

TERRITORY, BREEDING DENSITY, AND FALL DEPARTURE IN CASSIN'S FINCH

FRED B. SAMSON

WHETHER territory during the breeding season acts as a mechanism to regulate breeding density or total numbers within a population of birds has aroused much interest (Hinde 1956, Wynne-Edwards 1962, Lack 1966, Brown 1969, Klomp 1972, Von Haartman 1972, Watson 1973), but controversy remains. Kluyver (1970), after studying Great Tit (*Parus major*) populations on the Dutch Island of Vlieland in the North Sea, indicated that tit numbers are regulated in early autumn after breeding. In the present investigation, different populations of Cassin's Finch (*Carpodacus cassinii*) were studied during the breeding season and early autumn of 3 years, to determine factors influencing breeding density and population numbers.

I selected Cassin's Finch to study because little is known of its breeding biology or postbreeding behavior. Published descriptions of reproductive activities are few, most often by resident naturalists or those engaged in faunistic surveys (Ridgway 1877, Henshaw 1879, Grinnell 1908, Taylor 1912, Dawson 1923, Bailey 1928, Grinnell and Miller 1944, Jones and Baylor 1969), presumably because accessibility to montane breeding populations is limited. Fall studies are restricted to noting numbers seen or distributional lists (Orr 1968).

The breeding range for Cassin's Finch extends from southern British Columbia, Alberta, and Manitoba into northern Arizona and Baja California (Bailey and Neidrach 1965). These authors suggested that Cassin's Finch, like the crossbill (*Loxia* spp.), breed wherever an abundance of food exists within their range, with specific locations changing from year to year. For breeding, Cassin's Finch prefers a mixed forest habitat of the alpine meadow zone generally above 1500 m (Salt 1952). Most nests are located on ends of upper branches in tall pines (Orr 1968), and pairs may nest in colonies or singly (Lack 1968). After breeding, Cassin's Finch moves to lower elevations, with congregations as large as 5000 reported in December (Chapin 1958).

Two plumages are evident in Cassin's Finch. All females and males until approximately 14 months old have a streaked gray-brown plumage, but they are separable by winglength. Older males are mainly reddish pink and are easily distinguished.

STUDY AREAS AND METHODS

I investigated Cassin's Finch's breeding biology principally near the Beaver Mountain ski area in the Cache National Forest, Cache County, Utah. This study area of

approximately 250 ha involves a northeast-facing slope located in the Bear River Mountains 48 km northeast of Logan, Utah, at an elevation of 2225 m. Lodgepole pine (*Pinus contorta*), quaking aspen (*Populus tremuloides*), subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea Engelmannii*), limber pine (*Pinus flexilis*), and Douglas fir (*Pseudotsuga menziesii*) form a discontinuous forest canopy. Meadows interspersed among timbered areas are covered with sagebrush (*Artemisia tridentata*), grasses (*Bromus* spp., *Festuca* spp., *Agropyron* sp.), sedges (*Carex* spp.), and other annual and perennial herbs. I also used a second tract of approximately 20 ha, 4.6 km southeast of Beaver Mountain, referred to as site 143. This tract is similar in altitude and vegetation to the Beaver Mountain site but is separated on all sides from surrounding forested areas by open shrubland. Snow commonly remains on the ground at both sites until late May with open bare patches of ground evident in mid- to late April. Snowstorms occur into June (17 June 1973 and 6 June 1974).

Finches were collected in the spring months of 1972 and 1973 at three other locations with similar vegetation and elevation: (1) Amazon Hollow, 2.5 km southeast of Beaver Mountain; (2) Limber Pine, 8.6 km east; and (3) Summer Camp, 8.8 km southwest.

The studies of finch breeding and fall departure were conducted from June to October 1971, February to October in 1972 and 1973, and April through June 1974. I visited the principal study area, Beaver Mountain, at least 4 days a week from July through August 1971, February through July in 1972 and 1973, and weekly in 1974. Other study areas were visited less frequently and only for specific purposes, such as collecting males.

To investigate total population size and sex and age ratios, finches were captured systematically and banded with USFWS numbered aluminum bands. Nearly 50% of these I marked with unique combinations of plastic colored leg bands permitting individual recognition without recapture. I used mist nets at Beaver Mountain at a site within the study area, setting the nets once a week for 3 h, usually 0700-1000, during July 1971, from early May through July 1972, and from late May through early August 1973. Banding started in the spring when finches began to appear regularly on the banding site and stopped in late summer when no finches were being taken. During the winter months, the banding site served as a parking lot for a ski area, and salt was used to remove snow. The species' salt-eating habit (Henshaw 1879, Kelley 1921, Bailey 1928) attracted birds to the site after late May.

Winglengths of birds netted at Beaver Mountain and site 143 were measured to the nearest 0.1 mm with a vernier caliper. Plumage color was described for all birds captured, and presence or absence of an incubation patch was noted. I collected 44 finches in 1972 and 20 more in 1973 by shooting throughout April, May, and June to compare testicular development in adult and yearling males and to determine if females were part of spring flocks. In 1972 all collecting was at the Summer Camp site, and finches were shot as encountered. Finches in 1973 were shot as seen at the Limber Pine and Amazon Hollow sites. I used no systematic approach either year, but rather tried to make the collecting as random as possible.

Events of the breeding cycle of Cassin's Finch (i.e. song, courtship activities, territory, and nesting) were recorded by studying and describing individual or flock behavior, movements, and activities with observations of color-marked birds emphasized. Field notes of location of events were transcribed later to maps of the study area for analysis; further details on methods will be presented in later sections. Common and scientific nomenclature for birds follows the A.O.U. check-list (1957) as amended by the Thirty-second supplement (A.O.U. 1973); for mammals, Blair

TABLE 1
NUMBERS OF CASSIN'S FINCH Banded AND RECAPTURED AT BEAVER MOUNTAIN
AND SITE 143, UTAH¹

	May		June		July		August	
	Number banded	Number recaptured	Number banded	Number recaptured	Number banded	Number recaptured	Number banded	Number recaptured
1971					38	1	33	2
1972	151	4	194	7	106	3		
1973	19		25	7	56	4	12	

¹All data from Beaver Mountain except for 57 birds banded and 3 recaptured at site 143 in 1971.

et al. (1957); and for plants, Holmgren (1965). Data were analyzed by a Burrows 6700 computer utilizing statistical programs of Hurst (1972). Tolerance limits and Chi-square tests were calculated following Dixon and Massey (1969).

BREEDING POPULATIONS, TERRITORY, AND BREEDING DENSITY

This paper considers four major aspects of Cassin's Finch breeding: (1) What were total numbers and sex and age ratios of finches present each summer? (2) Do all adult and yearling males breed or do differences in their testicular development or dominance-subordination relationships exist that limit their breeding? (3) Is delayed or restricted participation in breeding by females evident? (4) What effect does territory have upon breeding density?

1. *Population size and sex and age ratios.*—Population levels of finches varied from summer to summer. In 1971 at site 143 and Beaver Mountain, 71 finches were banded during 54 net h (6 days, 3 h/day, 3 nets) for a mean of 1.31 birds per net h. At Beaver Mountain in 1972, 451 finches were banded during 117 net h (13 days, 3 h/day, 3 nets) for a mean of 3.85 birds per net h; and in 1973, 112 finches in 90 net h (10 day, 3 h/day, 3 nets) for a mean of 1.24 birds per net h. Table 1 gives numbers banded and numbers recaptured.

Once caught, finches were wary of mist nets, and recaptures were few in any summer although banded finches continued to use the banding site. To estimate the percent of populations banded, proportions of banded to unbanded birds using the site over a 1-h period were recorded once weekly during the banding season in each of the three summers. Counts were made with 9 × 35 binoculars or a 20-power spotting scope usually at distances within 35 m. From these observations, mean monthly proportions of banded to unbanded birds were calculated (Table 2).

Estimates of total finch populations during each summer of study at Beaver Mountain were obtained with a modified Lincoln index (Lincoln

TABLE 2

MEAN MONTHLY PROPORTIONS¹ ON THE BANDING SITE AT BEAVER MOUNTAIN, UTAH

	May	June	July
1971			15.1%
1972	19.1%	22.3%	19.4%
1973	12.1%	24.9%	23.4%

¹ Expressed as percent of banded to unbanded birds.

1930), by dividing the mean proportion of marked birds visiting the banding site during a particular month into total banded prior to and during that month. If numbers of finches visiting the site during July 1971 and June 1972 and 1973 are estimated (95% confidence limits), the population in 1972, estimated at 1548 ($N_L = 27$, $N_U = 285$), exceeded that of 1973, estimated at 177 ($N_L = 3$, $N_U = 33$), and both are larger than the population in 1971, estimated at 93 ($N_L = 2$, $N_U = 17$). Confidence limits on N were estimated following Chapman (1948). These estimates and the number of birds caught per net hour suggest substantial changes in finch numbers from summer to summer. Farner (1952) also reported marked fluctuations of summer Cassin's Finch populations during eight summers from 1941 to 1952 at Crater Lake, Oregon.

Two assumptions of the Lincoln index are that the population sampled is well defined and that the average probability of observing a marked individual is equal to that of an unmarked individual. No exchange of banded birds was evident during the three springs and summers of study between Beaver Mountain and site 143 and their surrounding terrain. This suggests that finch populations, including breeders and nonbreeders, may limit themselves during breeding and postbreeding periods to certain topographical regions and, therefore, are defined populations; but conclusive evidence is lacking as interchange of finch flocks between Beaver Mountain and adjacent mountain terrain other than site 143, though possible, was not observed. The only change in behavior of banded birds noted was in the segment of the banding site used, always away from nets; and no change was evident until July when site use decreased. Thus prior to July the average probability of observing a marked bird is judged equal to that of an unmarked one.

During the breeding season female finches have an incubation patch. The winglengths of captured gray-brown birds with an incubation patch can be separated from those of other captured gray-brown birds (data pooled 1971, 1972, 1973; $P < 0.001$). Thus, on the breeding ground, females differ from yearling males by both winglength (see below) and possession of an incubation patch.

TABLE 3
SEX RATIOS FOR CASSIN'S FINCH AT BEAVER MOUNTAIN AND SITE 143, UTAH

	Adult males	Yearling males	Females	Male to female ratio ¹
1971				
May				
June				
July	25	7	6	
August	24	7	2	
Total	49	14	8	63:8
1972 ²				
May	76	51	24	
June	63	85	46	
July	43	36	26	
August				
Total	182	172	96	354:96
1973 ³				
May	12	4	3	
June	19	6		
July	38	14		
August	6	4	2	
Total	75	28	5	103:5
TOTALS	306	214	109	520:109

¹ All proportions vary significantly from expected 1:1 ($P < 0.001$).

² One brown bird escaped before its wing was measured and is excluded from the data.

³ Four brown birds escaped before their wings were measured and are excluded from the data.

During June and July in the San Bernadino Mountains in California Grinnell (1908: 89) reported an imbalance in Cassin's Finch sex ratios stating that "there seems to be a large excess of males." In all three summers of this study, the ratio of near 5:1 (Table 3) in favor of yearling and older males to females varies significantly ($P < 0.001$) from the expected 1:1 ratio. This may not reflect the actual ratio, as most banding occurred during the breeding season when the males feed the incubating females or females with young nestlings at or near their nests. Females are inactive in comparison to the foraging males and may be under-represented in May and June banding samples.

Of 57 pairs seen building nests in 3 years of study, 54 (94.6%) involved older males. Data indicate that all older males (see section 2) and females of all ages (see section 3) attempt to breed and, therefore, are presumed equally represented in breeding populations. By constructing a population wherein number of females of all ages equals number of older males captured ($n = 306$) and yearling males are represented by number caught ($n = 214$), females would then represent an estimated 37%, older males 37%, and yearling males 26%. These estimates are

significantly different ($P < 0.01$) from an expected sex ratio of 1:1. If sex ratios are adjusted using banding data for each summer to reflect the assumption that female numbers equal those of older males, a significant disparity in sex ratio would have existed in 1972 ($P < 0.001$) and 1973 ($P < 0.05$) but not in 1971. In 1971 banding was not started until 6 July, which may have influenced banding samples; and, more importantly, no data were obtained to determine if all adult males obtained mates.

My studies show that males attain adult plumage when approximately 14 months old. Over the 3 years, yearling males represented 41.1% of all males banded. In 1971 yearlings comprised 22.2% of the males; in 1972, 48.6%; and, in 1973, 27.2%.

2. *Breeding of males.*—The study of male Cassin's Finch breeding involves the relationship, both physiological and behavioral, between adult and first-year males and the extent of breeding or nonbreeding by these two groups.

To determine if yearling males were handicapped physiologically for breeding, first-year and adult male finches were collected during early spring 1972 and 1973 to compare testicular development. In the spring of 1972, 21 adult and 21 yearling males were collected at Summer Camp; and in the spring of 1973, 6 adult and 6 yearling males were collected at Limber Pine and 6 adult and 2 yearling males at Amazon Hollow. Testes were immediately removed, measured for length and width with a vernier caliper to the nearest 0.1 mm, and placed in individual vials of Bouin's solution. Left testis volumes were calculated using the formula for an ellipse, $V = 4/3 a.b^2$.

The rate (slope) of increase for testicular development in first-year males was less than that of adult males both years (Fig. 1). In both years, testis volume of adult males exceeded that of yearling males. These differences in testis volume suggest some advantage for adult males through earlier production by the testes of steroid hormones that influence reproductive behavior, particularly for pair formation; but testicular development of yearling males, although slightly delayed particularly in 1973, was adequate to allow them to breed.

To determine if adult males were competitively limiting yearling males from breeding, three adult males, each a member of a nesting pair, were shot in June 1973 (2 on 13 June and 1 on 17 June) at Amazon Hollow. All three nests were fully constructed, but it could not be determined if clutches were complete. Finches were present in Amazon Hollow during each spring of study but no estimates of population composition or size were possible. Two of the three adult males removed were replaced within a 3-day period by yearling males and both nests were successful in raising young. The third nest was abandoned for reasons unknown.

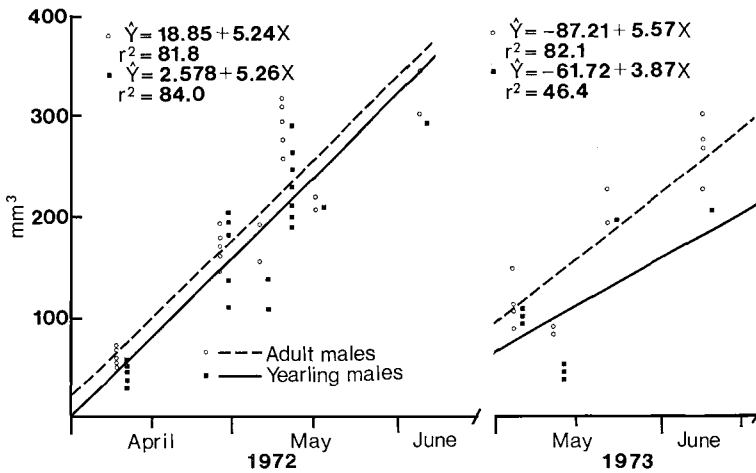


Fig. 1. Testis volumes of adult and yearling male Cassin's Finches.

In addition, two adult males with known histories, both paired and with nests completed, disappeared at Beaver Mountain in 1973. One adult, marked with a distinct leg-band combination, disappeared 1 June and was replaced by an unmarked first-year male within 3 days. The second adult male, unmarked but paired to a distinctively marked female, was not observed on 9 June and was replaced by an unmarked brown male, also within 3 days. No surplus adult males were seen on or near this study area after their disappearance, suggesting that both died. Such replacement patterns of adult males lost or removed from breeding populations suggest they do limit the participation of yearling males in competitive breeding. If not excluded, first-year males are both behaviorally and physiologically capable of breeding. The mechanisms of replacement are not clear.

In 18 of 20 pairs watched building nests at Beaver Mountain in 1972 the male was adult. No adult males appeared unpaired beyond mid-May. In 1973 at Beaver Mountain, all nine pairs that built nests initially involved an adult male, and no single adult males were seen by late May. At site 143 in 1973, 13 of 14 pairs starting nests were composed of an adult male and a female, and all adult males appeared paired by early June. At all 14 nests initiated at both sites in 1974 the male of each pair was an adult.

Several other observations substantiate that all adult males paired. At the onset of nest construction, mated males stop singing and do not use song to defend their territory. Weekly playback of adult male song

in the springs of 1972 and 1973 failed to elicit any response from territorial males. Male song is important in many avian species to attract unpaired females (Nottebohm 1972) and probably serves this function in Cassin's Finch populations. In 1972 the last nest was started 1 June, and no adult males were heard singing at Beaver Mountain after that date. Adult males at Beaver Mountain in 1973 stopped singing 16 June, and construction of the last nest began 18 June. At site 143 in 1973, no adult males sang after 12 June, and the last nest located was started 10 June. If any adult male remained unpaired, it is reasonable to assume that song would have continued. This was not observed; but numerous single, first-year males continued to sing near the colony at Beaver Mountain until 9 June 1972 and 11 August 1973, and at site 143 until 17 August 1973, suggesting that at both sites in these years yearling males remained unpaired.

These nonbreeding yearling males when not singing formed flocks of 7 to 50 birds and were seen regularly on or near the study area. Flock size varied with males leaving the flock to sing or forage at a particular location. No instances of any defense of a segment of habitat or of another brown bird were evident. These flocks traversed the breeding habitat without any interference unless they violated a male's territory. Estimation of total numbers forming these flocks was not possible even though they contained color-marked birds both in 1972 and 1973. As data suggest that all females and all adult males breed, these flocks were apparently composed entirely of yearling males. Estimates from banding data discussed above indicate that yearling males represent approximately 26% of the total finch population.

3. *Breeding of females.*—An important consideration is whether all females breed. Data from three sources, (1) the possession of incubation patches by a group of gray-brown birds exhibiting a discrete range of winglengths, (2) similar winglengths of age classes of males and females, and (3) composition of nonbreeding finch flocks, support the contention that all females breed.

Winglengths of all brown birds with incubation patches are significantly shorter ($P < 0.001$) than of those lacking incubation patches. This separation of all brown birds captured into two distinct groups indicates nearly all females breed. Second, at 95% confidence, 95% of the winglengths of first-year males are within a 3.8 mm span (91.9 ± 1.9 mm). For adult males, the 95% tolerance limits with confidence at 95% equals 93.4 ± 1.6 mm, for a tolerance interval of 3.2 mm. Thus for the two age classes, yearling males and adult males, winglength intervals extended from 90.0 to 95.0 mm or 5.0 mm. The 95% tolerance intervals at 95% confidence for females are 88.3 ± 2.3 mm or 4.6 mm. This similarity

in distribution of winglengths, 4.6 and 5.0 mm, between two age classes of males and all females suggests that two age classes, yearling females and adult females, were captured. As they possessed incubation patches, both yearling and adult females are presumed to have bred; and neither delayed maturation nor lack of participation in breeding by either age class of females was evident.

Third, if some females were not breeding, they should have been part of nonbreeding flocks. On 2 July 1973 I collected four birds at random from a nonbreeding flock of nine gray-brown finches and four more from a similar flock on 6 July. All birds were collected at site 143 and all were yearling males. This would be expected if females of all ages were on nests or were with their mate caring for young. The probability of collecting eight consecutive males is less than 1 in 10^5 when considering only gray-brown birds, of which yearling males are estimated to represent 27.2%. These data support the premise that all females breed.

4. *Territory*.—Conder (1949) described a "mated-female distance" for several avian species within which the male defends the female. The location, at least prior to nesting, is dependent upon the location of the female, which does change. Definitions of territory that include a moving datum rather than a localized topographical area are, as pointed out by Hinde (1956: 342), usually excluded in the common usage of "territory." Territory according to Tinbergen (1957) is the result of two distinct tendencies, site attachment and hostility. He asserted that, "Either can occur without the other."

For Cassin's Finch, territory is a mate-defended area with the male excluding other finch males from the vicinity of his mate by means of chases or threat postures, the defended area being defined by female location. The female does centralize her activity at the nest site, but this "attachment" does not appear to become an integral part of the male territorial behavior. A male will readily leave the nest site at any time during the nesting season if the female does. In addition, if the female disappears or is experimentally removed as two were on 18 June 1974, the male will not continue to defend the nest site actively nor attempt to attract a new female to the site. Rather, he abandons the nest site and presumably seeks an unmated female elsewhere.

Male territorial behavior involving defense of mate was not seen prior to nest site selection in any spring even though finch arrival preceded nesting by nearly 3 months in 1972 and 3-4 weeks in 1973 and 1974. Presumed pairs involving an adult male and a brown bird were noted in these early spring flocks each year. On 9 April 1972, two of these pairs were collected at Summer Camp. In both instances, the brown birds were females, providing evidence that at least for adult

males pair formation may occur either prior to or immediately after arrival on the breeding ground and while finches are still in flocks. As yearling males also were collected in early spring of 1972 and 1973, flocks arriving on the breeding ground were composed of females, yearling males, and older males.

Males began defense of mate when the female first sought a nest site. To measure the defended area, female location and the point of male defense were projected from the forest canopy to ground level, and intra-pair intervals were measured. In each breeding season, males extended their defended area from a mean radius of 4.1 m ($n = 31$, $SD = \pm 0.91$ m) during nest site selection to a mean of 15.6 m ($n = 35$, $SD = \pm 1.66$ m) during late stages of nest construction, which in many species of birds coincides with the peak in copulatory activity. Differences in length of defended radii were not evident between years, but the intensity of defense did vary. After nest construction the defended area around the female decreased, and defense ceased when incubation began.

Territorial behavior was particularly evident in the spring of 1972 at Beaver Mountain when the population level was high. That spring paired males invariably accompanied and defended their females against other males while the females foraged, selected the nest site, gathered nesting materials, and built the nests. In 1973 when the population of finches was substantially lower than in 1972, males always accompanied and defended females while foraging and during nest construction. In several instances while the female gathered nest material, males left the nest site with the female, perched in a tree near her and far closer to her than to the nest site, but did not join her on the ground as they did in 1972. This change in behavior pattern from 1972 to 1973 apparently was due to the presence of fewer bachelor males on or near the colony, which reduced the pressure on mate defense.

Whether spring territorial behavior limits density of breeding passerine birds has been tested experimentally by the removal of territory holders by Orians (1961) and Krebs (1971). In both studies, most replacement birds were first-year individuals. In this study two of three adult males collected at Amazon Hollow were replaced by yearling males. Neither replacement male exhibited any defense of mate. The lack of defense of mate by replacement males would be expected if clutches were complete, but this was not known. Yearling males also replaced two adult males that disappeared from the colony in 1973, each member of a pair in which at least one member was marked. The replacement yearling male of nest 3 did defend the female while she completed her clutch, and I saw this pair copulating. I noted no defense of mate by the other replacement male. Both replacement males did feed their females dur-

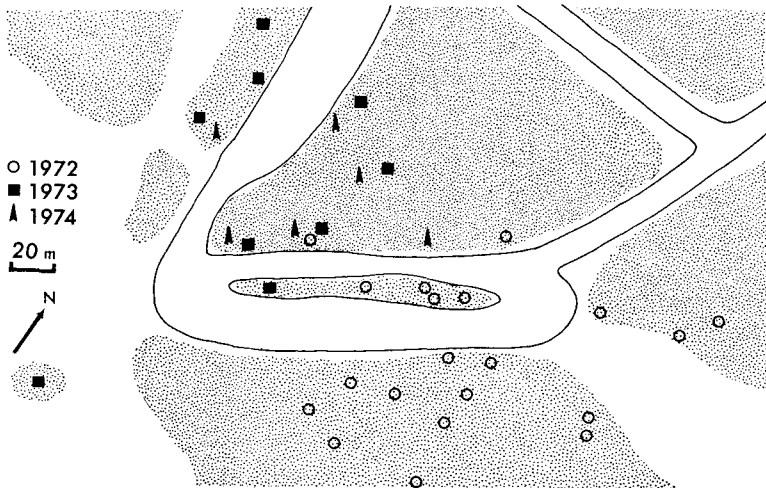


Fig. 2. Cassin's Finch nest locations at Beaver Mountain, Utah. Stippled area includes pine-aspen canopy.

ing incubation and the subsequent nestlings. This loss of two adult males and their replacement by two yearling males did not appear to influence the territorial behavior of other males. As one of the widowed females was marked, replacement was not by a pair. Along with the existence of bachelor flocks, these data suggest that some males capable of breeding were prevented from doing so.

As Brown (1969) pointed out, if total reproduction is to be limited by territorial behavior, some females must be prevented from breeding. Data already presented indicate that all females did attempt to breed and they were not replaced when lost or experimentally removed at nests as males were, suggesting that the mated-female form of behavior did not limit total reproductive effort in these finch populations. In 1972, 1973, and 1974, finches at Beaver Mountain nested in colonies using restricted areas of quaking aspen, lodgepole pine, and subalpine fir (Fig. 2). In each year, vacant habitat similar to that used for nesting extended on three sides of the colony for distances greater than 200 m. At site 143, finch colonies were in the same general 8-ha area of mixed aspen and conifer during 1972, 1973, and 1974 breeding seasons with extensive vacant but similar habitat adjacent to or close to breeding sites. Attempts to separate nesting habitat from vacant similar surrounding habitat by tree species present, foliage volume, or height were not successful. Habitat did not limit colony size or restrict colony location. The availability of suitable habitat is evident in that the site used

TABLE 4
INTERNEST AND NEST-TO-COLONY CENTROID DISTANCES¹

Year	Beaver Mountain		Site 143	
	Interne- st distances	Nest-to-colony centroid distances	Interne- st distances	Nest-to-colony centroid distances
1972	n = 20 22.2 ± 11.1 m	53.0 ± 33.9 m		
1973	n = 9 36.1 ± 32.5	47.3 ± 31.2	n = 14 34.4 ± 29.1 m	49.9 ± 44.4 m
1974	n = 6 37.0 ± 20.7	29.6 ± 22.8	n = 8 39.6 ± 22.8	40.3 ± 31.0

¹ ($\bar{x} \pm 1$ SD).

for colonial nesting at Beaver Mountain in 1973 and 1974 was available but not used in 1972, and the site used in 1972 was available to 1973 and 1974 nesters but not used.

Mean interne-
st distances and mean distances to colony centroid for all nests initiated were compared for the five colonies studied intensively (Table 4). No significant differences are evident among the mean interne-
st distances or nest distances to colony centroid, suggesting a rather uniform nest dispersion pattern within finch colonies. Interne-
st distances were larger in 1973 and 1974 when the colony size was smaller.

Nests were difficult to watch because they were usually on either the terminal end of upper branches of tall lodgepole pines or subalpine fir or against the tree trunks within 1 m of the top. Close observation of the few accessible nests was inadvisable because young finches left the nest before they were fully feathered if disturbed, causing needless mortality. Nest success was measured by whether or not pairs remained actively feeding young at the nest until the day the young left. At Beaver Mountain in 1972, 10 of 20 (50%) nests were successful; in 1973, 7 of 9 (77.8%); and at site 143 in 1973, 9 of 14 (64.3%). No particular pattern of nest loss was evident other than early nests were less successful (Table 5). Height of nests was not an influence.

Two of three nests initiated by pairs involving a yearling male were successful. These pairs all nested near the colony centroid. The male of the second pair to start nest construction at Beaver Mountain and site 143 and of the eighth pair found building a nest at Beaver Mountain in 1972 were yearlings.

Most nest construction at Beaver Mountain and site 143 was spaced sufficiently, either temporally or spatially, to preclude intense aggressive behavior. For those pairs attempting to build nests simultaneously within a limited segment of habitat, territorial behavior did temporally

TABLE 5
SUMMARY OF NESTING¹

	Beaver Mountain		Site 143
	1972	1973	1973
Number of nests	20	9	14
Height above ground			
< 15 m	5 (2) ²	2 (2)	1 (1)
> 15 m	12 (6)	7 (5)	11 (7)
> 25 m	3 (2)		2 (1)
Number successful	10	7	9
Number early nests lost ³	5	2	4
Number peripheral nests lost ⁴	5	1	3

¹ 1974 nesting data excluded as five nests were experimentally removed.

² Number successful.

³ Nests initiated before median date of nest construction. Beaver Mountain, 1972 = 26 May; 1973 = 9 June; site 143, 1973 = 8 June.

⁴ Outside mean distance to colony centroid.

space nesters within a segment of habitat. After completion of the clutch when defense of female ceased, males assumed a "sentinel" position (Mundinger 1971) at some distance from the nest. Another pair could then nest well within the original defended area of the first male. The male of the second pair tolerated the male of the first pair, traversing his defended area only when the first male was flying to his own nest to feed his mate and if he exhibited no overt aggressive behavior. The second male never interfered with the female of the first pair. An example occurred on 28 May 1972 when two females, both mated to adult males, had selected nesting sites 1 m apart. Vigorous chases and combat occurred over a 4-h period before one pair withdrew; 10 days later a pair also with an adult male nested 10.2 m away from the victor of the 28 May contest and was neither challenged nor interfered with.

Another example occurred at site 143 in 1972 after the mate of an adult male began building a nest near the top of a lodgepole pine on 25 May. On the same day the female of a yearling pair selected a nest site in the same tree but on a lower branch less than 2 m away. The adult male vigorously chased one brown bird assumed to be the male for over an hour before both brown birds left the site. By 16 June two more nests had been built by pairs with adult males, each well within the original defended area of the first male. The temporal spacing of nests allowed for increased density of breeding pairs within a segment of breeding habitat, but did not limit the total breeding pairs in a colony.

FALL DEPARTURE

After the breeding season in all three summers, one or more family groups of adults with young formed loose flocks of from 7 to 12 mem-

bers. These flocks dispersed from colony sites to forage. They were hard to follow and watch except when they returned to the banding site for salt. Observations of color-marked birds on the site and a few recaptures indicate that these flocks remained in the general vicinity of Beaver Mountain or site 143 throughout the summer and early fall.

What was evident in all three summers was an earlier departure from the study area by flocks of adult males, their mates, and young than by yearling male flocks. In 1971 adult males were last seen on 17 September whereas the flocks of yearling males remained until 2 October. In 1972, adult males were last noted on 16 September while yearling male flocks remained until 29 September. To verify if all members of non-adult flocks were males, 17 birds were collected at random at site 143 on 16 September. All were males molting into adult reddish plumage. In 1973 adult males, their mates, and young left the study area 22 September and yearling males departed 30 September. On 11 September I collected 6 males at random at site 143 from the remaining flocks. Utilizing the estimated sex ratios, the probability of collecting 17 consecutive males in 1972 would be less than 1 in 10^5 and less than 1 out of 1000 for the 6 males collected in 1973, again supporting the interpretation of essentially all male composition for these flocks.

DISCUSSION AND CONCLUSIONS

Findings of this study that warrant discussion are (1) the disparity in sex ratio observed in Cassin's Finch populations and its effect on (a) reproductive effort, (b) mated-female distance, and (c) timing of fall departure; and (2) the fluctuation of finch numbers from one breeding season to the next.

1. *Disparity in sex ratios.*—In the three summers of study, both the sex ratios observed from banding data and those estimated favored males. For 15,183 finches banded from 1955 to 1973 (data from Bird Banding Laboratory, USFWS), 39% were reported as males, nearly exclusively adult males, 31.3% as females, and 29.7% as unknown. Some banders (Sheppard pers. comm.) failed to recognize male dimorphism and reported all gray-brown birds as females. These data must then be viewed with considerable caution, but they do suggest similar percentages for adult males and females in other populations of Cassin's Finch to those estimated in this study.

Disparities in tertiary sex ratio favoring males in many species of birds are not uncommon (Lack 1966), but few data have been published for primary or secondary sex ratios in passerines. Morton et al. (1972) found more males than females being hatched in nests of White-crowned Sparrows (*Zonotrichia leucophrys oriantha*) during 3 years of study,

this imbalance lasting through adult life. Disparity in sex ratios favoring males in limited samples of juvenal Black Rosy Finches (*Leucosticte atrata*) shot by French (1959) suggests more males may have been produced in the nest, and their recruitment may have influenced the imbalance favoring males noted in adult sex ratios.

Data on secondary sex ratios obtained in this study are limited. Two nests at Beaver Mountain and 3 at site 143 were removed in spring 1974. No data were obtained for Beaver Mountain because nest contents were lost during removal. Three nests were accessible at site 143. Of the 13 nestlings and 1 egg removed, 8 were male, 5 were female, and 1 was unidentified. This sex ratio is not significantly different from the expected 1:1 ratio but does suggest that further investigation into secondary sex ratio in Cassin's Finch is needed.

Estimates of annual mortality and recruitment that may have influenced observed tertiary sex ratios are difficult to obtain for Cassin's Finch as populations appear nomadic to breeding grounds. Of 14 finches banded in 1971 at Beaver Mountain, 6 (42.9%) were recaptured or seen there in 1972. All 6 were males and 5 of the 6 were in adult plumage when banded. Of 57 finches banded at site 143 in 1971, 7 (12.2%) were recorded there again in 1972, and all were adult males when banded. In 1973, 6 adult males of 451 birds (1.3%) banded in 1972 were recaptured at Beaver Mountain. No birds banded in 1971 were noted in 1973. These data are insufficient to calculate annual mortality but suggest that year to year site attachment is strongest in adult males.

1a. Reproductive effort.—In some studies, Ribaut (1964) on European Blackbirds (*Turdus merula*), Delius (1965) on Skylarks (*Alauda arvensis*), and Carrick (1963) on Australian Magpies (*Gymnorhina tibicen*), females were prevented from breeding by territorial behavior; but this was not found in Cassin's Finch. The mated-female distance did not reduce reproductive effort by forcing pairs into marginal habitat, as indicated for many species (see reviews by Brown 1969, Klomp 1972, and Watson 1973). The colonies studied were very similar to the generalized colonial pattern provided by Newton (1972) for the subfamily Carduelinae and for members of the subfamily including *Carduelis cannabina* by Tast (1970) and *Carduelis flammea* by Peiponen (1962) and Hilden (1969). Tast reported asynchrony in nesting within colonies and fluctuations in numbers of summer populations, both findings similar to what this study reports for Cassin's Finch.

Both banding data from all 3 years and the sexes of nonbreeding birds shot at random during the breeding and postbreeding seasons indicate that surplus flocks were composed entirely of males. All females at-

tempted to breed, as shown by the discrete distribution of winglengths of individuals that had incubation patches that included first-year and adult females. Unpaired yearling males, physiologically and behaviorally capable of breeding, expressed their readiness to breed beyond the nesting season, but their participation was limited by a shortage of females. Females also were not replaced at nests as males were. Polygyny was not observed and is not a characteristic of the subfamily Carduelinae (Lack 1968, Newton 1972). Number of females is considered limiting for reproductive effort in this study.

1b. Mated-female distance.—With females and not habitat the limiting factor, it would be advantageous for a male to defend its mate and not a fixed segment of nesting habitat. A mobile defense of female similar to that seen in this study was described by Twining (1938) and French (1959) for the Black Rosy Finch, Johnson (1960) for the Gray-crowned Rosy Finch (*Leucosticte tephrocotis*), Thompson (1960) for the House Finch (*Carpodacus mexicanus*), Marler and Mundiger (pers. comm.) for the Twite (*Carduelis flavirostris*), and is generally characteristic of Cardueline finches (Newton 1972). Some nest defense when it contained young was suggested in the studies of Johnson and Thompson but was not noted in this study. Males were estimated to outnumber females by 5:1 or 6:1 by French and 4:1 by Johnson, ratios that exceed those estimated in this study. Both authors considered number of females limiting for breeding population size similar to the results of this study.

Lacking site attachment, certain functions of territory (i.e. knowledge of terrain to avoid predation, to ensure an adequate supply of food for young, or to facilitate pair formation) appear unimportant. Without an intimate familiarity to reduce predation within a territory via site attachment, Cassin's Finch has reduced both visual and auditory cues for predators through cryptic coloration of females and nests, lack of conspicuous displays near the nest, and cessation of song at onset of nesting. Female exposure to predation may also be reduced when females are fed at the nest during incubation and when with very young nestlings. These patterns do suggest that predation is important in female mortality.

Possible predators at Beaver Mountain include the Goshawk (*Accipiter gentilis*), Cooper's Hawk (*A. cooperii*), Sharp-shinned Hawk (*A. striatus*), American Kestrel (*Falco sparverius*), Pygmy Owl (*Glaucidium gnoma*), and red squirrel (*Tamiasciurus hudsonicus*), but no predation on free-flying or nesting finches was actually seen. A Sharp-shinned Hawk did select an adult male from several adult males and brown birds caught in a mist net 8 June 1972, but this was the only instance of predation on a Cassin's Finch noted during the breeding seasons.

During nest construction and when the female was completing her clutch, finch pairs invariably fed away from the nest and colony site. Distances of feeding sites from the colony varied from 30 to 300 m, but were generally at some distance from the colony. When feeding females or young, males always foraged at some distance, usually more than 100 m, from the colony site. Females feeding young were seen foraging near the nest on several occasions, but generally joined their mates and fed away from the colony. The radius of defended area did not vary from year to year even though both total numbers and colony size varied. Based on the preceding, and because of the limited interval of preincubation expression, the mated-female distance does not function to ensure an adequate food supply for young.

In many passerine species, males arrive before females and establish territories. This did not occur in Cassin's Finch nor was any defense of site by a single male noted. Certain reproductive activities of Cassin's Finch, including courtship behavior and copulation, are limited only by the female's location and male and female interest. Courtship feeding and copulation were both seen at considerable distances, often exceeding 100 m, from nests and colony site. Pair formation is not a function of or facilitated by the mated-female distance.

Three functions of the mated-female distance appear important: (1) The male gains an advantage in ensuring the passage of his genes to future generations by defending his mate wherever her location may be when she is most receptive to fertilization. (2) The protection provided the female allows her to feed without interference from other males when energy must be mobilized to build a nest and, more importantly, to complete production of eggs. (3) The female is provided continuous protection from predation by both the watchfulness of the accompanying male and, if paired with an adult male, a potentially more visible target for predators to select. The finch breeding population would benefit with each of these functions. Adult males having survived at least 20 months provide a genetic contribution reflecting a capability for resource location and exploitation, predator avoidance, and possible prior breeding experience that yearling males may lack. For a breeding population with number of females limiting the reproductive effort, female survival is important, and the mated-female distance provides for this.

1c. Timing of fall departure.—The importance of numbers of females may also be reflected in the timing of departure from the study area. Each fall adult males, females, and young left the study areas prior to yearling males. Magee (1924) reported a similar differential fall departure for another North American member of the genus *Carpodacus*,

the Purple Finch (*C. purpureus*), when after a particular date in early fall, no adult males were captured but yearling finches continued to be caught. Peiponen (1974) reports that Scarlet Rosefinches (*C. e. erythrinus*) older than 1 year leave southern Finland before juveniles.

Birds gain two advantages by leaving earlier. If food supplies after breeding and molt are diminished, earlier departure allows exploitation of new food resources at places away from the breeding ground in early fall. Second these flocks gain an advantage in locating winter food supplies and in familiarity with their location. If great distances to wintering grounds exist as in the Scarlet Rosefinch, the earlier departure would be beneficial (Peiponen 1974). Because of the differential departure, these advantages benefit survival of females, adult males, and young in the early nonbreeding seasons. As no hostility was observed between Cassin's Finch flocks of breeding birds with young and yearling male flocks, the reason for differential departure is not entirely evident.

Yearling male molt (duration of all molts estimated by regression analysis) was complete 3 days prior to departure of adults and young in 1971 and 10 days prior in 1973 (Samson 1974). Yearling male molt in 1972 extended 4 days beyond adult and young departure and thereby may have delayed their departure. This is questionable as molt for adults is estimated to have extended beyond their fall departure date in 1973. The differential departure may represent a genetically influenced behavior selected particularly to favor female survival. This favorability may also be reflected in the female dominance and associated low mortality found in Cassin's Finch winter flocks during 1972-1973 and 1973-1974 (Samson 1974).

2. *Annual fluctuation in breeding numbers.*—Cassin's Finch numbers fluctuated substantially from one breeding season to the next. Other cardueline finch populations also fluctuate from year to year, apparently in relation to food supply (Newton 1969, 1972). Contents of digestive tracts from 58 of 61 finches collected prior to and during the early nesting season in 1972 and 1973 were over 94% by volume staminate buds of quaking aspen. No animal material was evident in any digestive tract. It is known (Graham et al. 1963, Bogdanov 1968) that aspen pollen production varies from year to year with an unusually large production every third or fourth year. Conceivably finch utilization of region for breeding and lack of total annual fidelity to a breeding site may be influenced by availability and change in aspen staminate bud production, but total Cassin's Finch numbers in a breeding season may be influenced by other factors including winter food supply similar to the Bullfinch (*Pyrrhula pyrrhula*) (Newton 1964).

ACKNOWLEDGMENTS

Appreciation is extended to Keith L. Dixon for the helpful suggestions and advice throughout the study. The use of equipment and facilities of the Department of Biology, Utah State University, and that of Allen W. Stokes greatly facilitated the research. Keith L. Dixon, Ian Newton, and Peter Marler improved an earlier draft with constructive comments. Special thanks are extended to Sue Samson for her assistance throughout the study and in preparation of figures. The research was partially financed by grants from Sigma Xi and the Chapman Fund, American Museum of Natural History, New York, New York.

SUMMARY

Breeding populations, the mated-female distance form of territorial behavior and its effect on nesting density and fall departure of Cassin's Finch are described. Finch numbers varied from year to year with an estimated 15-fold increase from 1971 to 1972 and a decrease in 1973 to near the 1971 level. Males significantly outnumbered females in 2 of 3 years, and the female is considered the limiting resource for reproductive effort. Male territorial behavior, expressed as a mated-female distance, centers around the female and her location. It does not limit total breeding numbers but may space nesting pairs temporally. Finches nested in colonies, and habitat did not appear limiting for colony size or location. Adults with young left the study area prior to yearling males in each of three summers.

LITERATURE CITED

- AMERICAN ORNITHOLOGISTS' UNION. 1957. Check-list of North American birds, fifth ed. Baltimore, Amer. Ornithol. Union.
- AMERICAN ORNITHOLOGISTS' UNION. 1973. Thirty-second supplement to the American Ornithologists' Union check-list of North American birds. *Auk* 90: 411-419.
- BAILEY, A. M., AND R. J. NEIDRACH. 1965. Birds of Colorado, vol. 2. Denver, Denver Mus. Nat. Hist.
- BAILEY, F. M. 1928. The birds of New Mexico. Washington, D. C., Judd and Detweiler Press.
- BLAIR, W. F., A. P. BLAIR, P. BRODKORB, F. CAGLE, AND G. MOORE. 1957. Vertebrates of the United States, first ed. New York, McGraw-Hill.
- BOGDANOV, P. L. 1968. Poplars and their cultivation. Jerusalem, Israel Program for Sci. Transl.
- BROWN, J. L. 1969. Territorial behavior and population regulation in birds. A review and re-evaluation. *Wilson Bull.* 81: 293-329.
- CARRICK, R. 1963. Ecological significance of territory in the Australian Magpie, *Gymnorhina tibicen*. *Proc. 13th Intern. Ornithol. Congr.*: 740-753.
- CHAPIN, J. 1958. The 1957 Christmas counts in Colorado. *Colorado Bird Notes* 5: 29-31.
- CHAPMAN, D. G. 1948. A mathematical study of confidence limits of salmon populations calculated from sample tag ratios. *Intern. Pacific Salmon Fish. Comm. Bull.* 2: 69-85.

- CONDER, P. J. 1949. Individual distance. *Ibis* 91: 649-655.
- DAWSON, W. L. 1923. The birds of California, vol. 1. San Diego, South Moulton Co.
- DELIUS, J. D. 1965. A population study of Skylarks, *Alauda arvensis*. *Ibis* 107: 466-492.
- DIXON, W. J., AND F. J. MASSEY, JR. 1969. Introduction to statistical analysis, third ed. New York, McGraw-Hill.
- FARNER, D. S. 1952. The birds of Crater Lake National Park. Lawrence, Univ. Kansas Press.
- FRENCH, N. R. 1959. Life history of the Black Rosy Finch. *Auk* 79: 159-180.
- GRAHAM, S. A., R. P. HARRISON, JR., AND C. W. WESTELL, JR. 1963. Aspens: phoenix trees of the Great Lakes Region. Ann Arbor, Univ. Michigan Press.
- GRINNELL, J. 1908. The biota of the San Bernardino Mountains. Univ. California Publ. Zool. 5.
- GRINNELL, J., AND A. H. MILLER. 1944. The distribution of the birds of California. Pacific Coast Avifauna No. 27.
- HENSHAW, H. W. 1879. Ornithological report from observations and collections made in portions of California, Nevada, and Oregon. Appendix L, Ann. Rept. Chief Engineers for 1879 (Feb. 1880), Ann. Rept. Geogr. Surv. West 100th Meridian, by George M. Wheeler, pp. 282-335.
- HILDEN, O. 1969. Über vorkommen und brutibiologie des Birkenzeisigs (*Carduelis flammea*) in Finnisch-Lapland in Sommer 1968. *Ornis Fennica* 46: 93-112.
- HINDE, R. A. 1956. The biological significance of the territories of birds. *Ibis* 98: 340-369.
- HOLMGREN, A. H. 1965. Handbook of the vascular plants of the northern Wasatch. Palo Alto, National Press.
- HURST, R. L. 1972. Statistical program package. Logan, Utah State Univ. (mimeo).
- JOHNSON, R. E. 1960. Reproductive activities of Rosy Finches with special reference to Montana. *Auk* 82: 190-205.
- JONES, V. E., AND L. M. BAYLOR. 1969. Nesting of the Cassin's Finch at Pocatello Idaho. *Tebiwa* 12: 64-68.
- KELLY, J. W. 1921. Cassin Purple Finches eating salt. *Condor* 23: 165.
- KLOMP, H. 1972. Regulation of the size of bird populations by means of territorial behavior. *Netherlands J. Zool.* 22: 456-488.
- KLUYVER, N. H. 1970. Regulation of numbers in populations of Great Tits (*Parus m. major*). Proc. Advan. Study Inst. Dynamics Numbers Popul. Ocsterbeek: 507-523.
- KREBS, J. R. 1971. Territory and breeding density in the Great Tit *Parus major* L. *Ecology* 52: 2-22.
- LACK, D. 1966. Population studies of birds. Oxford, Clarendon Press.
- LACK, D. 1968. Ecological adaptations for breeding in birds. Bristol, Western Printing Service, Ltd.
- LINCOLN, F. C. 1930. Calculating waterfowl abundance on the basis of banding returns. U.S. Dept. Agr. Circ. No. 118.
- MAGEE, M. J. 1924. Notes on the Purple Finch. *Auk* 41: 606-610.
- MORTON, M. L., J. L. HORSTMANN, AND J. M. OSBORN. 1972. Reproductive cycle and nesting success of the Mountain White-crowned Sparrow (*Zonotrichia leucophrys oriantha*) in central Sierra Nevada. *Condor* 74: 152-163.

- MUNDINGER, P. C. 1971. Vocal, social and reproductive behavior in the continental Twite (*Carduelis f. flaverrostris*). Logan, Utah, Anim. Behav. Soc. Meeting.
- NEWTON, I. 1964. Bud-eating by Bullfinches in relation to the natural food supply. *J. Appl. Ecol.* 1: 265-279.
- NEWTON, I. 1969. Irruptions of crossbills in Europe. Pp. 337-357 in *Animal populations in relation to their food resources* (A. Watson, Ed.). *Brit. Ecol. Soc. Symp.* No. 10. Oxford, Blackwell Sci. Publ.
- NEWTON, I. 1972. *Finches*. Taplinger Publ. Co., New York.
- NOTTEBOHM, F. 1972. The origins of vocal learning. *Amer. Naturalist* 106: 116-140.
- ORIAN, G. H. 1961. The ecology of blackbird (*Agelaius*) social systems. *Ecol. Monogr.* 31: 285-312.
- ORR, R. T. 1968. Cassin's Finch (*Carpodacus cassinii* Baird). Pp. 280-289 in *Life histories of North American Cardinals, grosbeaks, buntings, towhees, finches, sparrows, and allies* (A. C. Bent and collaborators). *U.S. Natl. Mus. Bull.* 237.
- PEIPONEN, V. A. 1962. Über brutbiologie nahrung und geographische verbreitung des Birkenzeisigs (*Carduelis flammea*). *Ornis Fennica* 39: 37-60.
- PEIPONEN, V. A. 1974. Food and breeding of the Scarlet Rosefinch (*Carpodacus e. erythrinus* Pall.) in southern Finland. *Ann. Zool. Fennica* 11: 155-165.
- RIBAUT, J. 1964. Dynamique d'une population de Merles noirs *Turdus merula* L. *Rev. Suisse Zool.* 71: 815-902.
- RIDGWAY, R. 1877. *Ornithology*. Pp. 303-669 in *Ornithology and paleontology*, part 3. *U.S. Geol. Expl. of the fortieth parallel*.
- SALT, G. W. 1952. The relation of metabolism to climate and distribution in three finches of the genus *Carpodacus*. *Ecol. Monogr.* 22: 121-152.
- SAMSON, F. B. 1974. *Social organization of Cassin's Finch in Northern Utah*. Unpublished Ph.D. dissertation, Logan, Utah State Univ.
- TAST, J. 1970. Group nesting and the breeding season of the Linnet. *Carduelis cannabina* L. in Finland. *Ornis Fennica* 47: 74-82.
- TAYLOR, W. P. 1912. Field notes on amphibians, reptiles and birds of northern Humboldt County, Nevada with a discussion of some faunal features of the region. *Univ. California Publ. Zool.* 7: 319-436.
- THOMPSON, W. L. 1960. Agonistic behavior in the House Finch. Part 1: Annual cycle and display patterns. *Condor* 62: 245-271.
- TINBERGEN, N. 1957. The functions of territory. *Bird Study* 4: 14-27.
- TWINING, H. 1938. The significance of combat in male Rosy Finches. *Condor* 40: 246-247.
- VON HAARTMAN, L. 1972. Influence of territory upon structure and dynamics of bird populations. Pp. 101-110 in *Population ecology of migratory birds, a symposium*. *U.S. Dept. Interior Wildl. Res. Rept.* 2.
- WATSON, A. 1973. A review of population dynamics in birds. *Brit. Birds* 66: 417-437.
- WYNNE-EDWARDS, V. C. 1962. *Animal dispersion in relation to social behavior*. Edinburgh, Oliver and Boyd.

Department of Zoology, Ecology Center, Utah State University, Logan, Utah 84321. Present address: School of Forest Resources, The Pennsylvania State University, University Park, Pennsylvania 16802. Accepted 31 January 1975.