ANALYSIS OF SPRING MIGRATION OF LAPLAND LONGSPURS TO ALASKA[1]

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IN tracing the progress of Lapland Longspurs (*Calcarius lapponicus alascensis*) from the Teslin River–Atlin area of Yukon and British Columbia to many points in Alaska, Irving (1961) demonstrated by observed and reported dates that thousands of these birds migrated in flocks of 50 to 100 birds westward from the mountains of Northwest British Columbia along the route of the Alaska Highway, which follows the low levels of the Yukon watershed. In Alaska they proceed to their breeding grounds north and west of the forest. Irving postulated that longspurs nesting in the Mackenzie River Delta came from farther east in Alberta while those nesting in the Aleutians migrated along the coast or over the Gulf of Alaska, because their early arrival in the west precluded their passage through the mountains of British Columbia.

It was inferred that the longspurs use both interior and coastwise routes of migration to Alaska. Reports and our observations during several migrations show that longspurs migrate in large numbers northward and westward from the prairies of Alberta through Yukon Territory but we do not know what proportions of prairie birds continue westward into western and northern Alaska or diverge northward to the Mackenzie Valley. The mountain trenches of British Columbia also appear to offer favorable northward migration routes parallel to the prairie migration to enter the stream moving westward along the headwaters of the Yukon River in Yukon Territory. Although longspurs are reported in the mountains of British Columbia (Munro and McCowan, 1947) the data are insufficient to indicate migratory programs.

Observation suggests that longspurs are daytime migrants; we have seen them settling to roost at dusk and frequently on the wing during the day. The distinctive male longspur plumage permits discrimination of sex in flocks even at considerable distance. Irving noted that the majority of early migrant longspurs along the Alaska Highway and arriving on their nesting grounds at Anaktuvuk Pass were male birds, but he did not record significant numbers of females. On the nesting grounds the female birds are so secretive that their arrival and numbers are obscure. Except for the unlikely case that the females pursue a different route than the males they are to breed with, the proportions of sexes in the flocks along the migratory path should reveal the movement of a population adequate for nesting. Conversely the proportion of sexes in migrating flocks should

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TABLE 1

SCHEDULE AND ROUTES OF TRIPS ON ALASKA HIGHWAY 1965–67

	1965	1966	1967
19 April	Fairbanks, Alaska (mile 1520)[1]		
20 April	Beaver Creek, Y.T. (mile 1202)		
21 April	Whitehorse, Y.T. (mile 918)		
22 April	mile 674, Y.T.		
23 April	Fort Nelson, B.C. (mile 300)		
24 April	Dawson Creek, B.C. (mile 0)		
25 April	Dawson Creek, B.C. (mile 0)		
26 April	Dawson Creek, B.C. (mile 0)		
27 April	Dawson Creek, B.C. (mile 0)		
28 April	mile 116, B.C.		
29 April	mile 496, B.C.		Fairbanks, Alaska (mile 1520)
30 April	Watson Lake, Y.T. (mile 635)		mile 1119, Y.T.
1 May	Atlin, B.C.	Fairbanks, Alaska (mile 1520)	mile 813, Y.T.
2 May	Whitehorse, Y.T. (mile 918)	Tok, Alaska (mile 1310)	Watson Lake, Y.T. (mile 635)
3 May	Haines, Alaska	mile 955, Y.T.	Watson Lake, Y.T. (mile 635)
4 May	Kluane Lake, Y.T. (mile 1060)	mile 760, Y.T.	Watson Lake, Y.T. (mile 635)
5 May	Fairbanks, Alaska (mile 1520)	Watson Lake, Y.T. (mile 635)	Watson Lake, Y.T. (mile 635)
6 May		Watson Lake, Y.T. (mile 635)	Watson Lake, Y.T. (mile 635)
7 May		Watson Lake, Y.T. (mile 635)	Watson Lake, Y.T. (mile 635)
8 May		Watson Lake, Y.T. (mile 635)	Watson Lake, Y.T. (mile 635)
9 May		Watson Lake, Y.T. (mile 635)	Watson Lake, Y.T. (mile 635)
10 May		Whitehorse, Y.T. (mile 918)	Watson Lake, Y.T. (mile 635)
11 May		Tok, Alaska (mile 1310)	Johnson's Crossing, Y.T. (mile 835)
12 May		Fairbanks, Alaska (mile 1520)	Whitehorse, Y.T. (mile 918)
13 May			mile 1147, Y.T.
14 May			Fairbanks, Alaska (mile 1520)

[1] Mile of Alaska Highway from Dawson Creek, B.C.

register whether they are early or late in the migratory program, and hence the schedule of that population.

The prior arrival of males on the breeding grounds occurs also in many other arctic and subarctic species (Irving, 1960), but changing proportions of male and female birds along the migration route have not been recorded for any arctic passerine. We have noted that age and sex groups of Willow Ptarmigan (*Lagopus lagopus alascensis*) pursue their own programs of migration independently although they are gregarious and migrate in coherent aggregations (Irving et al., 1967). Through the following study of the dates of movements and sex composition of flocks, it became obvious that longspurs maintain distinguishable schedules during migration over several geographical routes.

In order to resolve the timing and extent of the several migrations of longspurs into Alaska and to determine the structure of migrating populations, we made observations and collections along the Alaska Highway and adjacent roadways in the springs of 1965, 1966, and 1967. Several specimens obtained for skins are housed at the Institute of Arctic Biology.

Methods

We traveled from and to Fairbanks according to the schedule and route listed in Table 1. Careful records were kept of each longspur flock observed as to number of birds, per cent of male birds in the flock, and direction of flight if obvious. Birds were collected with shotgun and mist net from many flocks for marking, to determine sex ratios where the birds could not easily be counted, to obtain stomach content samples and to assess depot fat content and fatty acid composition.

Results and Discussion

Routes.—Irving (1961) suggested that an interior and a coastal migration could be distinguished through dates of arrival at specific Alaskan points. From consideration of the physiography of Alberta, British Columbia, Yukon Territory, and Alaska we thought we could postulate that longspurs move along routes easily distinguishable both to them and to us (Figure 1). These are:

(1) Coastwise from interior British Columbia northward through the islands to enter Alaska near Ketchikan and Juneau, swinging inland at several localities such as the Lynn Canal, entering interior Alaska through Haines or Skagway and then traveling over the mountain passes (Chilkat Pass to Haines Junction or Chilkoot Pass to Carcross and Whitehorse) to enter the Yukon drainage.

(2) The mountain trenches of northern British Columbia and southern Yukon: a. east of the Cassiar Mountains entering the Yukon Territory at Watson Lake, b. between the Cassiar (Stikine) Range and the coast range to Teslin Lake and the Teslin River, and c. along Atlin Lake through Tagish to the Yukon River at Whitehorse.

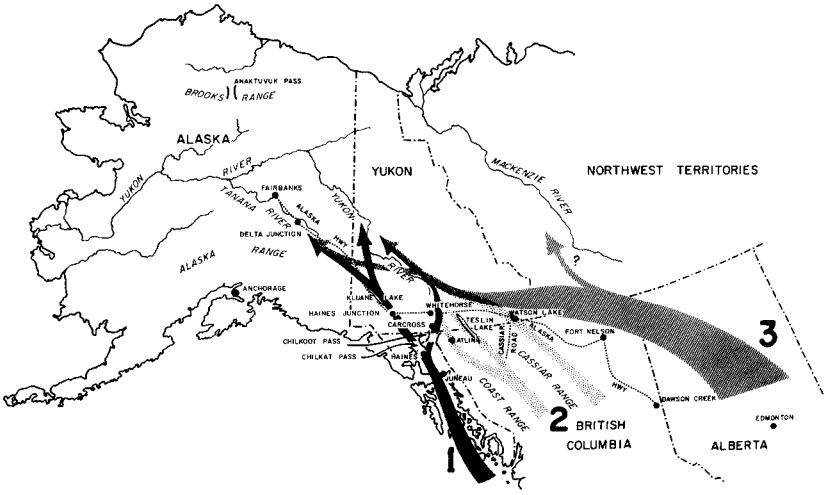

Figure 1. Map of Alaska and Western Canada showing the Alaska Highway, locations of observations and collections of Lapland Longspurs, and the suspected major migratory routes of longspurs mentioned in the text. 1, Coastal route; 2, intermountain route; 3, prairie route.

(3) From the prairies of Alberta northwest into the prairies of northeastern British Columbia, thence along the line of the Alaska Highway westward and northward to the Yukon River through the shallow valleys of the southern and western mountains of Yukon Territory.

Differing weather regimes in the three approach routes could separate the total migration into distinguishable pulses. The initial pulses of the three migrating populations could readily be distinguished by the date of arrival of male birds. Similarly, successive pulses along the routes could be detected by the changing proportions of male and female longspurs.

Migration observed in 1965.—In 1965 we went to the Yukon Territory early and did not see any longspurs until 29 April. We had already spent from 23 to 28 April south and east of Watson Lake (mile 635) at Dawson Creek (mile 0) and had seen no evidence of longspurs arriving from the prairies. At 1800 hours on 29 April we drove south along the Cassiar Road (which leaves the Alaska Highway at mile 648) to mile 36, but saw no birds and returned northward. At 2000 hours we sighted 25 longspurs along the roadside at mile 11; we counted 20 males. At mile 8 we counted 30 longspurs and collected three males. As we had seen no longspurs along the prairie section of the highway, we thought these birds had arrived through the mountains from the southeast and entered the Yukon Territory over the proposed intermountain trench route (No. 2, Figure 1).

The next day, 30 April, there were still no longspurs in the immediate

vicinity of Watson Lake, which we later learned was visited commonly by the prairie as well as later mountain migrants. We sighted a small flock of 12 at mile 636, and the same two flocks where we had seen them on the Cassiar Road the preceding afternoon. On 1 May we proceeded westward along the Alaska Highway and found scattered flocks of longspurs along the road to Teslin Lake (mile 805). The general direction of their movement was westward. We then traveled south to Atlin and there saw two small flocks of male longspurs.

We saw no other longspurs west of Whitehorse (mile 918) or until 3 May when we again turned south at Haines Junction (mile 1016) toward Haines over Chilkat Pass. Here we encountered several flocks of predominantly male longspurs obviously moving northward. We suspected that these birds had moved up the coast between the islands and along the grassy flats of river outwashes to Haines.

The next group of longspur flocks was found along the northwestern edge of Kluane Lake (mile 1106), which is on the northeast side of the St. Elias Range and on a straight-line course northwestward from Haines and Haines Junction. As we saw no birds between Whitehorse and Haines Junction in 1965 or 1966, we suspected that flocks approaching from the east turn northward either at Whitehorse or at the Takhini River (mile 946) west of Whitehorse to join the Yukon where migrating flocks have been reported (Rand, 1946). The two groups seen on the Haines Road and at Kluane Lake suggest a coastal component of migration into interior Alaska (No. 1, Figure 1). Thus the 1965 trip gave evidence for both an early intermountain and an early coastal component of migration by the appearance of predominantly male flocks arriving from the south.

Migration observed in 1967.—In 1967 we encountered a similar situation that gives further evidence for these two routes. The weather in southern Alberta was unseasonably cold and snowy during April and early May. Migration of all birds was delayed; the usual large flocks of longspurs were not seen passing through the Edmonton area (R. Lister, in litt.) and they did not arrive in the Yellowknife area until 27 May. We reached Watson Lake on 1 May and saw the first longspur on 2 May but the first flocks did not appear until 5 May. We worked with the few flocks present in Watson Lake, on the Cassiar Road, and at mile 679 from 5 to 10 May when they left the areas. On 9 May we drove 100 miles east of Watson Lake and saw no longspurs; a telephone call to Lister in Edmonton confirmed that the prairie population had not yet arrived. The birds we saw were predominantly males and must have come to the Watson Lake area via the intermountain trenches.

We saw large flocks of longspurs in the Whitehorse area and a flock of 500 at Haines Junction on 11 and 12 May. Scattered flocks of from

50 to 200 birds were seen northwest of Kluane Lake (mile 1065) and along the Alaska Highway and Tanana River northwest as far as Tanacross, Alaska (mile 1324). The proportion of male birds showed a slight diminishing by 10 to 13 May. These flocks seen in 1967 were obviously the initial waves entering Alaska through the mountains and from the coast.

We learned later from residents of Watson Lake that the usual large flocks of longspurs entered Watson Lake on approximately 18 May and remained 4 to 5 days. These birds from the prairies did not stop at Edmonton according to Lister, but apparently hurried through the northern prairies towards the breeding grounds.

Migration observed in 1966.—In 1966 we encountered an entirely different situation. We first saw longspurs on our way south along the highway on 2 May near the Kluane River (mile 1113) at the northwest end of Kluane Lake. These and others seen near Haines Junction (mile 1016) on 3 May were predominantly males. We did not encounter longspurs again until we found male flocks at Teslin Lake (mile 810). We believe that these flocks were the initial waves of the coastal (via Haines and Haines Junction) and mountain trench (via Teslin Lake) migrants respectively. On 4 May we approached the Watson Lake area and found 25 flocks that averaged 46 birds per flock between miles 679 and 635. As the proportion of male birds averaged almost 90 per cent, we believe these flocks constituted the first wave of prairie migrants arriving from the east, undoubtedly now mixed with the mountain population that had already arrived. Large numbers of longspurs continued to pass through the Watson Lake area until we left on 9 May. As we traveled west along the highway 9 May, we encountered 60 flocks of longspurs averaging 39 birds per flock between mile 680 and Whitehorse (mile 918). These flocks evidently consisted of birds that had been moving from the prairies westward plus the tail end of the mountain migration. Therefore it was not surprising to find the proportion of males averaged only 30 per cent. We do not know whether birds entering over the three migration routes intermingle in common flocks, as we have not yet discovered any morphological differences to distinguish them.

The fact that no longspurs were seen between Whitehorse (mile 918) and Haines Junction (mile 1016) on 10 May indicates that the mass of the combined migration had moved northward in the Yukon River Valley. Two flocks at Haines Junction (20, 50 birds) consisting of 40 per cent males, were probably part of the latter half of the mountain or coastal migration. Significant numbers of longspurs were not seen again until 11 May when a heavy snowstorm between Tok Junction (mile 1310) and Delta Junction (mile 1422) prevented hundreds of longspurs from continuing northward and westward in the Tanana Valley. Between mile 1323

TABLE 2

DAILY ESTIMATES OF LONGSPUR FLOCK SIZES BETWEEN MILES 630 AND 680, ALASKA HIGHWAY, 4 TO 9 MAY 1966

	Date, May					
Mile	4	5	6	7	8	9
633	100	200	50	75		100
634	100	50	75	100	100	
640		30	40			
644		20		10		
652			25	30	20	25
656	25	50	35		50	75
659					25	25
660		40		40	50	15
661			35	30	500	1000
662	60	40	10	80	25	15
663	70	20	65	50	50	28
664		100	90	75	50	
665		40	85	60	40	25
668	100	200	215	75	150	30
671	80		75		20	
672		75	25			
673	25		100	100	120	125
674			30	30	75	
677	30		30	15		25
678				25	50	
679	30			80	75	30
Total	620	865	985	875	1400	1515

and 1422 we encountered an estimated 5,120 longspurs averaging 50 birds per mile. Between mile 1355 and 1417 the birds were so dense along the roadside we could not define individual flocks accurately. We estimated the proportion of males in these flocks to be 24 per cent. The large numbers of longspurs held up southeast of Delta Junction represented the latter portion of the prairie component and would normally have been moving northwest along the Tanana River.

Thus through the 3 years of observations we have been able to distinguish three apparently distinct migrating components, each entering Alaska from a different route and following a common course over several miles along the Yukon and Tanana River systems to move northward to the tundra on the Arctic Slope and westward to the shores of the Bering and Chukchi Seas. No evidence has been found for an important migration of longspurs from the Yukon watershed northward into interior Yukon Territory (Rand, 1946; Irving, 1960).

The great variation in the arrival dates from year to year probably

TABLE 3

COLOR MARKED LONGSPURS OBSERVED AND ADDED TO FLOCKS FROM MILE 634 TO 679 ALASKA HIGHWAY, 4 TO 9 MAY 1966

	Date, May											
	4		5		6		7		8		9	
Miles	obs	add	obs	add	obs	add	obs	add	obs	add	obs	add
635–656	0	14	0	0	0	3	0	5	3	0	2	0
660–665	–	–	–	–	0	3	2	9	2	96	30	0
666–669	–	–	0	38	0	7	3	1	4	1	2	0
670–679	–	–	–	–	0	4	0	10	4	3	1	0

arises from the variety of routes taken and the vagaries of weather along the different routes. Usually the coastal route opens before the mountain or prairie route. Our early frustrations over explanations of marked annual variation in passage through the Yukon are explained by a population which, while not conspicuously polymorphic, is polyodic (*hodos* = way).

Evidence for movement and length of stay.—While the actual migration is usually difficult to observe directly in most small birds, indirect evidence can be obtained by marking individuals and noting their gradual disappearance from a local sedentary population.

Table 2 shows the flock sizes of longspurs recorded daily in 1966 for 50 miles west of Watson Lake in early May. Despite some day to day variation, Table 2 gives the impression that the numbers of birds in coherent flocks at specific locations remained relatively constant from 4 to 9 May. Excluding a marked influx in one area (mile 661) on 8 and 9 May when a large field became clear of snow, the populations in the 50 miles of roadside remained fairly constant over the 5 days at about 710 birds per day.

Birds were netted from these flocks, color marked and released on 5 days at several locations along the highway (Table 3). Long colored hackle feathers glued to a central rectrix were easily visible from a distance and marked individuals could be spotted with binoculars in flight or on the ground. A different color was used each day and each bird received a standard U. S. F. & W. S. aluminum leg band.

Initially birds were captured from a single flock and then released one or two at a time into other flocks along the road. In this manner we had hoped to mark individual flocks that we thought were long-term coherent aggregations. Release was made by throwing the marked bird into the air at the same time that a flock was scared up from the roadside only 5 to 10 meters away. In about 80 per cent of the cases, the marked bird joined the flock and was apparently accepted with no sign of discrimina-

TABLE 4
DAILY ESTIMATES OF LONGSPUR FLOCK SIZES BETWEEN MILES 630 AND 679, ALASKA HIGHWAY, 1 TO 10 MAY 1967

	Date, May									
Mile	1	2	3	4	5	6	7	8	9	10
630		1						10	2	
631						20		15		
634					100	200	40	100	100	
642					50					
660				1			7	12	10	
667						20	12			
668							20			
679					100	100	150	75	75	
Total	0	1	0	1	150	340	231	212	187	0

tion, but after marking a number of flocks on 4 and 5 May 1966 and finding no marked birds in the flock occupying the same location on the road on 5 and 6 May (Table 3), we subsequently released marked birds only into the flocks from which they were captured in 1966 and 1967.

The reason for the immediate disappearance of birds in early May 1966 may have been due to one of two factors: (1) The experience of handling, marking, and release into an "unfamiliar" flock caused the bird to depart or (2) the whole flock containing the marked bird left the area and was replaced by another flock of the same size in the same location the next day. The first of these explanations seems the more likely. After 5 May 1966, marked birds remained in the flock from which they were captured for periods of time up to 3 days. The marked birds gradually disappeared from the flocks, yet the flocks remained at about the same size and in the same location (Table 2).

In 1967 inclement weather in Alberta delayed the regular prairie migration considerably. The initial wave of longspurs at Watson Lake consisted predominantly of males. Table 4 shows that flocks entered the Watson

TABLE 5
COLOR MARKED LONGSPURS OBSERVED AND ADDED TO FLOCKS AT MILE 679 ALASKA HIGHWAY, 5 TO 10 MAY 1967

	Date, May											
	5		6		7		8		9		10	
Mile	obs	add	obs	add	obs	add	obs	add	obs	add	obs	add
679	0	10	3	54	9	29	25	0	–	0	0	0

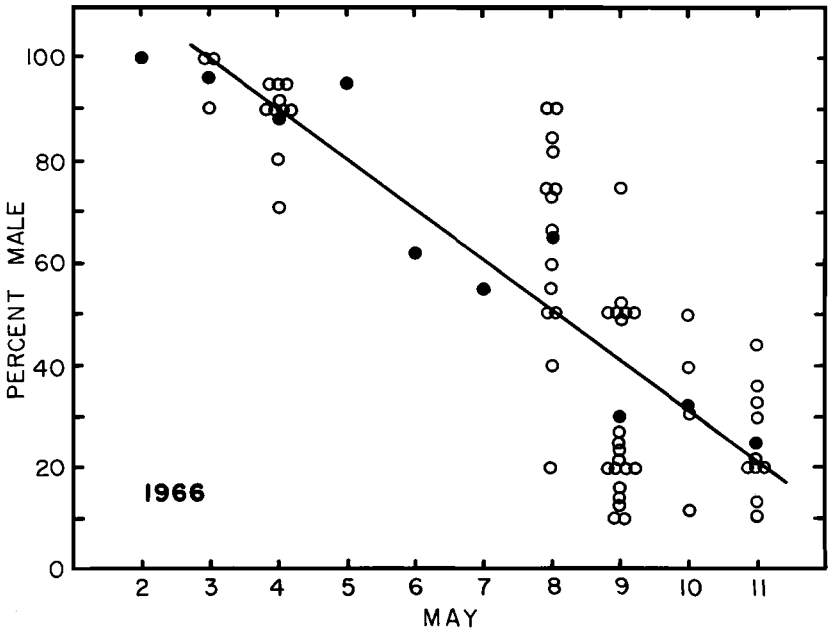

Figure 2. Sex ratios of Lapland Longspur flocks observed along the Alaska Highway, 2 to 11 May 1966. Solid circles indicate the average for each date.

Lake area on 5 and 6 May and remained until 9 or 10 May, presumably to feed and prepare for the next flight in their migration. Population size remained approximately the same in these flocks and averaged 224 birds per day in 49 miles near Watson Lake. Color marking was done only at mile 679 in 1967 (Table 5) and the results given in the table are not clear. For example, on 6 May, 54 birds were released in several groups. We noticed that one large group flew south out of sight over the trees and probably did not return to mile 679. On 7 May an additional 29 birds were marked and the following birds were seen on 8 May: 5 marked on 5 May; 6 marked on 6 May; and 14 marked on 7 May. As one-half of the birds marked on 5 and 7 May were still present on 8 May, we believe that the longspurs we observed in 1967 arrived on 4 May probably late in the evening and left 10 May in the very early morning. This indicates a length of stay of about 5 days at this stage of the migration to prepare for the next flight for this flock.

Changing sex ratio.—We noted that male longspurs preceded females both along the migration route and on the breeding grounds. The evidence for a gradual shift in sex ratio with date and geographical position came with an observation of longspurs from 2 to 11 May 1966 (Figure 2). The

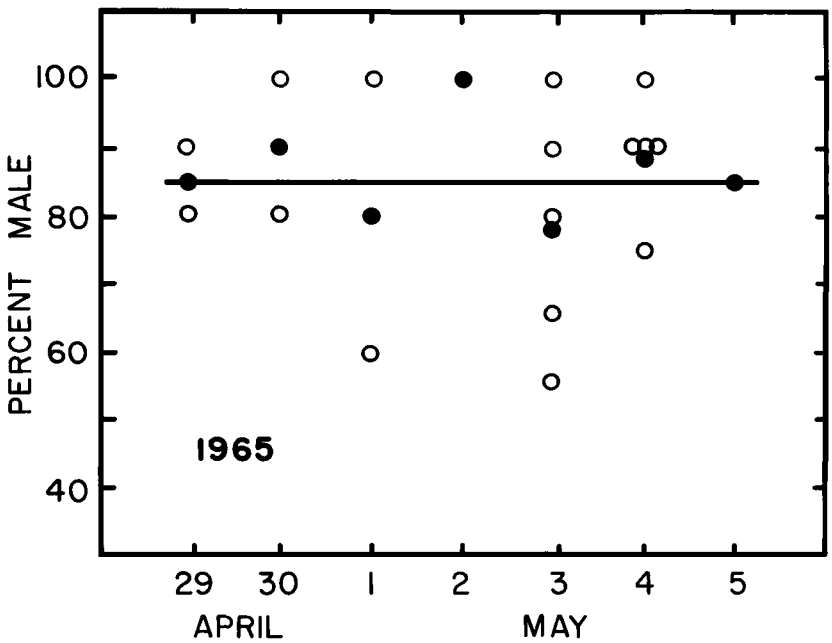

Figure 3. Sex ratios of Lapland Longspur flocks observed along the Alaska Highway, 29 April to 5 May 1965. Solid circles indicate the average for each date.

percentage of male birds declined gradually throughout the period 5 to 9 May while we were in the Watson Lake vicinity. In addition, the birds seen northwest of Watson Lake were 90 per cent male on 2–4 May while those seen northwest of Watson Lake 9–11 May were only 29 per cent male.

The compilation of data in Figure 2 combines birds from all three migration routes which were, of course, indistinguishable once the prairie population had overrun the mountain and coastal flocks. The clear decline in proportion of males allows a generalization that the stage of the migration can be predicted by the sex ratios of flocks observed at any one day and at any one point along the route. For example a flock of 90 per cent males indicates the initial wave, a 50–50 per cent ratio indicates the middle, and 10 per cent males the terminus of the migrating population. Undoubtedly the total time for the migration to pass any one point differs from year to year, and we have no observations that mark both beginning and end of a migration at a single locality. In 1967 the first flock of male longspurs was seen in Watson Lake on 5 May and the last flocks of prairie migrants passed through approximately on 22–24 May or in an elapsed time of 17 to 19 days. In 1966 we could estimate that because of more favorable weather conditions the elapsed time was much

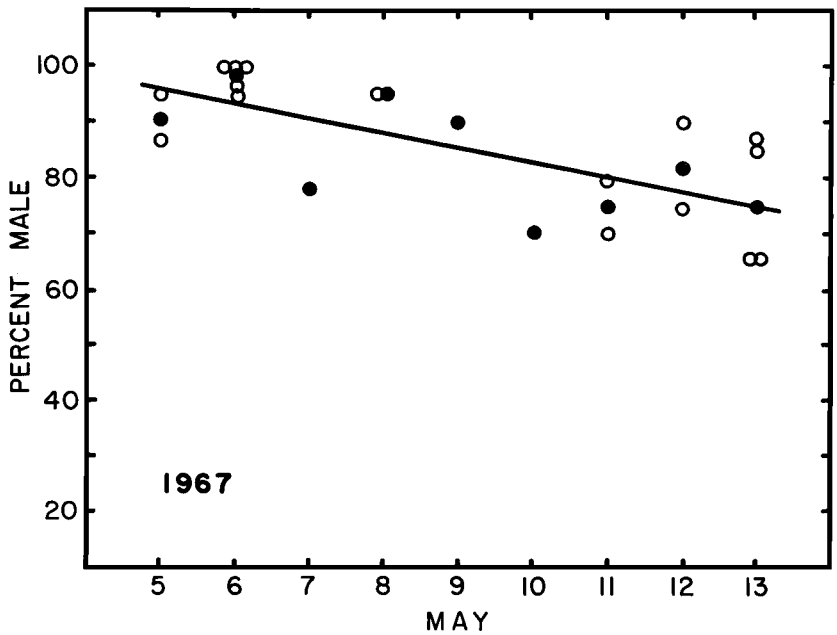

Figure 4. Sex ratios of Lapland Longspur flocks observed along the Alaska Highway, 5 to 13 May 1967. Solid circles indicate the average for each date.

shorter. Extrapolating from Figure 2, we can postulate that the migration through Watson Lake began about 2 May and terminated by 13 May or a total of only 11 days.

Figures 3 and 4 show the observed sex ratios of flocks of longspurs sighted in 1965 and 1967. From the above discussion, it is obvious that in 1965 we saw only the initial waves of migrants because the ratio of males remained constant and averaged about 87 per cent. The lack of a decline can be explained by the fact that we did not remain in one place but watched longspurs going northwest as we also traveled rapidly northwestward with the initial wave. In 1967 (Figure 4) the slight decline explained by the slow initial passage of birds through the Watson Lake area was due to poor weather in the prairies that delayed the prairie population. Again we observed only the initial one-fifth of the migration and the remaining decline in percentage of males must have occurred in the populations that moved through Watson Lake on 18–24 May.

Simon Paneak (in litt.) regards Lapland Longspurs as among the most variable migrants in arrival date at Anaktuvuk Pass (68° 19′ N, 151° 26′ W) that he has noted there over the past 9 years. It is not surprising that these birds vary in their time of arrival on their breeding grounds

TABLE 6

WEIGHT BY VISUAL FAT CLASS OF MALE LAPLAND LONGSPURS CAUGHT AT WATSON LAKE, Y. T. IN 1967

May 5			May 9		
Fat class	n	wt g	Fat class	n	wt g
Light	8	27.52	Light	4	27.85
Moderate	4	29.00	Moderate	21	31.36
Heavy	0	–	Heavy	5	32.20
Average	12	28.00	Average	30	31.03

when we find that their passage through southern Yukon Territory varies so greatly.

From the observation of the gradual disappearance of color marked birds from stably located flocks and from the gradually changing sex ratio in the same flocks, it appears that in a rapidly moving migratory longspur population, each individual pursues his own program of migratory flight, arriving, feeding, fattening, and departing a given area. Other individuals in the same and adjacent flocks are on the same schedule, so that those individuals whose programs are synchronized to migrate on a certain day leave together and migrate as a coherent flock, while others who have left flocks farther south and east enter the flock positions just vacated by the departing individuals. This theory is in accord with evidence obtained on Willow Ptarmigan (Irving et al., 1967) and redpolls (West et al., 1968).

Deposition of body fat.—Birds making long migrations deposit fat before leaving the wintering ground in spring (Helms, 1959; King and Farner, 1959, 1965; Kendeigh et al., 1960; Odum, 1960; Nisbet et al., 1963) and many replenish fat utilized en route as their original deposits cannot sustain their entire travel to the breeding ground in spring or to the wintering grounds in fall (Odum et al., 1961; Johnston, 1966). Further evidence of replenishment is given by Irving's (1960) data showing that males of many species arrive on their arctic breeding ground with fat that is not depleted in males until courtship and territorial activities occur, and females remain fat until egg laying.

We obtained evidence on fat replenishment during migration from a flock of longspurs at Watson Lake in 1967. On 5 May we netted, weighed, checked fat class (light, moderate, heavy), and banded 12 male longspurs in Watson Lake. The same flock remained in the vicinity of Watson Lake until the night of 9 May. At 1800 hours on 9 May we caught 30 male longspurs in the same location at Watson Lake. The weights

and fat classes are given in Table 6. If we assume that there is a relatively constant nonfat component (Odum and Perkinson, 1951), and only a negligible increase in water (Hicks, 1967) the differences in weight among the fat classes represents differences in lipid content. On 5 May 75 per cent of the males had light fat, but by 9 May 87 per cent had moderate to heavy fat deposits. The average increase in weight was 3.03 g in 4 days, or an average gain in fat of 0.76 g per day.

Judging from the fatness of arrivals on the nesting grounds and these figures during migration, longspur flights proceed at a pace consistent with their ability to maintain fatness until they reach the breeding grounds.

ACKNOWLEDGMENTS

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SUMMARY

Lapland Longspurs (*Calcarius lapponicus alascensis*) migrate in large numbers northwestward from their wintering grounds in western United States and southwestern Canada to Alaska in spring to breed on the treeless arctic and alpine tundra. The migrations follow three general routes as determined by dates of first arrivals of males which make up over 90 per cent of the initial component of the migrating population: (1) the coastal route along the Pacific shore of British Columbia and Alaska, some entering the state through mountain passes towards the Yukon River in the eastern part of Alaska, (2) the intermountain route in the mountain trenches of British Columbia and southern Yukon Territory and Alaska, also reaching the southeastern portion of the Yukon River drainage, and (3) the prairie route, from the prairies of Alberta and eastern British Columbia west and north to the Yukon drainage and probably also north to the Mackenzie River Delta.

The sex ratio changes gradually; initial flocks on each route are composed of 90 per cent males, the last flocks seen consist of about 25 per cent males. The total time for the population to pass a given point varies from year to year and the rate of sex ratio change varies accordingly. Consequently it is possible to determine the stage of migration by examining the sex ratio of flocks at any given place and time.

From the gradual disappearance of color marked birds and the changing sex ratio in apparently stably located flocks of constant size, it is proposed that individual longspurs pursue their own program of migration. Each

is impelled by his own changing physiological state in the time sequence of migration. They arrive, feed, and leave an area as they are ready, probably joining in migratory flocks composed of individuals in synchronous condition. Longspurs deposit fat en route; in one example the rate of deposition was 0.76 g of fat per day for 4 days.

The analysis of the migration of longspurs to Alaska has provided us with a new insight into the orderly progress of an organized population during migration and a means to identify the stage of migration from the composition of individual flocks.

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