

THE ALTITUDE OF BIRD MIGRATION IN EAST-CENTRAL ALASKA: A RADAR AND VISUAL STUDY

BRIAN A. COOPER

ABR, Inc.

P.O. Box 249

Forest Grove, Oregon 97116 USA

ROBERT J. RITCHIE

ABR, Inc.

P.O. Box 80410

Fairbanks, Alaska 99708 USA

Abstract.—Flight altitudes of birds were monitored in east-central Alaska during spring and fall migration periods with visual (1987–1989) and radar (1988–1989) methods. Visual observations indicated that diurnal flights occurred primarily below 300 m above ground level (agl). Radar observations indicated that nocturnal flights generally occurred below 500 m agl. Flight altitudes were significantly higher in fall than in spring, and there were interannual differences in both seasons. There was high night-to-night variability in nocturnal flight altitudes during both seasons. This night-to-night variability probably was not related to daily changes in the magnitude of migration: there was a very low correlation between mean nightly flight altitudes and mean nightly migration rates. Nocturnal flight altitudes were higher from April to early May than from mid- to late May and higher from late August to early September than from mid-September to mid-October. These seasonal differences in flight altitudes largely were due to changing species composition within a season. When spring radar data were partitioned among light conditions, flight altitudes were found to be similar between daylight and crepuscular periods and between daylight and nocturnal periods, but birds flew significantly higher in crepuscular than nocturnal periods. In fall, nocturnal altitudes were significantly higher than crepuscular and daylight altitudes, which were similar. Within a night, there was no near-midnight peak in flight altitudes in either spring or fall.

LA ALTITUD DE LA MIGRACIÓN DE AVES EN LA ALASKA CENTRO-ORIENTAL: UN ESTUDIO VISUAL Y DE RADAR

Sinopsis.—Se monitorearon las altitudes de vuelo de aves en la región centro-oriental de Alaska durante los períodos de migración de la primavera y el otoño con métodos visuales (de 1987 a 1989) y de radar (en 1988 y 1989). Observaciones visuales indicaron que los vuelos diurnos ocurrieron principalmente bajo los 300 m sobre el nivel del terreno (snt). Observaciones de radar indicaron que los vuelos nocturnos generalmente ocurrieron sobre los 500 m snt. Las alturas de los vuelos fueron significativamente más altas en otoño que en primavera, y existieron diferencias interanuales en ambos períodos. Se documentó una alta variabilidad en las alturas de vuelo de noche a noche en ambas estaciones. La probabilidad de esta variabilidad entre noche y noche no estuvo relacionada a cambios diarios en la magnitud de la migración: se obtuvo una correlación muy pobre entre el promedio de las altitudes de vuelo nocturnos y el promedio de las tasas de migración nocturna. Las altitudes de vuelo nocturno fueron mayores entre abril y principios de mayo que entre mitad y finales de mayo y fueron mayores entre finales de agosto y principios de septiembre que entre mediados de septiembre y mediados de octubre. Estas diferencias estacionales en altitudes de vuelo fueron causadas principalmente a los cambios en la composición de especies dentro de una estación. Cuando los datos primaverales de radar se dividieron entre las condiciones de luz, se halló que las alturas de vuelo eran similares entre luz de día y los períodos crepusculares y entre luz de día y períodos nocturnos, pero pocas aves volaron significativamente más alto en períodos crepusculares que en períodos nocturnos. En otoño, las altitudes noc-

turnas fueron significativamente mayores que las altitudes crepusculares y diurnas, las cuales fueron similares. Dentro de una noche no se evidenciaron picos en altitudes de vuelo cercanos a la medianoche en primavera o en otoño.

Several species of birds are prone to collisions with structures (Avery et al. 1980, Banks 1979, Weir 1976). Collectively, these collisions may be a significant mortality factor for some populations: approximately 1.25 million birds are killed each year in collisions with tall structures (Banks 1979). Declines of several species of Neotropical migrants in recent decades (Robbins et al. 1989, Terborgh 1989) suggest that reducing collision-caused mortality in these species may even be more critical than was previously thought. Consequently, information on the altitude at which birds fly is important, not only for understanding bird migration but when planning the construction of tall structures and utility lines, to minimize bird collisions.

Unfortunately, the altitude of migration is extremely variable, depending upon species, location, geographic feature, season, time of day and weather condition (Alerstam 1992, Kerlinger 1989). Despite numerous studies, our knowledge of species-specific, diel, seasonal and geographic variation in migration altitude is limited. Further, few data on the migration altitude of birds are available for Alaska.

The purpose of this paper is to summarize seasonal, diel and species-specific patterns of flight altitude of birds during spring and fall migration in east-central Alaska, determined from visual observations during 1987 to 1989 and from radar observations in 1988 and 1989. The visual observations provided data on flight altitudes for individual species, whereas the radar data provided more precise altitudinal information for both day and night (when visual observations were not possible). These data were collected as part of a study designed to assess the potential impact of a large antenna array on birds during migration. Detailed analyses of the effects of weather and other variables on flight altitude will be presented in another paper.

STUDY AREA

The study area was located in the upper Tanana River Valley, near Tok, Alaska (63°20'N, 142°59'W; Fig. 1). The Tanana River Valley, which extends northwestward from the Yukon Territory of Canada into central Alaska, is a major migration corridor for many species of birds (e.g., Bellrose 1976, Gabrielson and Lincoln 1959, Irving 1961, Kessel 1984, Sladen 1973, Spindler and Hall 1991, West et al. 1968).

The study area is part of the Northway-Tanacross Lowland (Wahrhaftig 1965) and is nearly flat, ranging in elevation from 530 to 560 m asl (above sea level). In the study area, the valley is approximately 15 km wide and is bordered to the north by broad hills (the Yukon-Tanana Uplands) that crest at approximately 750 m asl and to the south by mountains of the Alaska Range that crest at 2000–3000 m asl. The area is forested with large tracts of black spruce (*Picea mariana*), white spruce (*Picea glauca*), and quaking aspen (*Populus tremuloides*).

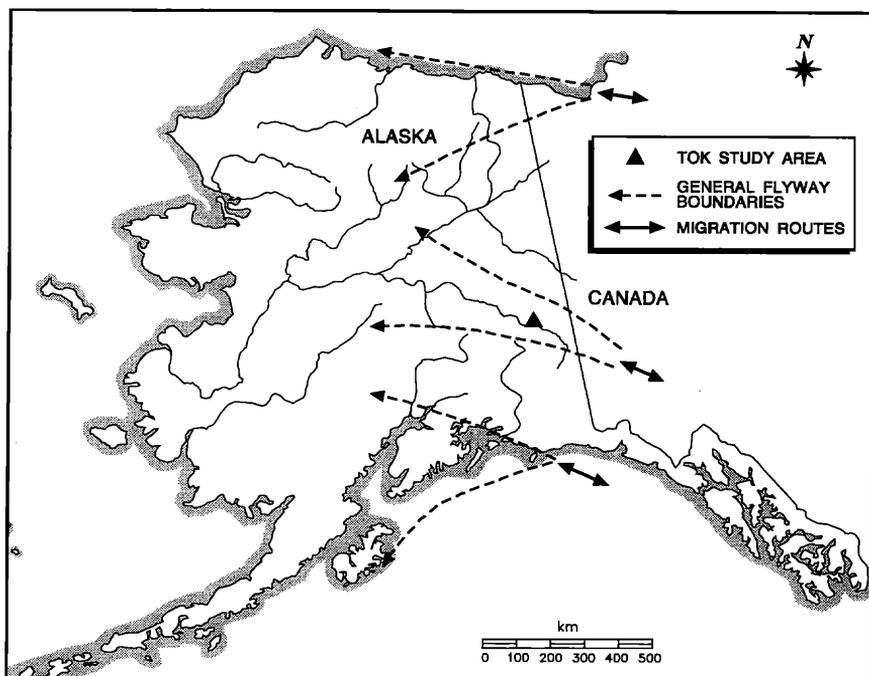


FIGURE 1. Map of Alaska showing location of study area and major migration pathways. Locations of pathways determined from Bellrose (1976), Gabrielson and Lincoln (1959), Irving (1961), Kessel (1984), Sladen (1973), Spindler and Hall (1991), West et al. (1968), S. Ambrose (USFWS, pers. comm.), J. King (USFWS, retired, pers. comm.) and R. King (USFWS, pers. comm.).

METHODS

Visual.—Visual observations were conducted daily 10 Apr.–24 May 1987, 16 Aug.–6 Oct. 1987, 6 Apr.–21 May 1988, 16 Aug.–17 Oct. 1988, 5 Apr.–25 May 1989, and 16 Aug.–15 Oct. 1989. Observers equipped with binoculars and a variable-power spotting scope made observations from a 6-m-high tower or from natural vantage points for the entire daylight period during peak migration (i.e., approximately 20 April to 20 May and 15 August to 5–15 October) and for approximately 6–10 h/d at other times. Systematic scans from zenith to horizon in all directions were made when searching for birds. Data were recorded as each flock of birds (migrant species only) crossed an imaginary North/South transect extending from the observer (or an East/West line for birds headed to the North or South; note that the predominant direction of flight is westward or northwestward in spring and eastward or southeastward in fall). For each flock, the following data were recorded: time, species, number of birds, flight altitude category above ground level (agl; 0–15 m, 16–30 m, 31–

150 m, 151–300 m, and >300 m agl), distance to bird, and flight direction.

Flight altitude and distance to birds were estimated with the aid of several reference points of known height and distance: trees marked with colored flagging, human-made structures (e.g., 220-m-tall Loran towers and 15-m-tall telephone poles) and nearby geological features (e.g., mountains and hills). When possible, visual estimates of altitude were checked against altitudes measured with radar.

For all statistical analyses, “flocks” and not birds were used as the sampling unit, because of problems of independence among individuals within a flock. A “flock” was defined as two or more birds flying in proximity, or any birds flying singly. Thus, individual birds and different-sized flocks had equal weight for statistical tests. Further, our data set was restricted to migrant species that flew <500 m horizontal distance from the observer, because it was difficult to detect low-flying birds at greater distances. This lack of detection would bias the altitude data and, hence, would inflate our estimates of mean flight altitudes.

Mean flight altitudes were computed by using the midpoint of the flight altitude category in which a flock was observed. The upper flight altitude category (>300 m) was problematic because it did not have an upper boundary. To solve this problem, we computed a median flight altitude for targets above 300 m that were observed during daylight hours on radar. Half of all flights measured on radar above 300 m during daylight hours occurred below 350 m in spring and below 650 m in fall. Thus, 350 m was used as the midpoint of the >300 m altitude category for spring observations and 650 m was used as the midpoint for fall.

Radar.—Three models of Furuno X-band marine radars (FR-1900, FR-8050 and FR-8100) also were used to measure flight altitudes. Different models were used in different seasons, depending upon their availability. Each was modified with a fixed, vertically-aligned parabolic antenna. Peak power output was 3 kW, 5 kW and 10 kW for these three models, respectively. The maximal range of detection for birds on these radars was unknown; however, small individual passerines could be detected to approximately 1 km, and large species and flocks of passerines could be detected at higher altitudes. For a description of the radar systems, see Cooper et al. (1991).

We operated the radar 2–15 h/d during 6 Apr.–21 May 1988 (FR-1900), 17 Aug.–17 Oct. 1988 (FR-1900), 12 Apr.–23 May 1989 (FR-8050) and 16 Aug.–17 Oct. 1989 (FR-8100). During periods of peak migration, we operated the radar from dusk to dawn and for at least 2 h during daylight, to provide information on diel patterns of flight altitude. Data could not be collected during periods of rain or wet snow. We recorded the following information for each radar target: time, altitude and light condition. Information on light condition (daylight, crepuscular [the dawn/dusk period between sunrise/sunset and nocturnal periods], and nocturnal [the periods when it was dark enough that one could not read a typed

page at arms' length]) was collected at the beginning of each hour of sampling.

We used the 1.4-km range setting (actual range = 1900 m) on the FR-8100 and FR-8050 radars and the 0.9-km range setting (actual range = 1000 m) on the FR-1900 radar, which did not have a 1.4-km setting. As 0.2% (51) of the targets observed in spring 1989 and 0.1% (7) of the targets observed in fall 1989 (when we used the FR-8050 and FR-8100 models, respectively) flew above 1000 m (the vertical range of the FR-1900 that we used in 1988 was 1000 m), all analyses were restricted to include only those observations below 1000 m agl, so that data from both 1988 and 1989 could be combined into a single data set.

The species composition and size of a flock of birds observed on the radar usually was unknown. Therefore, the term "target," rather than "flock" or "individual" is used to describe birds detected by the radar. For data summaries and analyses, flight altitude data were corrected because the vertical radar had a beam that was approximately cone-shaped at the altitudes we sampled, which meant that the area sampled increased with increasing altitude. Refer to Blokpoel (1971) for a detailed explanation of correction factors for a vertically-aligned radar.

As the lower limit of detection for the vertical radar was approximately 30 m agl, we sampled the 0–29-m agl zone at night with a 5× Noctron V night-vision scope from a 6-m-high tower. Observations were conducted for 1–2 h/night within the seasonal peak of migration for 30 nights in 1988 (16 nights in spring and 14 in fall) and 32 nights in 1989 (6 in spring and 26 in fall). Observers oriented the night-vision scope toward the northeast (perpendicular to the main axis of migration), at a slight angle above horizontal, so that the upper edge of the field of view was at 30 m agl at the distance where we discontinued night-vision sampling (100 m). To determine the proportion of birds that flew below 30 m agl, the night-vision data were converted to flocks per m², which was multiplied by the area that the vertical radar would have sampled below 30 m. Applying the correction factor for sampling area of a vertically-aligned radar to this number allowed us to determine the number of birds that would have been detected by the radar below 30 m agl (if that was possible). By dividing this corrected number (x) by $x +$ total corrected number of targets concurrently observed with vertical radar, we could estimate the proportion of birds that flew below 30 m agl during concurrent radar and night-vision sampling.

RESULTS

Visual.—Flight altitudes varied among species groups, although the majority of birds in all groups flew below 300 m agl (Fig. 2). In general, swans, geese, ducks and cranes flew higher than did raptors, shorebirds and passerines. There was a great amount of variability in flight altitudes among species within each group (Appendix 1). For instance, the bimodal distribution in altitude of raptors (Fig. 2) largely reflected the differ-

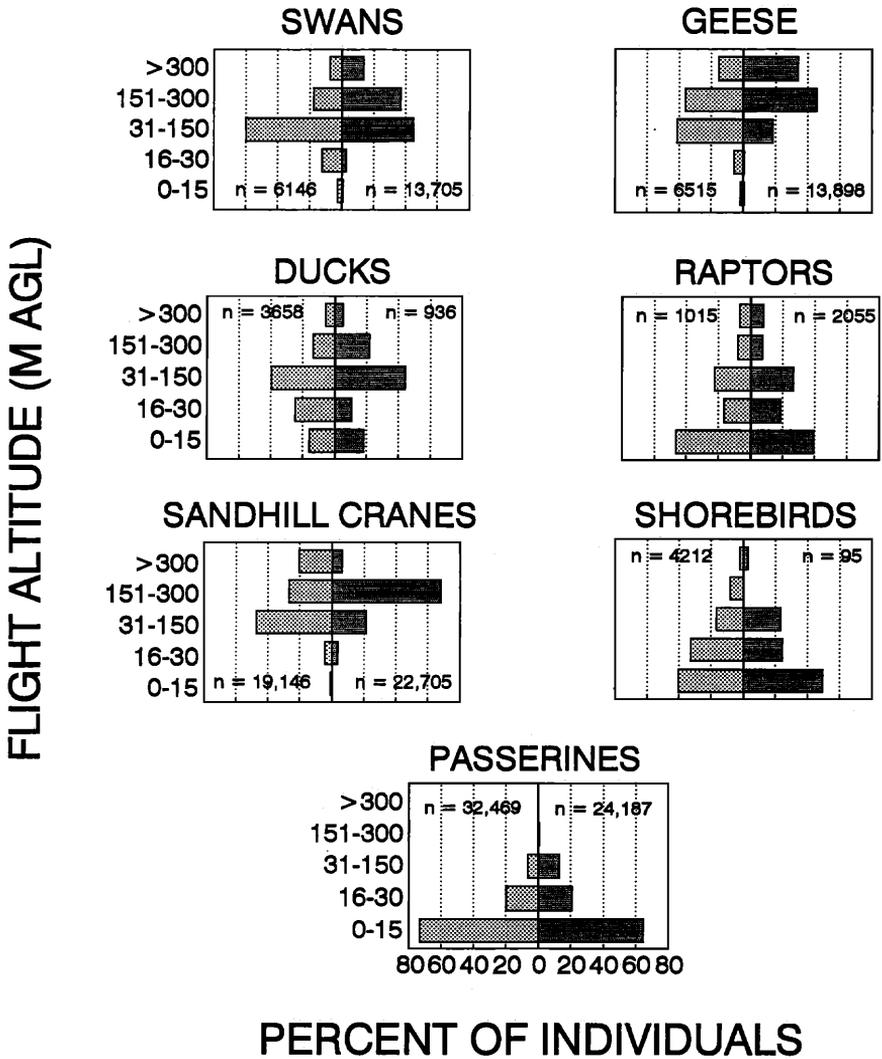


FIGURE 2. Flight altitudes of birds observed in east-central Alaska during spring (light shading) and fall (dark shading) 1987-1989. These data include only diurnal, visual observations of birds recorded within 500 m (horizontal distance) of the observer.

ence between low-flying Northern Harriers (see Appendix 1 for scientific names) and high-flying buteos.

Seasonal and/or annual differences in flight altitudes were found for all species groups (2-way ANOVA; Tables 1 and 2). Flight altitudes of most species groups tended to be higher in fall than spring and lower in 1989 than in other years.

TABLE 1. Mean flight altitude (m agl) of flocks^a of birds observed visually in east-central Alaska during spring and fall 1987–1989. These data include only daytime observations of flocks within 500 m.

Year	Species group	Spring			Fall		
		Mean	SD	<i>n</i>	Mean	SD	<i>n</i>
1987	Swans	126	97	60	143	124	48
	Geese	170	119	91	353	248	73
	Ducks	63	90	139	49	66	12
	Raptors	82	110	365	80	140	664
	Cranes	173	108	127	224	169	61
	Shorebirds	53	62	182	71	145	19
	Passerines	17	23	1567	32	69	1001
1988	Swans	138	115	73	204	169	317
	Geese	147	113	59	354	256	61
	Ducks	56	81	162	108	163	72
	Raptors	67	100	309	123	205	609
	Cranes	201	129	44	349	258	23
	Shorebirds	32	46	192	59	150	18
	Passerines	21	30	1362	23	37	1534
1989	Swans	89	61	147	150	164	125
	Geese	109	81	83	294	226	120
	Ducks	47	55	231	27	45	30
	Raptors	52	78	252	63	126	533
	Cranes	113	92	43	155	131	25
	Shorebirds	30	46	626	12	18	20
	Passerines	17	23	2466	27	38	2251

^a A flock was defined as two or more birds flying in proximity or any birds flying singly.

To determine if our visual observations were biased toward low-flying birds, we compared them with concurrent radar observations, which do not have this bias for observations below 1000 m. When we divided concurrent visual and diurnal radar observations into three altitudinal categories (31–150, 151–300 and 301–1000 m agl; no birds were observed

TABLE 2. Two-factor analysis of variance of daytime flight altitudes of flocks^a of birds observed visually in east-central Alaska during spring and fall 1987–1989. Refer to Table 1 for mean (\pm SD) flight altitudes for each season and year.

Species group	Season			Year			Season \times year		
	df	<i>F</i>	<i>P</i>	df	<i>F</i>	<i>P</i>	df	<i>F</i>	<i>P</i>
Swans	1	15.02	<0.001	2	8.65	<0.001	2	1.24	0.290
Geese	1	119.57	<0.001	2	5.10	0.006	2	0.16	0.850
Ducks	1	0.24	0.624	2	9.51	<0.001	2	6.96	0.001
Raptors	1	14.37	<0.001	2	12.87	<0.001	2	9.35	<0.001
Cranes	1	19.58	<0.001	2	15.87	<0.001	2	3.06	0.048
Shorebirds	1	1.40	0.237	2	10.47	<0.001	2	3.43	0.033
Passerines	1	142.75	<0.001	2	3.97	0.019	2	22.95	<0.001

^a See Table 1 for definition of flock.

TABLE 3. Mean (\pm SD) flight altitudes (m agl) of bird targets measured on radar at night in east-central Alaska during spring and fall 1988–1989.

Year	Spring			Fall		
	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>
1988	184	133	211	426	189	1064
1989	146	120	1198	341	199	2835

above 1000 m during concurrent observations), we found that flocks had a significantly higher distribution on radar than were recorded visually, both in spring ($\chi^2 = 56.5$, *df* = 2, $P < 0.001$) and fall ($\chi^2 = 140.5$, *df* = 2, $P < 0.001$). In spring, 10% of the visual sightings and 14% of the radar observations were above 300 m agl. In fall, 12% of the visual sightings and 28% of the radar observations were above 300 m agl. These results indicate that lower-flying birds were detected better than higher-flying birds when using visual observation techniques.

Radar.—Nocturnal flight altitudes on radar were significantly higher in the fall than spring and altitudes were higher in 1988 than in 1989 (2-way ANOVA; Tables 3 and 4; Fig. 3). Night-to-night variability in nocturnal flight altitudes was high for both spring and fall; mean flight altitudes commonly differed by 100–200 m on consecutive nights.

The night-vision data indicated that a small percentage of birds flew <30 m agl during nocturnal hours in both spring (0.7% of all targets) and fall (2.4%). In 1989, we also were able to obtain information on flight altitudes between 1000 and 1900 m agl. Only a small percentage of the targets observed in spring 1989 (0.2%) and fall 1989 (0.1%) flew >1000 m agl.

We also compared radar observations of nocturnal flight altitudes among early, mid- and late spring periods (10–25 April, 26 April–10 May, and 11–25 May, respectively) and among early, mid- and late fall (15 August–5 September, 6–21 September, and 22 September–15 October, respectively). Flight altitudes were significantly higher in early and mid-spring than in late spring (Table 5). In fall, altitudes were significantly higher in early fall than in mid-fall and late fall.

Both these within-season patterns of flight altitudes and day-to-day variability in nocturnal flight altitudes apparently were not related to seasonal

TABLE 4. Two-factor analysis of variance of nocturnal flight altitudes of bird targets measured on radar in east-central Alaska during spring and fall 1988–1989. Refer to Table 3 for mean (\pm SD) flight altitudes for each season and year.

Source	<i>df</i>	<i>F</i>	<i>P</i>
Season	1	1216.2	<0.001
Year	1	95.3	<0.001
Season \times year	1	14.2	<0.001

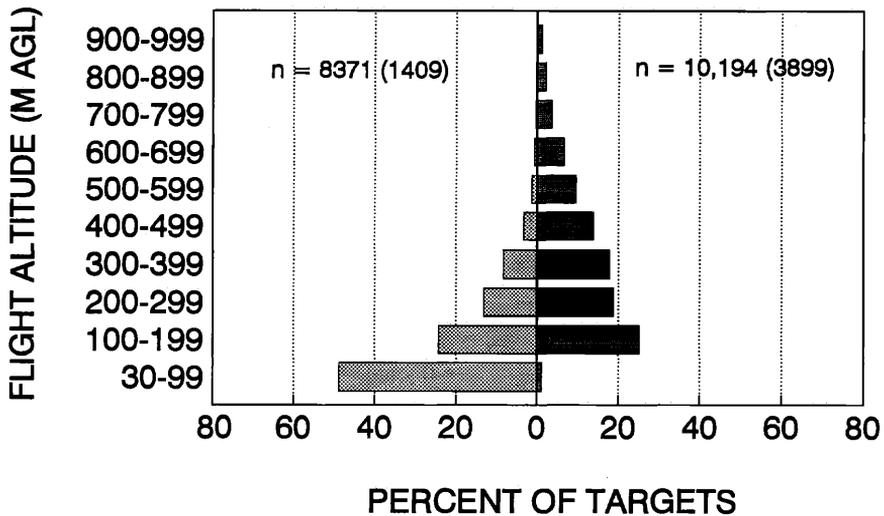


FIGURE 3. Nocturnal flight altitudes of bird targets detected by radar (corrected for sampling area) in east-central Alaska during spring (light shading) and fall (dark shading) 1988-1989. Numbers in parentheses are the actual number of targets observed.

changes in the magnitude of migration; the correlation between mean nightly flight altitudes and mean nightly migration rates (targets/hour) was very low in both spring ($r = -0.252$, $n = 46$, $P = 0.091$) and fall ($r = 0.146$, $n = 82$, $P = 0.192$).

Mean altitudes of flight for each hour of the day and night were highly variable and there was no strong near-midnight peak in flight altitudes (Fig. 4). Flight altitudes during daylight, crepuscular and nocturnal periods also were compared. Flight altitudes in spring were similar between daylight and crepuscular periods and between daylight and nocturnal periods, but crepuscular altitudes were significantly higher than nocturnal altitudes (Table 6). In fall, nocturnal altitudes were significantly higher than were crepuscular and daylight altitudes, which were similar.

TABLE 5. Comparisons of nocturnal flight altitudes (m agl) of bird targets observed by radar during early, mid- and late spring and fall periods in east-central Alaska during spring and fall 1988-1989.

Season	Period						<i>n</i>	<i>H'</i>	<i>P</i>
	Early		Mid		Late				
	Mean	SD	Mean	SD	Mean	SD			
Spring	140	132	157	125	133	107	1409	62.4	<0.001
Fall	449	197	340	189	355	206	3899	121.9	<0.001

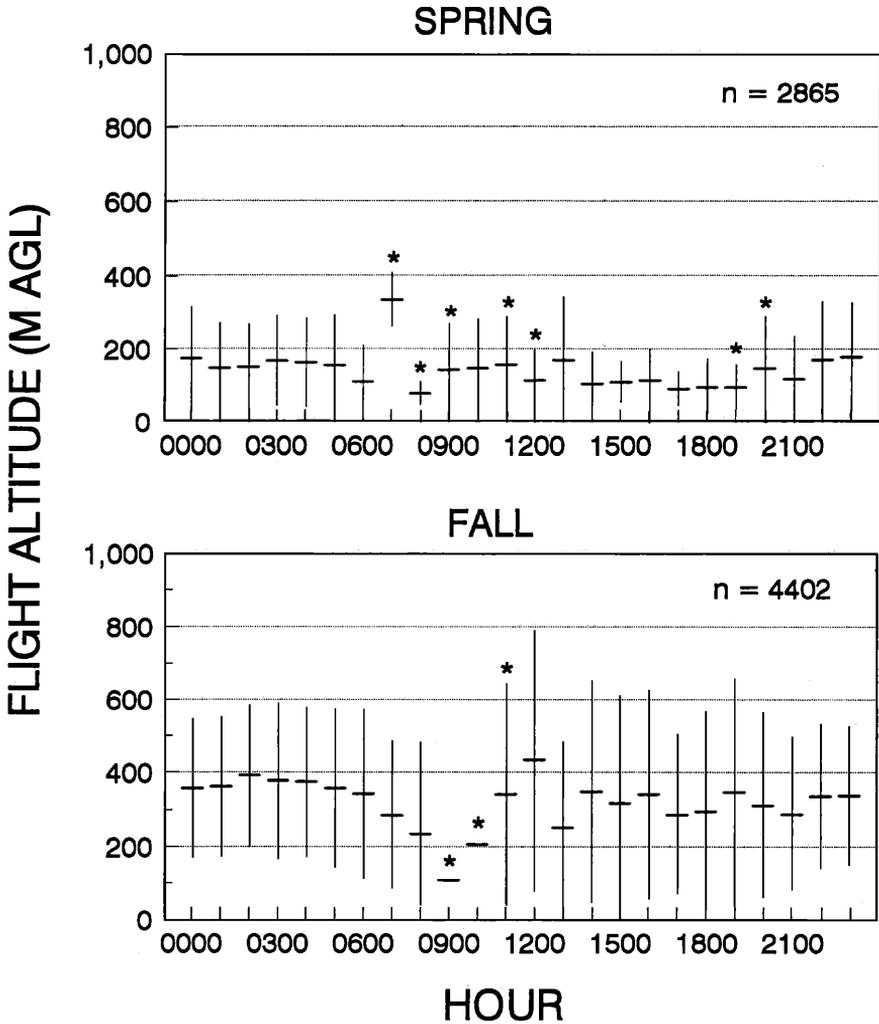


FIGURE 4. Mean (\pm SD) flight altitudes of bird targets by hour of the day, as measured by radar (corrected for sampling area) in east-central Alaska during spring and fall 1988–1989. (* = sample size \leq 5)

DISCUSSION

Diurnal altitudes of flight.—The flight altitudes of the birds we studied visually in east-central Alaska generally were lower than altitudes reported in the literature. For example, most swans flew \leq 300 m agl, whereas Bellrose (1976) stated that most Tundra Swans migrate at 900–1500 m agl. Most of the geese we studied flew \leq 300 m agl; others report that geese migrate mostly at 100–1110 m agl (e.g., Bellrose 1976, Blokpoel 1974,

TABLE 6. Comparisons of flight altitudes (m agl) of bird targets observed on radar during daylight, crepuscular and nocturnal periods in east-central Alaska during spring and fall 1988–1989.

Season	Light condition						<i>n</i>	<i>H'</i>	<i>P</i>
	Daylight		Crepuscular		Nocturnal				
	Mean	SD	Mean	SD	Mean	SD			
Spring	155	128	168	134	150	122	2865	19.9	<0.001
Fall	319	278	314	227	361	200	4402	50.8	<0.001

Cooch 1955, Meinertzhagen 1955). In addition, most of the ducks that we studied during daylight hours flew ≤ 150 m agl. Seaducks migrating along the northern coast of Alaska also flew < 150 m agl (Johnson and Richardson 1982). Ducks migrating during the "grand passage" along the Central Flyway generally flew at 460–850 m agl during the day and dropped to a minimum of 150 m at night (Bellrose and Sieh 1960).

Flight altitudes of raptors also were lower in this study (most flew ≤ 150 m agl) than in many others. Flights below 50 m agl are common along some ridges and coastal areas in North America, however (Kerlinger 1989). Migrating raptors in North America previously have been reported to migrate at 200–1100 m agl (e.g., Kerlinger 1980; Kerlinger and Gauthreaux 1984, 1985; Kerlinger et al. 1985).

The flight altitudes of the other species groups that we studied also were lower than those in the literature. For example, most of the Sandhill Cranes we observed flew 30–300 m agl, whereas Kessel (1984) reported that most cranes in east-central Alaska migrated at 300–900 m agl. The shorebirds that we observed generally flew < 150 m agl, but others report flights between ~ 200 m and 4000 m agl (e.g., Kerlinger and Moore 1989, Mascher 1962). Most of the passerines that we observed during the day flew below 30 m agl. Similarly, Bingman (1980), Wiedner et al. (1992), and several of the sources cited by Kerlinger and Moore (1989) observed diurnal passerine migration below 50–150 m agl. Others report that passerines generally migrate below 1000 m agl but that some have been observed at much greater heights (e.g., Gauthreaux 1972, Kerlinger and Moore 1989, Lack 1960, Meinertzhagen 1955).

The primary reason for the low diurnal flight altitudes that we observed visually may be related to location: the study area is near the northern terminus of migration for many species. Thus, these species are not in the middle of a long, non-stop trip as they pass over the study area, and many may linger before and after the breeding season for feeding or resting, especially if breeding areas are frozen or snow-covered. If birds did stop to use the area, one would expect to observe lower flight altitudes as they flew down into, or out of, the area. The extensive wetlands in the Tanana River Valley attract large numbers of migrant waterbirds, and many of the flights that we observed for those species probably repre-

sented low-level flights of birds that had used this area on their way to or from the breeding grounds.

It is likely that only a small portion of the differences in diurnal flight altitudes between this study and others occurred because some of the individuals (especially passerines) we observed were local breeders making low-altitude foraging flights. Flight directions indicated that most of our records were of migrating birds, even though it was daylight. For all species groups combined, over 90% of the birds that we observed flew toward the West or Northwest in spring, and over 90% flew toward the East or Southeast in fall.

Another reason why diurnal flight altitudes were lower for this study is because our visual observations are biased to low-flying birds, although some of the other visual studies we cite may also have had this bias. This bias probably was greatest for the smaller or less vocal species (i.e., shorebirds, passerines, some of the smaller raptors) and was greater in fall than in spring. Other authors also report that visual observers tend to miss the higher flying birds (e.g., Kerlinger et al. 1985; Kerlinger and Gauthreaux 1984, 1985; Meinertzhagen 1955). Comparisons of our concurrent radar and visual observations did not indicate that this bias in our visual data was great enough to account entirely for the large differences in flight altitudes between our study and others, however.

Nocturnal altitudes of flight.—At night, a large proportion (98% in spring and 77% in fall) of the radar targets were flying <500 m agl. Nocturnal flight altitudes in spring and fall at two other locations in interior Alaska (Fairbanks in 1992 and Gulkana in 1989) also indicated that most birds in the area flew below 500 m agl at night (Cooper, unpubl. data). Likewise, several other radar studies have found that nocturnal migration usually occurs below 500 m agl (e.g., Bellrose 1971; Bruderer and Steidinger 1972; Gauthreaux 1972, 1978, 1991). Large kills of birds at tall structures also indicate that nocturnal migrants fly <500 m on at least some nights (Avery et al. 1980). In contrast, others have found that peak nocturnal densities extend over a broad altitudinal range below approximately 2000 m (e.g., Eastwood and Rider 1965; Nisbet 1963; Richardson 1971, 1972). We suspect that differences between the two groups of studies are due to differences in location, species composition of migrant birds, and perhaps weather conditions. We do not believe that differences between our study and the studies that report higher altitudes occurred because birds flew above the zone we sampled (i.e., >1000 m agl), because we also sampled 1000–1800 m agl in 1989 and found that <0.3% of the targets occurred in that zone. Further, we do not believe that the differences were due to range limitations of the radars. Our radars (especially the FR-1900 model) probably could not detect some of the smallest birds that were flying singly at 1000–1800 m agl; however, the distribution of flight altitudes (Fig. 3) shows that the number of birds dropped off to nearly zero well below the minimum range of 1000 m agl. Additionally, if large numbers of birds were migrating at 1000–1800 m agl we should have had more numerous observations of the large-bodied or

flocked bird targets, which we know were detectable at those altitudes. Thus, we believe that it is extremely unlikely that a large proportion of birds were flying at 1000–1800 m agl. The relatively low flight altitudes we observed probably were due in large part to the location of our study area near the northern terminus of migration.

Seasonal patterns in altitude of flight.—Both radar and visual observations indicated that flight altitudes generally were higher in fall than in spring, as has been observed elsewhere (e.g., Bellrose 1976, Bellrose and Graber 1963, Blokpoel and Burton 1975, Gauthreaux 1978). In contrast, other studies found that migration occurred at lower altitudes in fall than in spring (Eastwood and Rider 1965, Kessel 1984, Lack 1960) and a third group of studies found that flight altitudes of both small birds and waterfowl did not differ between spring and fall (Bellrose 1971; Richardson 1971, 1972).

Bellrose (1976) noted that, in general, the longer the migratory flight, the higher the altitude at which it occurs. Perhaps spring flight altitudes in east-central Alaska were lower because spring migrants made shorter migration flights than did fall migrants. In spring, migrants to Alaska encounter ice- or snow-covered habitat and low food availability as they advance northward. These barriers are not present in fall, which may lead to lengthier, higher flights over the area.

We observed high night-to-night variability in nocturnal flight altitudes for both spring and fall. Judging by the low correlation between mean nightly flight altitude and migration rates, the day-to-day variability was not related to daily changes in the magnitude of migration. This variability may have been related to changing species composition and changes in vertical structure of the atmosphere, however. Birds tend to migrate at altitudes where favorable winds minimize the cost of migration (Bruderer et al. 1995, Gauthreaux 1991, Kerlinger and Moore 1989). As mentioned, we plan to discuss the effects of atmospheric structure on flight altitude in a different paper.

In addition to the high day-to-day variability, there were within-season patterns of nocturnal flight altitudes among early, mid, and late periods of the spring and the fall. These patterns were not related to seasonal changes in the magnitude of migration but probably were related to changing species composition. In spring, flight altitudes were highest in April and early May, when waterfowl were the dominant migrants and lowest in mid-late May, when lower-flying passerines were the dominant migrants. The high flight altitudes observed during late August and early September probably were due to Greater White-fronted Geese, which were one of the most numerous fall migrants and had the highest mean flight altitudes of all species in fall (Appendix 1).

Diel patterns in altitude of flight.—The radar data indicated that flight altitudes within a day were highly variable and that there was no near-midnight peak in flight altitudes. Further, birds flew higher at night than during daylight or crepuscular conditions in fall but not in spring. Although a few studies have found that flight altitudes of birds are highest

during the day (Bellrose and Sieh 1960, Gauthreaux 1972), most have found that altitudes tend to be lowest during the day (e.g., Bruderer and Steidinger 1972, Eastwood and Rider 1965, Gauthreaux 1978, Lack 1960). Further, flight altitudes of migrating birds generally are highest near or just before midnight and decline slowly until dawn (e.g., Able 1970, Blokpoel and Burton 1975, Nisbet 1963, Richardson 1971).

The lack of a near-midnight peak in flight altitudes may be related to the rapidly changing day length in Alaska. During both fall and spring in Alaska, the amount of daylight can change by up to 8 min/d (nearly 1 h/wk), so times of sunrise and sunset change dramatically (compared with lower latitudes) over the course of a spring or fall study period. Such changes would tend to dampen hourly trends in flight altitudes, if altitudes were related to the amount of time elapsed since sunset.

In summary, results of this study indicate that substantial numbers of birds migrated at low altitudes in east-central Alaska. The relatively low altitudes we observed are a good example of the high degree of geographic variability in flight altitudes of birds during migration. Given this variability and the geographic variability in bird abundance, we recommend that site-specific field studies, in conjunction with regional assessments (e.g., literature reviews) be conducted to assess the potential for bird collisions at sites where tall structures are to be constructed. In addition to addressing conservation concerns, there clearly is a need for more studies of flight altitude in a variety of geographic locations before we will fully understand this important facet of bird migration.

ACKNOWLEDGMENTS

Funding for this study was provided by the U.S. Air Force. The study was administered by Metcalf & Eddy/Holmes & Narver, the Alaska Environmental and Information and Data Center, and the Stanford Research Institute, International. Our radars were operated under radio station license 901106N-6-1-1B. We thank the numerous personnel from ABR who were involved in this study. Special thanks go to P. W. Banyas, C. L. Cranor, C. B. Johnson, J. G. King, B. E. Lawhead, S. M. Murphy, R. J. Rohleder and J. R. Rose. We thank L. C. Byrne, for help with analyses. W. C. Kappleman (Metcalf & Eddy/Holmes & Narver) provided thorough reviews of the study and valuable input into study design. We thank H. Blokpoel, R. H. Day, P. Kerlinger, K. Yasukawa and the anonymous reviewers for their valuable comments.

LITERATURE CITED

- ABLE, K. P. 1970. A radar study of the altitude of nocturnal passerine migration. *Bird-Banding* 41:282-290.
- ALERSTAM, T. 1992. *Bird migration*. Cambridge Univ. Press, Cambridge, United Kingdom. 420 pp.
- AVERY, M. L., P. F. SPRINGER, AND N. S. DAILEY. 1980. *Avian mortality at manmade structures: an annotated bibliography (revised)*. U.S. Fish and Wildlife Service, Biological Services Program, Rep. No. FWS/OBS-80/54. 152 pp.
- BANKS, R. C. 1979. Human related mortality of birds in the United States. U.S. Fish and Wildlife Service, Spec. Sci. Rep.—Wildl. No. 215:1-16.
- BELLROSE, F. C. 1971. The distribution of nocturnal migration in the air space. *Auk* 88:397-424.
- . 1976. *Ducks, geese, and swans of North America*, 2nd ed. Stackpole Co., Harrisburg, Pennsylvania. 540 pp.

- , AND R. R. GRABER. 1963. A radar study of flight directions of nocturnal migrants. Proc. XIII Intl. Ornithol. Congr.:362-389.
- , AND J. G. STEH. 1960. Waterfowl flights in the Mississippi Flyway, 1956 and 1957. Wilson Bull. 72:29-59.
- BINGMAN, V. P. 1980. Inland morning flight behavior of nocturnal passerine migrants in eastern New York. Auk 97:465-472.
- BLOKPOEL, H. 1971. The M33C track radar (3-cm) as a tool to study height and density of bird migration. Can. Wildl. Serv. Rep. Ser. 14:77-94.
- . 1974. Migration of lesser snow and blue geese in spring across southern Manitoba, Part I: distribution, chronology, direction, numbers, height, and species. Can. Wildl. Serv. Rep. 28:1-30.
- BLOKPOEL, H., AND J. BURTON. 1975. Weather and the height of nocturnal migration in east-central Alberta: a radar study. Bird-Banding 46:311-328.
- BRUDERER, B., AND P. STEIDINGER. 1972. Methods of quantitative and qualitative analysis of bird migration with a tracking radar. Pp. 151-168, in S. E. Galler, K. Schmidt-Koenig, G. J. Jacobs, and R. E. Belleville, eds. Animal orientation and navigation: a symposium. NASA SP262. U.S. Government Printing Office, Washington, D.C.
- BRUDERER, B., L. G. UNDERHILL, AND F. LIECHTI. 1995. Altitude choice by night migrants in a high desert area predicted by meteorological factors. Ibis 137:44-55.
- COOCH, F. G. 1995. Observation on the autumn migration of Blue Geese. Wilson Bull. 67: 171-174.
- COOPER, B. A., R. H. DAY, R. J. RITCHIE, AND C. L. CRANOR. 1991. An improved marine radar system for studies of bird migration. J. Field Ornithol. 62:367-377.
- EASTWOOD, E., AND G. C. RIDER. 1965. Some radar measurements of the altitude of bird flight. Brit. Birds 58:393-426.
- GABRIELSON, I. N., AND F. C. LINCOLN. 1959. The birds of Alaska. Stackpole Co., Harrisburg, Pennsylvania. 932 pp.
- GAUTHREAUX, S. A., JR. 1972. Behavioral responses of migrating birds to daylight and darkness: a radar and direct visual study. Wilson Bull. 84:136-148.
- . 1978. Migratory behavior and flight patterns. Pp. 12-26, in M. Avery, ed. Impacts of transmission lines on birds in flight. U.S. Fish and Wildlife Service, Office of Biological Services, Washington, D.C. Rep. No. FWS/OBS-78/48.
- . 1991. The flight behavior of migrating birds in changing wind fields: radar and visual analyses. Am. Zool. 31:187-204.
- IRVING, L. 1961. The migration of Lapland Longspurs to Alaska. Auk 78:327-342.
- JOHNSON, S. R., AND W. J. RICHARDSON. 1982. Waterbird migration near the Yukon and Alaska coast of the Beaufort Sea: II. Moulting migration of seaducks in summer. Arctic 35: 291-301.
- KERLINGER, P. 1980. A tracking radar study of bird migration. J. Hawk Migr. Assoc. N. Am. 2:34-42.
- . 1989. Flight strategies of migrating hawks. Univ. Chicago Press, Chicago, Illinois. 375 pp.
- , V. P. BINGHAM, AND K. P. ABLE. 1985. Comparative flight behavior of migrating hawks studied with tracking radar during autumn in central New York. Can. J. Zool. 63:755-761.
- , AND S. A. GAUTHREAUX, JR. 1984. Flight behavior of Sharp-shinned Hawks during migration, I: over land. Anim. Behav. 32:1021-1028.
- , AND ———. 1985. Flight behavior of raptors during spring migration in south Texas studied with radar and visual observations. J. Field Ornithol. 56:394-402.
- , AND F. R. MOORE. 1989. Atmospheric structure and avian migration. Pp. 109-141, in D. M. Power, ed. Current ornithology, Vol. 6. Plenum Press, New York, New York.
- KESSEL, B. 1984. Migration of sandhill cranes, *Grus canadensis*, in east-central Alaska, with routes through Alaska and western Canada. Can. Field-Nat. 98:279-292.
- LACK, D. 1960. The height of bird migration. Brit. Birds 53:5-10.
- MASCHER, J. M., B. STOLT, AND L. WALLIN. 1962. Migration in spring recorded by radar and by field observations in Sweden. Ibis 104:205-215.

- MEINERTZHAGEN, R. 1955. The speed and altitude of bird flight (with notes on other animals). *Ibis* 97:81-117.
- NISBET, I. C. T. 1963. Measurements with radar of the height of nocturnal migration over Cape Cod, Massachusetts. *Bird-Banding* 34:57-67.
- RICHARDSON, W. J. 1971. Spring migration and weather in eastern Canada: a radar study. *Am. Birds* 25:684-690.
- . 1972. Autumn migration and weather in eastern Canada: a radar study. *Am. Birds* 26:10-16.
- ROBBINS, C. S., J. R. SAUER, R. GREENBURG, AND S. DROEGE. 1989. Population declines in North American birds that migrate to the Neotropics. *Proc. Natl. Acad. Sci. U.S.A.* 86: 7658-7662.
- SLADEN, W. S. L. 1973. A continental study of Whistling Swans using neck collars. *Wildfowl* 24:8-14.
- SPINDLER, M. A., AND K. F. HALL. 1991. Local movements and habitat use of Tundra or Whistling Swans *Cygnus columbianus* in the Kobuk-Selawik Lowlands of northwest Alaska. *Wildfowl* 42:17-32.
- STEARNS, E. I. 1949. The study of hawks in flight from a blimp. *Wilson Bull.* 61:110.
- TERBORGH, J. W. 1989. *Where have all the birds gone?* Princeton Univ. Press, Princeton, New Jersey. 207 pp.
- U.S. FISH AND WILDLIFE SERVICE. 1990. Alaska Trumpeter Swan census—1990. U.S. Fish and Wildlife Service, Migratory Bird Management, Juneau, Alaska. 4 pp.
- WAHRHAFTIG, C. 1965. Physiographic divisions of Alaska. *U.S. Geol. Surv. Prof. Pap.* 482:1-52.
- WEGE, M. L., AND D. G. RAVELING. 1984. Flight speed and directional response to wind by Canada Geese. *Auk* 101:342-348.
- WEST, G. C., L. J. PEYTON, AND L. IRVING. 1968. Analysis of spring migration of Lapland Longspurs to Alaska. *Auk* 85:639-653.
- WEIR, R. D. 1976. Annotated bibliography of bird kills at man-made obstacles: a review of the state of the art and solutions. *Can. Wildl. Serv., Ottawa, Ontario, Canada.* 85 pp.
- WIEDNER, D. S., P. KERLINGER, D. A. SIBLEY, P. HOLT, J. HOUGH, AND R. CROSSLEY. 1992. Visible flight of neotropical landbird migrants at Cape May, New Jersey. *Auk* 109:500-510.

Received 29 Aug. 1994; accepted 23 Mar. 1995.

APPENDIX I

Common and scientific names, mean flight altitudes (\pm SD) in meters above ground level and numbers of flocks* (n) of migrant birds observed visually during daylight hours in east-central Alaska, spring and fall 1987-1989. Does not include species for which <10 flocks were observed in both spring and fall.

Common name	Scientific name	Spring			Fall		
		Mean	SD	n	Mean	SD	n
Tundra Swan	<i>Cygnus columbianus</i>	114	87	136	188	169	233
Trumpeter Swan	<i>Cygnus buccinator</i>	100	90	90	164	146	206
Gr. White-fronted Goose	<i>Anser albifrons</i>	158	103	104	319	226	152
Canada Goose	<i>Branta canadensis</i>	114	104	103	285	259	66
Green-winged Teal	<i>Anas crecca</i>	14	18	45	41	45	5
Mallard	<i>Anas platyrhynchos</i>	31	44	133	47	137	22
Northern Pintail	<i>Anas acuta</i>	89	95	152	92	150	18
Northern Shoveler	<i>Anas clypeata</i>	62	90	18	101	242	7
American Wigeon	<i>Anas americana</i>	51	83	44	90	0	1
Common Merganser	<i>Mergus merganser</i>	22	53	17	8	0	2
Bald Eagle	<i>Haliaeetus leucocephalus</i>	130	113	39	77	119	43
Northern Harrier	<i>Circus cyaneus</i>	29	54	429	65	142	526
Sharp-shinned Hawk	<i>Accipiter striatus</i>	76	93	80	115	186	340
Northern Goshawk	<i>Accipiter gentilis</i>	42	75	23	32	97	92
Red-tailed Hawk	<i>Buteo jamaicensis</i>	116	112	115	135	198	119
Rough-legged Hawk	<i>Buteo lagopus</i>	149	120	59	115	162	224
Golden Eagle	<i>Aquila chrysaetos</i>	220	126	20	239	258	19
American Kestrel	<i>Falco sparverius</i>	14	16	30	33	86	131
Merlin	<i>Falco columbarius</i>	22	27	17	35	85	61
Peregrine Falcon	<i>Falco peregrinus</i>	51	43	6	181	231	12
Sandhill Crane	<i>Grus canadensis</i>	166	113	214	235	194	109
Lesser Golden-Plover	<i>Pluvialis dominica</i>	47	90	37	8	0	1
Semipalmated Plover	<i>Charadrius semipalmatus</i>	27	32	11	8	0	1
Lesser Yellowlegs	<i>Tringa flavipes</i>	29	30	55	—	—	0
Solitary Sandpiper	<i>Tringa solitaria</i>	17	29	80	—	—	0
Spotted Sandpiper	<i>Actitis macularia</i>	8	0	35	8	0	11
Baird's Sandpiper	<i>Calidris bairdii</i>	16	24	12	—	—	0

APPENDIX 1. Continued

Common name	Scientific name	Spring			Fall		
		Mean	SD	n	Mean	SD	n
Pectoral Sandpiper	<i>Calidris melanotos</i>	27	39	50	—	—	0
Long-billed Dowitcher	<i>Limnodromus scolopaceus</i>	43	36	12	23	0	1
Common Snipe	<i>Gallinago gallinago</i>	55	61	122	45	37	21
Bonaparte's Gull	<i>Larus philadelphia</i>	40	39	14	—	—	0
Mew Gull	<i>Larus canus</i>	39	54	171	10	6	6
Herring Gull	<i>Larus argentatus</i>	37	53	94	29	35	9
Short-eared Owl	<i>Asio flammeus</i>	39	90	19	18	25	11
Belted Kingfisher	<i>Ceryle alcyon</i>	30	34	5	9	5	19
Northern Flicker	<i>Colaptes auratus</i>	11	11	128	19	26	45
Say's Phoebe	<i>Sayornis saya</i>	8	0	29	8	0	5
Horned Lark	<i>Eremophila alpestris</i>	16	24	22	8	0	7
Tree Swallow	<i>Tachycineta bicolor</i>	14	20	279	15	11	2
Violet-green Swallow	<i>Tachycineta thalassina</i>	14	25	104	23	0	2
Bank Swallow	<i>Riparia riparia</i>	19	21	55	31	40	7
Cliff Swallow	<i>Hirundo pyrrhonota</i>	18	18	40	8	0	2
Ruby-crowned Kinglet	<i>Regulus calendula</i>	8	3	20	10	12	55
Swainson's Thrush	<i>Catharus ustulatus</i>	8	3	20	40	74	9
Hermit Thrush	<i>Catharus guttatus</i>	8	0	12	8	0	1
American Robin	<i>Turdus migratorius</i>	14	21	457	33	79	233
Variied Thrush	<i>Ixoreus naevius</i>	20	24	51	38	55	277
American Pipit	<i>Anthus rubescens</i>	19	27	217	15	19	340
Bohemian Waxwing	<i>Bombicilla garrulus</i>	23	24	258	8	0	8
Northern Shrike	<i>Lanius excubitor</i>	24	37	5	12	7	14
Orange-crowned Warbler	<i>Vermivora celata</i>	8	3	21	11	16	27
Yellow Warbler	<i>Dendroica petechia</i>	9	12	46	23	33	11
Yellow-rumped Warbler	<i>Dendroica coronata</i>	11	13	177	15	20	87
Blackpoll Warbler	<i>Dendroica striata</i>	8	0	11	8	0	3
Wilson's Warbler	<i>Wilsonia pusilla</i>	8	0	19	16	26	10
American Tree Sparrow	<i>Spizella arborea</i>	9	12	51	16	72	80
Savannah Sparrow	<i>Passerculus sandwichensis</i>	10	14	33	8	0	8

APPENDIX 1. Continued

Common name	Scientific name	Spring			Fall		
		Mean	SD	n	Mean	SD	n
Fox Sparrow	<i>Passerella iliaca</i>	9	4	12	8	0	13
White-crowned Sparrow	<i>Zonotrichia leucophrys</i>	8	3	81	8	2	40
Dark-eyed Junco	<i>Junco hyemalis</i>	9	6	237	9	9	402
Lapland Longspur	<i>Calcarius lapponicus</i>	12	13	684	14	18	187
Snow Bunting	<i>Plectrophenax nivalis</i>	10	11	61	9	5	50
Rusty Blackbird	<i>Euphagus carolinus</i>	21	27	325	26	30	495
Unidentified redpoll	<i>Carduelis spp.</i>	23	26	215	17	23	277

^a Flock defined as two or more birds flying in proximity, or any birds flying singly.