine the relationship between migration volume and one weather variable at a time when only those days with one or more other variables in certain restricted ranges of values are considered.

Regrettably, none of the above methods allows us to determine conclusively which parameters the birds respond to and which they ignore. Nevertheless, some indications have been obtained.

(i) There is an obvious simple correlation between intensity and *wind direction*

for NW spring, SE autumn, and most other types of movement (Fig. 14). More importantly, this correlation persisted in 10°F-temperature categories and in 10 per cent humidity ranges. Wind direction has been considered by most North American authors to show the strongest simple correlation of any parameter with the volume of migration. Of the several parameters which have been found by various authors to be correlated with migration volume, only wind direction and rain show the same direction of correlation for all types of broad-front movement. That is, migration is almost always heavier with following than with opposing winds regardless of season or direction of movement, whereas at different times and places intensity may be positively or negatively correlated (or uncorrelated) with temperature, humidity, pressure change, wind speed, cloud extent, and atmospheric stability.

(ii) *Pressure trend* shows clear simple correlation with intensity, but at least in autumn this trend disappears when only nights with following (or opposing) wind are considered (Table 8). If birds were reacting to pressure changes *per se*, one would expect the correlation to persist, since not all nights with following (or opposing) winds have similar pressure trends.

(iii) Intensity of normal direction migration was not obviously related to *temperature* (Tables 6 and 7). This was unexpected, in view of the correlation between intense migration and S winds in spring and NW winds in autumn (Fig. 14). Several previous studies of migration in North America have found correlations between intensity and temperature (e.g., Mueller and Berger, 1961; Richardson, 1966; Nisbet and Drury, 1968; Richardson and Haight, 1970), but some have not (e.g., Raynor, 1956; Hassler *et al.*, 1963). In contrast to the situation with normal migration, we did find relationships between intensity of reverse migration and temperature in both spring and autumn. The unexpected direction of the autumn correlation was the result of very low temperature

on the few nights having reverse migration with opposing winds (Table 6).

(iv) *Wind speed* and *cloud extent* show no obvious simple correlation with intensity nor any correlation when only nights with following winds were considered. Again, if the birds were strongly influenced by either of these factors, correlation on nights with following wind would be expected.

(v) In spring, the relationship between high intensity of NW movement and low humidity persisted when only nights with SE wind were considered (Table 13). The correlation was also not the result of autocorrelation of humidity and temperature or pressure trend (Table 13). This indicates that these birds may be using low humidity as an indicator of the preferred time for NW migration. Nisbet and Drury (1968) found a negative partial correlation between intensity and humidity using the multiple regression method. Richardson (1966) found that, on the average, spring "waves" of migrants in Ontario occurred with rising but near-normal humidity. How humidity might be measured by the birds is not clear.

The above results suggest but do not prove that birds flying over Cold Lake respond to wind direction and (at least for spring NW movement) humidity. They also suggest that pressure trend, temperature, wind speed, and cloud extent are not major cues used in the system which determines whether or not to fly on a given night. However, the absence of any apparent correlation with one factor may mean only that birds respond to that parameter and also to another correlated with the first in an opposing manner. We suspect that at least some of the last four parameters listed above may have modifying influences on the responses to other factors by the Alberta birds and that they may be more important in some birds than others.

In general, we believe that birds have evolved short-term migration timing mechanisms placing different weights on the separate weather parameters depending

upon season and species. More specifically, the particular pattern of weights would depend primarily upon the "preferred" direction. The pattern would serve to initiate migration in synoptic situations optimal for survival. Since most birds in most situations seem more likely to fly with following than with opposing winds, and since there are obvious energetic reasons for flying with tail winds, we believe that wind direction is a key factor in the timing mechanisms of most birds. The other factors involved are less clear and vary from situation to situation. At present, it is probably safest to describe the typical values of all weather parameters when heavy migration of a given type occurs rather than to attempt to single out individual factors besides wind direction. We agree with Curtis (1969:244) that "the effects of specific weather components on migration should be examined in relation to the general weather situation rather than independently". Thus we find the following:

(i) *Heavy SE autumn migration in Alberta* usually occurs with a high to the W, SW, or S and/or a low to the E or NE. The wind is from the NW and the pressure is higher than the previous day. The temperature is relatively stable and not different from that on days of little movement. The humidity situation is unclear (Table 11). These conditions are somewhat different from those prevailing when there is SE reverse movement in spring (see below). It is not obvious why temperature should not be lower with heavy than with light migration in view of the strong correlation between heavy migration and NW wind.

(ii) *Heavy SW autumn starling migration in Ontario* usually occurs on days with geostrophic winds between N and E (surface winds between NW and E) on the E, SE, or S sides of highs or on the NW or W sides of lows. The temperature is both low and lower than the previous day; the humidity is near normal.

(iii) *SE spring reverse migration in Alberta* almost never occurs unless there is a high to the W or SW and/or a low to

the NE or E. The winds are from the NW, the temperature is low and falling, and the pressure is rising. The humidity is high and it is on the average cloudier than when no reverse movement occurs. These humidity, temperature, and cloud correlations were not found with autumn SE migration, probably because spring reverse SE movement tends to occur closer to the low than heavy autumn SE migration (Fig. 12 and 13).

(iv) *Winter NW and SE movements in Alberta* occur in similar conditions to reverse autumn and spring migration respectively, except for temperature relationships. Both winter and reverse movements rarely occur without following winds while forward migration in spring and autumn is frequent with side as well as following winds (Table 3). Lack (1963b) also found that winter movements are very closely correlated with wind direction. While he believed that lapwings (*Vanellus vanellus*) undertake northward flights to Britain in winter to take advantage of unfrozen areas farther north, this is obviously not the case at Cold Lake in midwinter.

(v) *Heavy NW spring migration in Alberta* typically occurs with SE winds on the W or SW side of a high or the SE, E, NE, or N side of a low. The temperature is moderate and not increasing much more than when little movement occurs; the pressure is falling. The humidity is typically lower than when little migration occurs and perhaps slightly lower than the previous day. The intensity is greater on the average on days with SE wind and low humidity than on days with SE wind and higher humidity.

(vi) *Heavy NE spring starling migration in Ontario* typically occurs with SW winds SE or S of a low. On these days the temperature is high and rising (compared to low and falling on days without movement), but the humidity is not obviously different from days with no movement (Richardson and Haight, 1970). The temperature averages higher relative to normal here than with heavy Alberta NW movement because heavy starling flights occur later in the

transition from high to low pressure than NW flights at Cold Lake, probably because the wind shifts from SE to SW as a high moves away and a low approaches. Also, increases in temperature with southerly airflows are likely to be greater in southern Ontario than in Alberta, since flows of maritime tropical air from the Gulf of Mexico frequently reach Ontario but do not reach Cold Lake. For the same reasons, the Alberta movements probably have lower humidity relative to days with no movement than the movements of Ontario starlings.

(vii) *NW autumn reverse migration in Alberta* occurs near the centres of highs and in the area of S flow and falling pressure when there is a high to the E and/or a low to the W or NW. Most flights have the near-normal and stable temperature and humidity found on the west side of a high. However, the few flights occurring with NW winds just before the high passed by had low temperatures. The usual conditions when NW autumn reverse migration occurred more closely resemble the typical conditions when spring NW movement occurred in Alberta than the situation when NE starling migration occurred in Ontario.

By the hypothesis proposed earlier involving selection of conditions with falling pressure gradient from right to left and following winds, heavy NE spring migration in Massachusetts would be expected to occur in the same conditions as NE starling migration in Ontario. However, it apparently occurs in conditions intermediate between those of heavy Alberta NW and Ontario NE migration (Nisbet and Drury, 1968). As in Alberta, it is associated with SE winds and low humidity. However, it is also associated with rising humidity and high temperature, which are to be expected later in the transition from high to low pressure than is typical of heavy NW migration at Cold Lake. As noted earlier, perhaps it is more advantageous to avoid the warm sectors and the possibility of encountering a cold front while in flight near the coast than it is disadvantageous to fly with a side rather than a following wind.

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