OBSERVATIONS ON MIGRATION, ECOLOGY, AND POPULATION FLUX OF WINTERING ROSY FINCHES

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The eight recognized taxonomic forms of *Leucosticte* in North America include two northern resident races (*Leucosticte tephrocotis umbrina* and *L. t. griseonucha*), two principally altitudinal migrants (*L. t. dawsoni* and *L. australis*), two altitudinal migrants with minor latitudinal displacement (*L. t. wallowa* and *L. atrata*), and two latitudinal migrants (*L. t. littoralis* and *L. t. tephrocotis*). This spectrum of migratory habits within a single genus holds much interest for students of migration and of the mechanisms controlling long-term physiologic cycles. Comparative investigations of the biology of the races potentially could aid in the identification of environmental factors which control the evolution of such diverse migratory habits and physiologic responses and which regulate their annual repetition. The productivity of this approach has already been illustrated by the results of investigation of the crowned sparrows, *Zonotrichia* spp. (for example, see Blanchard, 1941; Blanchard and Erickson, 1949; Mewaldt and Rose, 1960; Miller, 1960; Farner and Wilson, 1957; King and Farner, 1963).

We therefore initiated a program of field observations and laboratory experimentation on a wintering population of rosy finches near Salt Lake City, Utah. Although we have not been able to continue this study beyond the preliminary, descriptive phases, the data obtained are significant in identifying certain aspects of the biology of rosy finches which particularly merit additional investigation. In this paper we present data on the Black Rosy Finch (*Leucosticte atrata*), Hepburn Rosy Finch (*L. tephrocotis littoralis*), and Gray-crowned Rosy Finch (*L. t. tephrocotis*), which utilize as winter roosts the abandoned buildings and piers at Saltair, a former amusement park on the shore of the Great Salt Lake. We thus augment observations of this same population which were initiated by Behle (1944) and by French (1959*a*, 1959*b*). Our field work included occasional observations in the area in late October and early November of 1959, bi-weekly collections or observations from January to April, and a few additional collections in December of 1960, and in February of 1961.

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POPULATION MOVEMENTS

Autumnal arrival.—Rosy finches arrived at Saltair between October 31 and November 5 in 1959. In other years they have been first detected on November 9 (Behle, 1944), and on October 31 and November 16 (French, 1959*a*). All three races appear to arrive concurrently. Elsewhere in the winter range, *Leucosticte t. tephrocotis* has been detected first in autumn in Saskatchewan "about the beginning of November" (Potter, 1935: 213); in Montana on October 25 (Cameron, 1907), October 29 (Saunders, 1912), and November 6 to 7 (Thorne, 1895); in southern Washington, in successive years on October 28 (2 years), October 29, and November 6, 12, and 15 (Shaw, 1936); and in Wyoming on November 18 (McCreary and Mickey, 1935). The dates for autumnal arrival of *L. t. littoralis* are very similar. In Washington, flocks have been detected in the lowlands first on October 24 (Jewett *et al.*, 1953; see also Shaw, 1935); in Wyoming, the mean arrival date for seven years was November 17, the earliest date being October 25 (McCreary and Mickey, 1935); in Colorado, flocks have been seen in the winter areas first on October 27 (Packard, 1945).

These data suggest that *L. t. tephrocotis* and *L. t. littoralis* arrive in the winter areas with considerable annual regularity within a span of approximately three weeks in late October and early November. The data are too few to support this generalization for *L. atrata*.

Vernal departure.—In 1960, the population of rosy finches at Saltair began diminishing after March 20 and was entirely gone on March 28. Although our sample (17 birds) for this period is small, coupled with our observations it is sufficient to show that there was no large differential timing in the departure of the sexes or races. During three other years in which continuous observation yields reliable dates (Behle, 1944; French, 1959*a*), rosy finches were last seen in this area on March 27, 28, and 29, respectively. Elsewhere within the winter range, *L. t. tephrocotis* has been seen at the latest at "the end of March" in Saskatchewan (Potter, 1935:213); on March 26 in Washington (Shaw, 1936); on March 15, on the average, in Montana (Cameron, 1907); and in Wyoming the average date of departure for seven years was March 23 (McCreary and Mickey, 1935). The few data for *L. t. littoralis* (McCreary and Mickey, 1935; Shaw, 1936; Jewett *et al.*, 1953) fall within the span of those for *L. t. tephrocotis*. We have not found additional records for *L. atrata*.

Vernal departure from the winter roosts, at least in the Salt Lake Valley, thus appears to be timed annually with considerable precision. Within the winter range generally, departure occurs during the last two weeks of March, and principally within the last week.

Daily movements of the flocks and behavior at the roosts.—The departure of rosy finches from their roosts at Saltair occurred very inconspicuously before dawn. We did not detect any preliminary flocking but saw only birds leaving singly or in small groups. On several occasions the departure began before it was light enough to see the birds, and we could detect them only from the call notes overhead. By full daylight, only a few individuals remained; particularly during cold weather the structures at Saltair were entirely vacant during the midday. During more favorable periods in March we could find a few rosy finches at any time of the day.

The afternoon influx of birds began rather abruptly and, particularly during inclement weather, was very conspicuous. We did not keep systematic records of return times, but our field notes indicate a general shift in arrival time from *ca.* 3:30 to 3:40 p.m. in January to 4:00 to 4:20 p.m. in March. The birds returned often in mixed flocks of up to about 50 individuals and could be seen for a considerable distance at an altitude of 100 to 150 meters above the salt flats. Their behavior upon arrival was markedly influenced by the weather. In periods of heavy snow cover, the arriving flocks remained intact and congregated at the baited traps, feeding rapidly. There was much competition for the bait, engendering occasional agonistic challenges. At dusk, the flocks dissipated quickly and the birds went to their roosts. In late January and early February, the roosts were occupied by 5:00 p.m. or shortly thereafter. Observation of the distribution of excreta in the roosts and survey of the location of the birds by spotlighting at night clearly indicates that they roost individually and do not huddle as a mechanism of heat conservation.

The rosy finches display an astonishing tenacity in remaining in their roosts, and can be driven from them only momentarily and by persistent effort. This compulsion to occupy a protected roost has an obvious adaptive significance in increasing the probability that the birds will survive the thermal impact of the cold winter night (see beyond).

In warmer weather when there was no significant snow cover, many of the returning birds went directly to their roosts without joining the aggregation at the traps. In such periods, we deduce that foraging had been easy and that many of the birds, being replete, were not attracted by the bait. The contrast between the voraciousness of the birds at the bait during inclement weather and the apparent indifference of the majority of them during favorable weather emphasizes the compelling drive to obtain maximum energy stores before settling down to roost.

COMPOSITION AND STABILITY OF THE WINTER FLOCKS

The wintering population was sampled during the afternoon influx to the roosts. Standard double Potter traps baited with millet seed were used. In many hours of observation of the flocks at the traps we did not detect any sampling bias with respect to sex or species. We therefore assume that we have sampled the flocks randomly.

Species composition of the winter population.—We did not attempt to census the winter population at Saltair. Estimates based upon observation of the flocks during the afternoon infiltration of the roosts are unreliable. During cold periods with much snow cover the birds congregate in large numbers at the baited traps; during warm periods, the returning birds display little interest in the bait, and most of them go directly to their roosts. At such times they are comparatively inconspicuous. Relatively large changes in the total size of the population thus may escape discovery.

For the detection of differential winter movements by the components of the population, we must rely upon inspection of the proportions of the three taxa in the samples. Because these proportions are related reciprocally, an apparent increase in one component of the population obviously could result from an actual decrease in one or both of the other components. Without a reliable method for assessing changes in the total size of the population there is no rigorous way to make the necessary discrimination. The conclusions which can be supported by the data in table 1 (see also French, 1959*a*)

TABLE 1

COMPOSITION OF WINTER FLOCK OF ROSY FINCHES AT SALTAIR, UTAH

Interval	Number of birds	Percentage of population Black	Hepburn	Gray-crowned	G/H
1960					
Jan. 20–31	98	9	39	52	1.3
Feb. 1–10	41	39	32	29	0.91
Feb. 11–20	68	54	21	25	1.2
Feb. 21–29	56	29	30	41	1.4
Mar. 1–10	32	37	16	47	2.9
Mar. 11–20	55	42	16	42	2.6
Mar. 21–31	12	42	16	42	2.6
Dec. 21–31	100	18	40	42	1.1
1961					
Feb. 1–10	72	14	47	39	0.83

are therefore limited. However, these indicate clearly enough that the proportions of the three taxa in the winter flocks vary among different years and also within a single year. The Black Rosy Finch appears to contribute the largest fraction of this change, varying from *ca.* 9 per cent of the sample (table 1) to *ca.* 82 per cent (French, 1959*a*) in different years. The relative numbers of Gray-crowned and Hepburn rosy finches are most conveniently examined in terms of the ratio of Gray-crowns to Hepburns, hereafter denoted as the G/H ratio. During the winters of 1952–1953 and 1953–1954, Hepburns apparently equalled or outnumbered Gray-crowns ($G/H = 0.3 - 1.0$) in the monthly samples (French, 1959*a*). This situation may have prevailed in 1959–1960 only in the sample from the first ten days of February, but the ratio is not significantly different ($P = 0.7$) from unity. In the other samples (table 1), Gray-crowns consistently outnumbered Hepburns, but the ratios, at the 5 per cent level of confidence, did not differ significantly from unity in any case, nor did they differ significantly from one another. By pooling the data by months, and thus increasing sample size, the G/H ratio becomes significantly greater than unity only in March ($P<0.01$; $G/H=43/16=2.7$), and is significantly greater ($0.05 < P > 0.02$) than the ratios in January (1.34) and February (1.18). We can thus state with reasonable confidence that between February and March there was an influx of Gray-crowned Rosy Finches and/or an efflux of Hepburn Rosy Finches. The data pooled by 10-day intervals suggest that this change occurred in early March.

Including the Black Rosy Finch, the changes in the composition of the samples were statistically significant only between February 1 to 10 and February 11 to 20 ($P<0.01$) and between February 11 to 20 and February 21 to 28 ($P<0.03$). The changes in G/H ratios between these intervals were not significant. We must therefore conclude that if these changes resulted, respectively, from a departure and return of Gray-crowned and Hepburn rosy finches, then these two components must have moved in proportional numbers. We believe that it is more probable that the changes resulted largely from an increase in the numbers of Black Rosy Finches at Saltair in early February followed by a decrease in late February. Although this opinion lacks satisfactory quantitative support, we are led by our field observations and impressions, to agree with French (1959*a*) that the Black Rosy Finch is the most mobile element of the winter population at Saltair, perhaps displacing southward, as French notes, toward its center of distribution in periods of particularly inclement weather. During such periods, as in early January, 1960, Black Rosy Finches could be found only in very small numbers or not at all for several days. It is very improbable that this situation would result simply from dilution of the population by an influx of Gray-crowns and Hepburns. It is reasonable to assume in such a case, if the population of Black Rosy Finches were stable, that numerous individuals could be found, even though comprising a smaller fraction of the population.

Correlations of weather conditions and population changes.—French (1959*a*) has suggested that the composition of the population of rosy finches at Saltair is affected by weather conditions, noting the large proportion of Black Rosy Finches (69 to 82 per cent) during the mild winter of 1952–1953 and the reduced proportion during the "normal" winter of 1953–1954. Our data for the winter of 1959–1960 support this viewpoint. In figure 1, we have displayed some indices of weather conditions concurrently with the changes in the proportions of Black Rosy Finches on the assumption that this group contributes the majority of the variation in the composition of the population. Whether or not this is true, this proportion will serve as an index of weather-influenced changes *per se*. In order to illustrate better the trends in population, we have plotted the data for daily samples rather than pooled samples, as given in table 1.

The initial samples in late January were taken near the end of a period of essentially normal air temperature but unusually prolonged snow cover. The ground was covered by one inch or more of snow for 26 days in January. There were no Black Rosy Finches in the first sample taken in late January, although this species had been observed in the population in November. The proportion of Black Rosy Finches increased steadily with the amelioration of weather conditions in early February. A series of

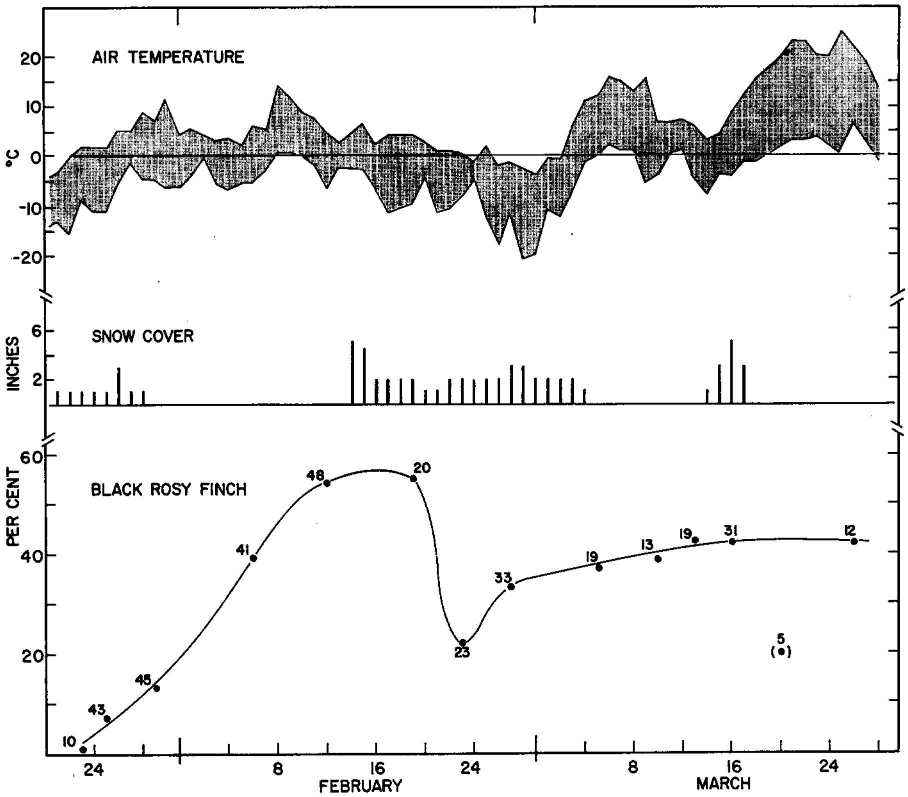

Fig. 1. Daily maximum and minimum air temperatures at Saltair, Utah, depth of snow cover on flat ground, and the proportions of Black Rosy Finches in trapped samples. The size of the total sample (all three taxa) is indicated by numerals at each point.

storms in mid-February then initiated a snow cover which persisted at a depth of one inch or more for 19 consecutive days. The average air temperature also declined steadily in February but remained above the normal average for the month. These conditions appeared to have no effect on the composition of the population for the first six days of snow cover, but between the sixth and tenth days there was a drastic and significant ($P<0.03$) decrease in the proportion of Black Rosy Finches. Although we believe that this resulted from an actual decrease in the number of Black Rosy Finches in the population, we cannot dismiss the possibility that it was caused entirely or in part by an influx of Gray-crowned or Hepburn rosy finches.

The changes in population composition after February 21 were not statistically significant, and the population was comparatively stable throughout March. We assume that the weather-correlated changes which we observed are related in a cause-and-effect manner. We cannot discriminate between the partial effects of change in temperature, snow cover, and perhaps other factors, in inducing these changes. It is noteworthy, however, that rosy finches avert much of the potential thermal stress of their winter environment by persistently utilizing nocturnal roosts which provide overhead cover, and thus heat loss, particularly by radiation to the cold night sky, is greatly reduced (see beyond). The proclivity of rosy finches for roosting in caves, mine shafts, abandoned buildings, and even cliff swallow nests in winter has been well documented (French, 1959*a*).

Sex ratios.—Ratios of males/females, determined by dissection, in the total sample from 1959–1960 were as follows: Black Rosy Finch, 46/14 = 3.3; Hepburn, 24/27 = 0.89; Gray-crowned, 56/18 = 3.1. The ratios were significantly different than unity ($P<0.01$) in the Black and the Gray-crowned rosy finches, but not in the Hepburns. The excess of male Black Rosy Finches at Saltair has been noted previously by French (1959*a*), who found a ratio of 79/14 = 5.6, based on plumage inspection, in 1953–1954. Based on plumage inspection, we found 82/27 = 3.0 (compared with 3.1 by dissection), indicating only a slight tendency to judge equivocal specimens in favor of females. French found that this disparity apparently prevails also on the breeding grounds; he reports ratios of 6 to 8, based on observation of the breeding populations. We have no data on the sex ratios of Hepburn and Gray-crowned rosy finches on the breeding grounds. A surplus of breeding males has been suggested for *Leucosticte tephrocotis dawsoni* (Dawson, 1923; Twining, 1938) and for *L. t. griseonucha* (Hanna, 1922), but the lack of conspicuous sexual dimorphism in these forms makes it necessary to identify sexes on the basis of behavior. The suggestion accordingly awaits confirmation. In the case of the Gray-crowned Rosy Finch, it is plausible that the disparity of sexes at Saltair results from a tendency of the sexes to winter in different areas.

THE NOCTURNAL MICROCLIMATE AND CALORIC EXPENDITURE IN ROOSTING

Continuous thermograms which we obtained from typical but vacant roost sites in February and March of 1961 provide some insight into the thermoregulatory significance of the roosting habits of rosy finches. In February, the mean minimum temperature in roosting sites was 1.7° C., compared with a mean minimum air temperature equal to −2.6° outside. During the coldest night in February, air temperature was −12.2°, but roost temperature was only −1.1°. Roost temperature fell to 0° or less on 10 nights in February, with an absolute minimum of −4.4°. In March, the minimum roost temperature was 0° or less on 5 nights, with a mean minimum of 4.3°, and an absolute minimum of −1.7° on one night. The mean minimum air temperature outside during February was 0.2°.

The nocturnal microclimate of the roosting rosy finch is thus much less stressful than is indicated by outside air temperature and is undoubtedly made still more favorable by the heat production of the bird itself and by protection from wind. Because of this situation, we are inclined to believe that snow cover, which impedes feeding by these ground-foraging birds, is a more significant factor than temperature in limiting the winter distribution of rosy finches and in causing the temporary displacements of population indicated by our data. As Kendeigh (1934) has noted, the survival of birds at the northern limits of their winter range is a function of the duration of the night, when feeding is not possible, the minimum nocturnal temperature, and the magnitude of the energy stores at the beginning of the night. At the end of February, the mean ether-extractable fat per bird was 2.4 gm. for Black Rosy Finches, 2.7 gm. for Hepburns, and 2.1 gm. for Gray-crowns; these amounts are equivalent to *ca.* 23, 26, and 20 kcal/bird, respectively (unpublished data). Although we have no data on the resting energy metabolism of rosy finches, we can obtain a reasonably good estimate of the energy cost of a night of roosting by application of data on nocturnal, resting metabolism obtained from other well-insulated fringillids, such as the Cardinal, *Richmondena cardinalis* (Dawson, 1958) and the Evening Grosbeak, *Hesperiphona vespertina* (Dawson and Tordoff, 1959). Although these species are larger than forms of *Leucosticte,* and therefore have a slightly smaller weight-specific metabolic rate, the difference is insignificant in the present approximation. Resting heat production for one-hour intervals was calculated by reading from the thermograms the mean air temperature of the roost during a typical cold night (minimum roost temperature = – 3.3°); heat production for each hour at prevailing temperature was then computed on the basis of empirical values. By summing such data for each of the maximum of 15 hours (4 p.m. to 7 a.m.) which rosy finches spend in their roosts, we obtained estimates of the total nocturnal energy requirement. These were 8.4 kcal/night (data from *Hesperiphona*) and 8.9 kcal/night (data from *Richmondena*). The maximum reasonable value, based upon unpublished data from the White-crowned Sparrow (*Zonotrichia leucophrys gambelii*) obtained in our laboratory, appears to be *ca.* 10.7 kcal/night. Although equivalent to forms of *Leucosticte* in body weight, *Z. l. gambelii* has comparatively poor insulation.

In any case, it is evident that rosy finches arriving at their roosts in the afternoon carry sufficient energy stores in fat to sustain them through the most unfavorable night and to provide a significant surplus to initiate foraging on the following morning. It is likewise evident that several successive days of snow cover, during which foraging costs more and yields less calorically, can deplete energy reserves to a level which will not permit survival of a long, cold night. We can only speculate that the intricate interplay of decreasing air temperature, poor foraging conditions, and dwindling reserves of body fat "informs" at least some elements of the population that survival requires removal to more favorable surroundings. The consequent reduction of population at a roost, by decreasing the competition for food, may provide the margin of survival for the segment of the population which remains there.

SUMMARY

Black, Gray-crowned, and Hepburn rosy finches (respectively, *Leucosticte atrata, Leucosticte tephrocotis tephrocotis,* and *L. t. littoralis*) overwinter in mixed flocks in central Utah. They arrive at Saltair, near Salt Lake City, within a span of three weeks in late October and early November; they leave during the last two weeks of March. The evidence suggests a relatively precise annual regularity, particularly in spring. We did not detect any differential timing in the movements of the races.

Significant changes in the composition of the wintering population are associated with periods of prolonged snow cover and low ambient temperature. At such times there is an apparent decrease in the proportion of Black Rosy Finches and an apparent increase in Gray-crowns and Hepburns. Our observations suggest that this reflects an actual decrease in Black Rosy Finches. We surmise that deterioration of foraging conditions is a major ultimate cause of the change.

During the day, most birds leave the roost area to forage. At night they roost individually, without huddling, in structures providing overhead shelter. During periods of snow cover and difficult foraging, the birds returning to the roost in late afternoon congregate at baited traps, eating rapidly. When there is no snow cover, the returning birds, evidently replete, often go directly to their roosts. They are very tenacious in occupying the roost at dusk and can be driven out only momentarily by persistent harassment. Thermograms from vacant roost sites show that temperature in the nocturnal microclimate is relatively moderate (−4.4° C.) even when air temperature outside is at a seasonal minimum (−12.2°). Mean minimum temperature in vacant roosts in February was 1.7°. Occupied roosts are warmed by the bird and undoubtedly have higher temperatures. The conspicuous compulsion of the birds to remain in such roosts is evidently a behavioral adaptation which minimizes energy expenditure in nocturnal thermoregulation.

Estimates indicate that rosy finches returning to the roost have stored as fat a mimimum of somewhat more than twice the energy needed to sustain them through a typical cold night. Thus, they have accumulated the energy stores necessary to initiate foraging on the following day.

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