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FACTORS INFLUENCING THE TIMING, DISTANCE, AND PATH OF MIGRATIONS OF CANADA GEESE

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The ability of birds to migrate over long distances has for many years raised intriguing questions concerning the mechanisms of bird navigation. Experiments with caged birds and with artificially displaced wild and domestic species have identified potential orientation cues including landmarks, weather conditions, the sun, stars, geomagnetic fields, inertial forces, polarized light, barometric pressure, and infrasound (see Walcott 1974 and Emlen 1975 for reviews). Field observations have defined times and places of migratory movements and related weather phenomena (Emlen 1975). Few data are available on the exact path flown by individuals for which the origin and destination of migration were known (Griffin 1964, Cochran 1972). Theories concerned with the migration abilities of wild birds ultimately will depend on, and be tested by, such data.

By means of radio-location telemetry, we determined the exact path flown during autumn and spring migration by individual Canada Geese (*Branta canadensis*) whose destination was known. Knowledge of the destination of a migration flight allowed analysis of the flight path, and nature of the migration (nonstop vs interrupted flight) in relation to weather phenomena and habitat. Autumn and spring migrations were compared with respect to time required for completion, flight corridor, use of orientation cues, and weather patterns.

METHODS

Study areas and population.—Data were collected between 1973–1975 on the population of Canada Geese which nests between lakes Manitoba and Winnipeg in Manitoba, Canada, and migrates to Rochester, Minnesota (Raveling 1976a, b; 1978a). The travels of this population were thoroughly known as a result of color-marking over 1500 birds between 1968–1970 with individually identifiable, plastic neck collars (Raveling 1978a).

Autumn observations in 1973 and 1974 were made at the Marshy Point Goose Sanctuary (50°32′N, 98°7′W) on the southeast shore of Lake Manitoba about 105 km northwest of Winnipeg. This was the main autumn concentration area for the population. The main wintering area for the population was Silver Lake in Rochester (44°N, 92°20′W). Spring observations were made in the Rochester area in 1974 and 1975.

Study animals and transmitters.—Before each migration season, previously neck-banded geese with a history of migrating between Marshy Point and Rochester were captured in a drop-gate, walk-in trap or with a cannon net. These geese were outfitted with transmitters contained in a harness design that was modified from Cochran et al. (1963) and Raveling (1969) to accommodate a rigid, 30.5-cm whip antenna to increase signal strength. Total weight of transmitters (including harness) varied from 50–75 g (which was 1–3% of adult body weight) depending on the size and number of batteries used.

Social status and migration categories.—Daily observations with a spotting scope allowed the determination of the social status of most of the neck-banded geese on the study areas. Individuals were classified into three social categories (single, pair, or family; see Fischer 1965; Raveling 1969, 1970) and five migration departure and arrival categories based upon the migratory pattern of the total population (before first wave, first wave, between first and second wave, second wave, and after second wave).

Migration monitoring.—Migrations of transmitter-tagged geese were monitored with the use of a ground vehicle, an airplane, ground observers, and a base station (see Cochran et al. 1967). All times are Central Standard Time (CST).

Weather.—Weather conditions were recorded during migration flights and additional data were obtained from weather stations located along the migration route (Winnipeg, Manitoba; Grand Forks and Fargo, North Dakota; Thief River Falls, Detroit Lakes, Alexandria, St. Cloud, Minneapolis, Redwood Falls, and Rochester, Minnesota). Wind directions, unless otherwise indicated, were the directions from which the wind was blowing.

RESULTS

Autumn Migration

Timing.—Although some migration occurred almost continuously between 20 September and late November, the bulk of the population migrated in two brief periods (2–6 days each). These wave-like departures from Marshy Point were reflected in censuses taken in Rochester (Table 1). Departure waves occurred 14–15 October and 2–4 November 1973 and between 28 October–2 November and between 8–13 November 1974. Arrival waves at Rochester occurred during 14–20 October and 2–6 November 1973 and during 1–6 and 11–18 November 1974.

Nonstop vs interrupted migrations.—Data on the nature of the complete migration were obtained for seven transmitter-tagged geese in 1973 and for eight in 1974. In 1973, four of seven birds completed the 855-km trip in a nonstop flight. In 1974, however, only one of eight birds migrated nonstop. The range in flight time for these nonstop migrations was 7 h 52 min–11 h 38 min.

The 10 birds making an interrupted migration took 1–12 days to complete the migration. The magnitude of this range is misleading as, except for two birds which left during the final departure from Marshy Point (18 November 1973 and 13 November 1974), the migration was completed by the others in 1–2 days. The two birds departing at the end of the migration season took 8 and 12 days, respectively.

Nonstop or interrupted migrations did not appear to be related in any obvious manner to social status or departure date (i.e., migration category). The social status of five nonstop migrants included: family (3), pair (1), and unknown (1). Status of the 10 geese which did not migrate nonstop were: family (4), single (2), pair (1), and unknown (3). The migration category for nonstop migrants included three departures during the first wave and two during the second wave of migration. Four interrupted migrants

TABLE 1
ARRIVAL OF CANADA GEESE AT ROCHESTER, MINNESOTA

Dates	Mean peak population 1968–1974[a]	Peak population	
		1973	1974
	19,440	20,670	23,640
20–30 Sept.	9[b]	4	8
1–10 Oct.	12	6	8
11–20 Oct.	22	48	12
21–31 Oct.	9	10	5
1–10 Nov.	22	32	15
11–20 Nov.	22	—	42
21–30 Nov.	4	—	10
Total	100	100	100

[a] 1968–1972 data from Minnesota Department of Natural Resources and Raveling (unpubl.); 1973 and 1974 data from present study.
[b] Figures represent the percent of the peak population censused at Rochester in late November that arrived during that time period.

departed during the first wave, five during the second wave, and one after the second wave of migration. Nonstop flight departures occurred after sunset (20:15–22:22) and during mid-morning (08:00–10:03). While 2 of the 10 geese which interrupted their flight departed during mid-morning (08:00–09:30), six departed during mid-afternoon (13:05–14:58) and two after sunset (19:30–19:55). In addition, 8 of the 10 interrupted migrations were completed during daylight hours in contrast to the nocturnal flights of three of the nonstop migrants.

Migration onset time.—The time of departure for transmitter-tagged birds showed a similar pattern in both years. Departures in October occurred after sunset (19:30–22:22, N = 5), while all recorded departures in November occurred during the day (08:00–14:58, N = 8).

Migration path.—We characterized the autumn flight corridor as containing two sections: (1) from Marshy Point to the northwest corner of Minnesota; (2) from northwest Minnesota to Rochester (Fig. 1). The first migration section was similar for all flights as all geese that were tracked in this area (N = 7) flew 10–35 km west of Winnipeg. The points (N = 4) where transmitter-tagged geese crossed the Manitoba-Minnesota border were within 25 km of one another. The second section of the migration corridor steadily increased in width until it reached a maximum of 210 km between Minneapolis and Redwood Falls. The autumn migration corridor was generally located along the forest-prairie ecotone in Minnesota (see Taylor and Ludwig 1966, Wilson and Loomis 1967 for descriptions). The eastern and western boundaries of the corridor were the paths of diurnal flights of individuals that stopped before reaching Rochester.

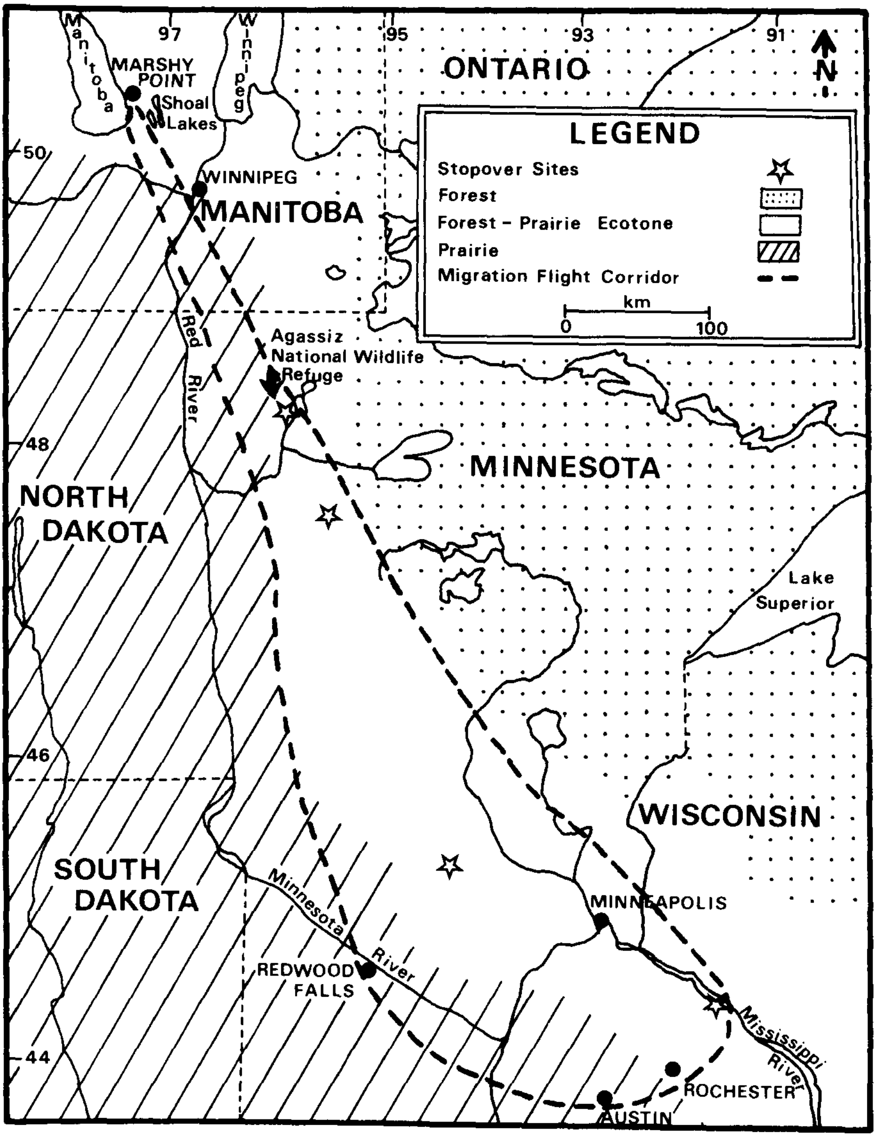

FIG. 1. Autumn migration flight corridor encompassing the 10 paths flown by transmitter-tagged Canada Geese.

Weather.—All 13 transmitter-tagged geese departed with a following surface wind, decreasing daily mean temperature, and increasing barometric pressure. Increasing relative humidity and no precipitation occurred during nine departures and eight occurred with a clear to partly cloudy sky.

The sun, moon or stars were visible for at least part of the time for 11 of the 13 tracked migration flights. Interrupted flights occurred with more and lower clouds than did nonstop flights (with one exception when a nonstop flight occurred during rain and low clouds; see Wege 1979 for more details on weather). After-sunset departures (N = 5) were within 4 days after a full moon and within 5 h after moonrise.

The enroute weather conditions encountered by transmitter-tagged birds differed for nonstop and interrupted flights. Three of the four nonstop migrations in 1973 were overnight flights made under favorable conditions of a following surface wind (270°–360°, 11–37 km/h), increasing barometric pressure, no precipitation, and a clear to partly cloudy sky. Two nonstop flights occurred during daylight under poorer conditions with the presence of rain, snow, and an overcast sky. Interrupted flights occurred when birds encountered snow (N = 3) or the onset of darkness (N = 5). Weather data at the time of interruption were available only for eight geese. Three of the 10 birds completed the migration on the following day while five birds took from 2–12 days. The time of completion of migration was not determined for two birds. Two of the three birds that completed the migration within 24 h had landed in northwestern Minnesota at sunset and departed on the following day with weather conditions that were favorable and similar to those at departure (decreasing temperature, increasing barometric pressure, following surface wind at 13–20 km/h, no precipitation, and a partly cloudy to overcast sky). The remaining bird landed after encountering snow along the Manitoba-Minnesota border, but resumed its migration on the following day when conditions improved (i.e., no precipitation, clear sky, following surface wind at 7–18 km/h). Of the five birds that took more than one day (i.e., >24 h, but 2 or more calendar days) to complete their migration, two stopped at sunset, one stopped 3 h after sunset, and two stopped after encountering snow around 22:00. The latter birds resumed their flight after the snow ended.

The last departing geese in both 1973 and 1974 took the longest to complete their migrations (12 and 8 days, respectively). In 1973, variable weather conditions including snow, head winds, and decreasing barometric pressure occurred at the stopover site between the 18 November departure date and 28 November. On 29 November a high pressure system with accompanying stable air including a wind shift from south to north, an end to the precipitation, a clear sky, and increasing barometric pressure moved into the area. Favorable conditions continued on 30 November when the migration was completed. A similar pattern occurred in 1974 when a bird remained at its stopover area from 13 November until a stable high pressure system moved in on 19 November when it then continued its migration. However, the migration was not completed until 21 November, even though conditions had remained favorable.

Spring Migration

Timing.—At the onset of thawing in late February or early March, geese dispersed from Silver Lake. Because geese no longer concentrated daily at Silver Lake, it was difficult to accurately census the population and to detect minor migration departures. Major departures of geese (i.e., >5000) were observed on 2 and 6 April 1974, and between 12 and 14 April 1975. The major departures of geese included 14 of 23 and 11 of 17 transmitter-tagged geese in 1974 and 1975, respectively. Major arrivals on the nesting grounds occurred from 8–12 April 1974 and 13–15 April 1975.

All spring migrations of radio-tagged geese were interrupted. The mean duration from departure from Rochester to arrival at Marshy Point, Manitoba was 10 days in 1973 (range = 6–14 days, N = 3) and 7 days in 1974 (range = 6–9 days, N = 4).

Migration onset time.—As observed in autumn, departure times occurred earlier in the day as the season progressed for the 1974 spring migration. The second major departure (6 April) occurred between 06:00–12:00, whereas previous departures were 17:50 on 13 March and 15:30, 16:00, and 17:00 on 2 April. This trend was not evident in 1975 as departures occurred at 04:55 on 8 April, 18:15 on 12 April, 04:00, 06:30, 16:30 on 13 April, and 06:40 on 16 April.

Migration path.—The spring migration path followed an arc from Rochester west-northwest through western Minnesota and eastern North Dakota, and then north into central Manitoba (Fig. 2). Stopover areas were pastures and grain fields containing water from snow melt.

Weather.—Major departure from Rochester in 1974 occurred when major rivers were free of ice in southern and southwestern Minnesota and melt water was abundant in western Minnesota and eastern North Dakota. Because the ground was still frozen, the water from melting snow gathered in low lying areas among the rolling hills of this area. Lakes and marshes located in the more vegetationally closed forest-prairie ecotone area in Minnesota (see Fig. 2) were still frozen. The departures of 11 transmitter-tagged geese that were tracked occurred under generally similar weather conditions, although there was greater variation in these conditions than was found for autumn departures. No precipitation and a following surface

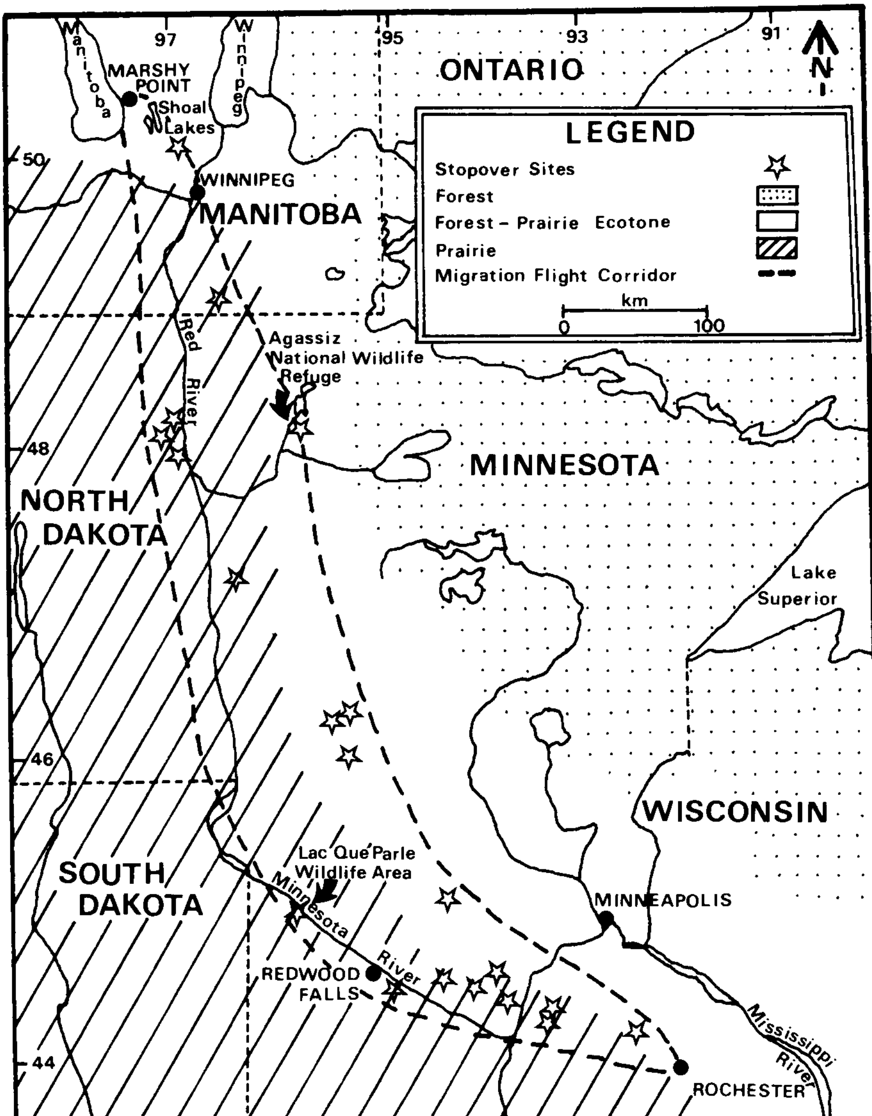

FIG. 2. Spring migration flight corridor encompassing the 16 paths flown by transmitter-tagged Canada Geese.

wind (60°–190°) occurred during 10 departures; nine migrations were initiated when the daily mean temperature was increasing; seven departures occurred with a completely overcast sky, and increasing relative humidity; and six occurred with decreasing barometric pressure.

On eight occasions, weather conditions encountered enroute by transmitter-tagged geese were recorded. They were similar to conditions at departure and included: seven occasions with no precipitation and decreasing barometric pressure, five with an increasing daily mean temperature and a following surface wind, four with increasing relative humidity and an overcast sky.

The weather conditions existing when spring migration flights were interrupted were recorded for five transmitter-tagged geese on six different occasions. Birds landed with continuing favorable conditions at 12:00, 13:00, 14:00, 18:30 (sunset), and 22:30; and with deteriorating weather (wind shifted to northeast and rain began) at 15:30.

The visibility of the sun, moon or stars was similar for spring migration flights in both 1974 (N = 11) and 1975 (N = 7). The total sample size (18) is greater than the number of birds tracked (N = 11) because some geese were tracked more than once before reaching their breeding grounds (i.e., they had interrupted their migration). The only after-sunset departure (in 1974) occurred after the setting of a half-moon under partly cloudy skies so that some stars were visible. Three 1974 daylight departures occurred under complete overcast, however, the sunrise had been visible, as had been the moon during the previous night. The other seven departures in 1974 occurred when the sun was visible. Similarly, 1975 departures under overcast conditions occurred after: (1) the sun and moonrise were visible during the previous day (N = 2); (2) the sunrise was visible on the day of departure (N = 1); and (3) complete overcast had obscured the sun and moon during the previous 2 days, except for the sun being visible for 3 h under $^{9}/_{10}$ cloud cover on the day before departure (N = 1). In general, the sun or moon and stars were visible during more than one-half (N = 10) of the flights and there was no precipitation during 17 of the 18 migration flights but many clouds were present during 14 of the flights.

DISCUSSION

Autumn vs spring migrations.—In autumn, this population tends to migrate between wildlife refuges which provide protection from hunters and to minimize the number of migration stopover locations (Raveling 1978a). Autumn migrations during this study tended to be characterized by direct flight paths, nonstop flights when departure time and weather conditions permitted, and the resumption of interrupted migrations as soon as weather conditions permitted. The last major departure of geese from Marshy Point occurred 2–3 days before final freeze-up of the marsh. Therefore, autumn migrations preceded the time at which water roosting areas became totally unavailable.

Successful reproduction in northern geese requires that nesting begin almost as soon as nest-sites become available in spring (Cooch 1961, Barry 1962, MacInnes 1962, Raveling 1978b). A delay in egg-laying due to a late spring thaw or to a goose not being in the proper physiological condition increases the probability of nesting failure (Cooch 1961, Barry 1962). Despite the relatively short distance between wintering and breeding areas (855 km) for this segment of the Giant Canada Goose population, spring phenology, and weather conditions experienced upon arrival on the breeding grounds are comparable to arctic nesting geese (see Cooper 1978:20). Although renesting may occur in this population, initial nesting attempts coincide with newly available nest-sites and open water (Cooper 1978) as reported for more northern geese (see above references).

Arrival on nesting grounds in close synchrony with soon to be available nest-sites involved undertaking short flights with favorable weather conditions to prairie locations offering open water. Initial migration flights were shorter and more days were required to complete spring migrations ($\bar{x}$ = 8.3 days, range 6–14 days) than were recorded for autumn migrations ($\bar{x}$ = 2.3 days, range 0.33–12 days) ($t = 3.65$, $P < 0.01$). Reverse migrations in spring occurred when geese were confronted with the lack of open water and food. Reverse migrations also occurred in autumn (Raveling 1976b).

Flight corridor.—The autumn migration corridor along the forest-prairie ecotone (Fig. 1) provided numerous suitable wetland stopover areas for migrating geese and a minimal energy expenditure as a result of a nearly direct flight path to their destination. The prairie to the west contained many fewer water areas in autumn. The spring migration corridor was 20–55 km west of the autumn corridor (Fig. 2). Two factors combined to cause suitable stopover areas to be first located in southwestern and extreme western Minnesota and eastern North Dakota. Firstly, spring storms passed through the Midwest on a generally southwest to northeast line (Barry and Chorley 1971:227). Secondly, the habitat in these areas was tall grass prairie (presently, cultivated grains and pasture). The rain and warm temperatures of spring storms, along with the open habitat, caused the early formation of melt water in pastures and grain fields. Snow melt and ice thaw on marshes and lakes occurred in the more closed conditions and permanent water bodies of the forest-prairie ecotone after spring migration had been completed. Therefore, open water and food were unavailable and this area was little used during spring. However, similar to autumn, the spring migration corridor was the most direct suitable path to the breeding grounds, resulting again in a minimum of expended energy.

Orientation cues.—The use of landscape features is variable among species and may be most important during migration in locating a specific wintering or breeding site (Bellrose 1972, Keeton 1974, Emlen 1975, Wiltschko and Wiltschko 1978). For nocturnal-diurnal migrants (e.g., Canada Geese), Bellrose (1967, 1972) concluded that landscape features were most important in maintaining the flight direction during diurnal flights. Visual cues provided by open water and cities could have been used to maintain the migratory direction by the geese in this study. In autumn, permanent lakes along the forest-prairie ecotone and the Red, Mississippi, and Minnesota rivers (Fig. 1) and, in spring, patterns of ice-free rivers and melt water in fields could have provided critical landscape cues. The paths of two birds which approached Rochester from the southwest, and one bird which followed the Mississippi River suggest that local landmarks influenced their final approach. One of these geese approached Austin (Fig. 1) from the north-northwest and when it was about 13 km north of the city, changed course abruptly and flew northeast for 28 km until encountering Rochester where it then landed at a small lake located in the southwest part of the city. The sky was completely overcast at the time but the cloud ceiling was 24,000–32,000 m with 25–30 km surface visibility. The second bird approached Austin from the west-northwest and, when it was about 6 km south of the city, turned and flew northeast. After flying 44 km it landed at Rochester. The sky was again completely overcast, and the ceiling (2200–3200 m) and visibility (15–20 km) were reduced. Austin may have been confused with Rochester by these birds. These two towns are similar in size and larger than any other town in this area of southeastern Minnesota.

Research has tested the effect of the earth's magnetic field on a bird's orientation ability, but little discussion has addressed the possible importance of the magnitude of magnetic activity in determining the time of migration departures (Richardson 1974, 1976). Multivariate analyses of 33 weather variables revealed that magnetic disturbance was correlated with migration departure (Wege 1979).

Variation within migrations.—While autumn and spring migrations were related to favorable weather periods, there was variation in departure and arrival dates of migration waves and in flights of transmitter-tagged birds. Band recoveries and previous field observations indicated that the autumn migration occurred between 20 September and 20 November and tended to be nonstop. About one-half of the population migrated by 1 November and about 66% of the population arrived at Rochester during two periods (10–20 October and 1–20 November) (Table 1). Major arrival in 1973 was the earliest and largest recorded between 1968–1974, while that in 1974 was the second latest.

The sequence of events during the 1975 spring migration demonstrated that the time required to complete the migration may be shorter in a late spring. The major departures from Rochester averaged 9 days later in 1975 than in 1974, but the major arrival at Marshy Point was only 4 days later. The apparent reduction in migration time is further indicated by the fact that transmitter-tagged geese took an average of 10 days to complete the migration in 1974 (N = 3) and 7 days in 1975 (N = 4). There was little delay in reproduction as the first egg was laid at Marshy Point just 1 day later in 1975 than in 1974.

Transmitter-tagged geese.—For the 1973 and 1974 autumn and the 1974 spring migrations, departures of transmitter-tagged geese were nocturnal early in the migration season and then diurnal later in the season. This change cannot be explained by any readily apparent difference in nocturnal vs diurnal weather conditions. Perhaps there are both nocturnal and diurnal migratory individuals or segments of the population, with the nocturnal geese tending to be early season migrants. Support for such an hypothesis comes from the fact that individuals (neck-banded) began migration in the same relative order each year (Wege 1979), and the interruption of migration around sunset by diurnal, transmitter-tagged migrants occurred on five of eight occasions (the other three interruptions occurred when geese encountered a snow storm). All eight of these geese completed their migrations with only diurnal flights.

No transmitter-tagged geese interrupted their migration at sunrise. Since all recorded nocturnal departures occurred before midnight, geese that flew all night were at least 75% of the way to Rochester by sunrise and would be able to complete their migration within a few hours. Bellrose (1964) observed that before nocturnal migrating waterfowl made a major change in direction, it appeared they needed to obtain landscape cues during the day. Similar behavior by geese in this study was not observed either because no major changes in direction were required and the recognition of local landmarks was sufficient to make minor changes in direction and to guide them to Rochester, or because migrating geese were readily able to change from using astral cues to celestial or landscape cues. The flight paths of three nocturnal, nonstop migrants indicated that an almost direct flight line was maintained between Marshy Point and Rochester.

SUMMARY

Canada Geese (*Branta canadensis*) with a known history of migrating between Marshy Point Goose Sanctuary, Manitoba, and Rochester, Minnesota, were fitted with 50–75 g radio transmitters between August 1973 and April 1975. Part or all of the migrations of 25 indi-

viduals were tracked with a ground vehicle and an aircraft. Autumn migrations were characterized by a relatively direct flight path, nonstop flights when departure time and weather conditions permitted, and the resumption of interrupted migrations as soon as weather conditions permitted. Spring migrations involved shorter flights along the edge of the snow melt which facilitated arrival on the nesting grounds in close synchrony with soon to be available nest-sites. There may be nocturnal and diurnal migratory individuals or segments of the population, with the nocturnal geese tending to be early season migrants.

The autumn migration corridor was on a direct path between Marshy Point and Rochester and was generally located along the forest-prairie ecotone in Minnesota where water was available in permanent potholes. Due to the path of spring storms in the Midwest and because snow on the prairie melted earlier than ice on the potholes, the formation of melt water occurred first on the prairie. The spring migration corridor was associated with this open water and was 20–55 km west of the autumn corridor. Thus, patches of open water served as major visual cues influencing the migration path. The paths of three birds indicated that the recognition of local landmarks probably determined their final approach to their destination. During nocturnal flights, when these landscape features may be unavailable, astral cues were available.

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