The Condor 87:494–510

BREEDING SITE FAITHFULNESS, REPRODUCTIVE BIOLOGY, AND ADULT SURVIVORSHIP IN AN ISOLATED POPULATION OF CASSIN'S FINCHES

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ABSTRACT.—We used mist nets in a capture-recapture demographic study of the birds of an isolated relict grove of ponderosa pines (Blue Sky) on Hart Mountain in southern Oregon. Cassin's Finches (*Carpodacus cassinii*), usually considered nomadic, returned each spring. Females were more faithful to breeding site than males. As evidenced by cloacal swelling and incubation patch formation, 96% of females laid eggs in the 18 days following 24 May. When June snow storms destroyed most nests in 1975 and 1979, many females attempted second nestings. Most apparently abandoned these second nestings in early July when the finches left Blue Sky to wander more widely over Hart Mountain while they underwent their annual molts. Most yearling females and males were sexually active and apparently nested. Although obscured by reduced mobility of females during incubation and early brooding, the sex ratio was close to 50/50. There were 20 to 25 pairs per hectare of suitable (pine) finch habitat. Breeding density may be limited by the zone around the female that is defended by the male during nest-site selection and nest building. The minimum annual survival rate for finches one year old and older was 0.64 (SE = ± 0.02) for males and 0.60 (SE = ± 0.03) for females.

Cassin's Finch (*Carpodacus cassinii*) inhabits open conifer woodlands of the interior mountains of western North America, generally nesting above an elevation of 1,500 m. It breeds from southern interior British Columbia, Montana, and northern Wyoming south to interior southern California, northern Arizona, and northern New Mexico. The finch is at least an altitudinal migrant in parts of its range, and migrates latitudinally as well. Wintering flocks have been reported in the lowland valleys as far north as southern British Columbia. Latitudinal migrants have been recorded regularly as far south as northern Baja California and the Mexican highlands to Durango, Zacatecas, and Coahuila (AOU 1983).

A limited literature (summarized by Salt 1958, Orr 1968, and Samson 1976a) conveys the impression that Cassin's Finch is an opportunistic species, characterized by a labile annual cycle, weak faithfulness to breeding site, and geared to exploit variable sources of food. The bird shares these characteristics with many other species of cardueline finches (Newton 1972). In the only systematic studies of the summer biology of the Cassin's Finch done thus far, Samson (1976a, b) found large annual fluctuations in breeding populations of northern Utah and regarded the species as nomadic.

In contrast, we found that a population of Cassin's Finches on Hart Mountain in southeastern Oregon varied little in size from year to year and that individuals showed high breeding site faithfulness. This stimulated us to examine and report here several related aspects of the summer biology and demography of this relatively little-known species. Our data on Cassin's Finches were obtained as a secondary result of a more extensive, seven-year survey of year-to-year variation in the breeding avifauna of Hart Mountain, conducted by systematic capture-recapture of birds in mist nets. Our analysis is, therefore, retrospective and confined to questions that can be examined with the aid of data obtained by such methods.

STUDY AREA

Hart Mountain, a part of Hart Mountain National Wildlife Refuge, is a typical block-fault basalt formation in the Great Basin country of southeastern Oregon. Elevations range from the 1,365-m lake surfaces in the Warner Valley to 2,444 m at Warner Peak. An escarpment of nearly 1,000 m faces westward. The Hart Mountain population of Cassin's Finches centers on the isolated grove of ponderosa pines, henceforth referred to as "Blue Sky," which is associated with riparian habitat on the comparatively gentle eastern slope of the mountain. Occupying a total area of about 136 ha, Blue Sky (Fig. 1) extends from about 1,830 to

FIGURE 1. Aerial view of the entire Blue Sky relict grove of ponderosa pines on the easterly slope of Hart Mountain, taken 07:45 on 10 June 1982. Warner Peak (2,444 m) is in the right center background. The Y-shaped Camp Creek study area extends along the left edge of the photograph. Post Meadow is in the left center foreground. To the right of and below Warner Peak are the headwaters of Guano Creek, which then flows to exit the photograph in the lower left corner. On 10 June, the aspens at Blue Sky and upper Guano Creek were not yet leafed-out.

1,950 m elevation. Three small permanent spring-fed creeks with their associated riparian strips, including several small meadows, encompass about 30 ha between the lateral edges of the tree canopy. At Blue Sky, the riparian habitat is dominated by ponderosa pines, quaking aspens (*Populus tremuloides*), willows (*Salix scouleriana*), and alders (*Alnus tenuifolia*). Of the greater study area, 106 ha is characterized by sagebrush (*Artemisia tridentata*), rabbit brush (*Chrysothamnus nauseosus*), bitterbrush (*Purshia tridentata*), grasses, forbs, and scattered western juniper (*Juniperus occidentalis*), continuous with the surrounding shrubsteppe.

We centered our study on Camp Creek (Fig. 1), the southernmost of three permanent, spring-fed streams that originate in and flow through Blue Sky. The Camp Creek springs, at about 1,950 m elevation, flow 1,300 m to join Guano Creek at 1,830 m elevation. The Y-shaped riparian habitat of Camp Creek includes 5.4 hectares within the lateral edges of the canopy of usually mixed pines and aspens. We made systematic studies during the summers of 1973–1979 and gathered supplemental data in summers of 1972, 1981, 1982, and 1984.

The ponderosa pine grove at Blue Sky was severely reduced, if not nearly demolished, in the fall and winter of 1866–1867, when the 11th Cavalry Regiment of the United States Army established Camp Warner on the site and cut trees for a stockade, shelters, and firewood. Camp Warner was abandoned in the early spring of 1867.

Representative core samples taken from among the 514 ponderosa pines counted along Camp Creek in 1974 show that all but four giants, each more than 250 years old, were no more than 100 years old. Examination of the additional 25 ha of the Blue Sky pine grove shows the same pattern; that is, a few old giants, but mostly trees of the same age as on Camp Creek. Given the rate of growth of these pines and the predilection of Cassin's Finches for nesting above 15 m in tall pines (Orr 1968, Samson 1976a), we believe that the present population of Cassin's Finches probably established itself, or more likely re-established itself, no more than 50 to 70 years ago.

During our periods of residence, variously April to October, we recorded weather data near our camp site (1,885 m elevation) on Camp Creek with a hygrothermograph, a pyranograph, and a rain gauge. We also have in

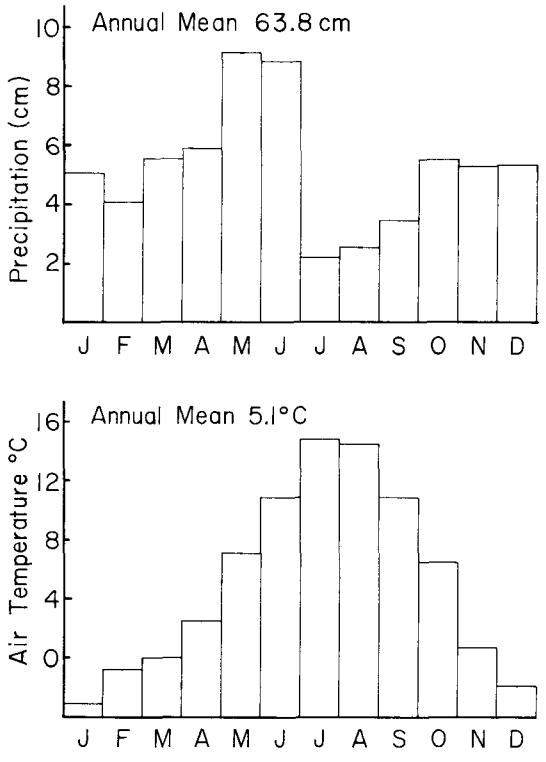

FIGURE 2. Estimated mean monthly precipitation and temperature on mid-Camp Creek, from records taken at Refuge headquarters 1940–1979 (precipitation) and 1971–1980 (air temperature), and from our records taken at Camp Creek during our tenure there (1973–1979).

hand long-term records (National Oceanic and Atmospheric Administration) of air temperature and precipitation that were taken by U.S. Fish and Wildlife Service personnel at the Hart Mountain Refuge headquarters (1,713 m elevation) on the open shrubsteppe plain 15 km NNE of Blue Sky. Our simultaneous records permitted us to estimate the annual patterns of temperature and precipitation at Blue Sky by correlation with the records from Refuge headquarters. We found precipitation at Blue Sky to be about 2.28 times greater than that at Refuge headquarters and established cognate correlations for air temperature (Fig. 2). The study area is on an ESE-facing slope that allows cold air to drain downslope to Post Meadow, especially on calm nights. Air temperatures on the mid- and upper portions of the Camp Creek riparian study area had higher minima, but lower maxima and means, than the surrounding shrubsteppe.

In the May–June period of greatest nesting activity, precipitation reached its annual maximum (Fig. 2) and air temperatures typically dropped below 0°C several nights each month. Daytime temperatures were mild, usually reaching 15° to 20°C in May and June, and 20° to 25°C in July and August.

Twice (1975 and 1979) during the study (1973–1979), storms in mid-June brought cold rain and substantial snow. Because in 1975 (17–19 June and 24–25 June) and again in 1979 (16–18 June) these storms lasted 36–48 hours, reproductive failure was nearly universal among species that were incubating eggs or with young in the nest at Blue Sky and higher on the mountain.

Aspen leaves of early clones on Camp Creek came from bud to full size in the period from 20 May to 3 June. Later clones moved through the same sequences 10 to 15 days later. We noted as much as 15-days difference in phenology among years, with an apparent relation to variable persistence of snow cover in the aspen groves. The production of forbs and grasses varied conspicuously among years and was especially luxuriant in 1974.

METHODS

To maximize captures, we established 64 net sites, eight to 10 of which we used each day in rotation (Fig. 3). Net sites accommodated from one to four black nylon 36-mm mesh, four-panel mist nets, 12 m long. Most nets were placed perpendicular to stream flow, and two or more nets at a site were placed end to end. Nets were set with the bottom trammel line about 0.15 m above the ground and the top 2.15 m high. The 64 sites accommodated 94 nets. Nets, open from dawn to usually about 11:00, were emptied hourly, the birds were banded and measured, and then were released near the site of capture. Data recorded at each capture and recapture included site, hour, age, sex, wing-length (first capture each season), weight, reproductive condition, and pertinent notes on plumage and molt. Overall capture efficiency of Cassin's Finches was 59 per 1,000 net hours (Table 1), but typically exceeded 100 per 1,000 net hours on most days in late May and early June.

AGE AND SEX DETERMINATION

Because we handled nearly all birds during May, June, and early July (Table 1), we were able to ascertain their age and sex by using methods described by Samson (1974, 1976b) and Balph (1977). Our designations of age and sex of individuals or of groups conformed to definitions in the *North American Bird Banding Manual* (1976): HY, a bird known to have hatched in that calendar year; SY, a bird known to be in its second calendar year of life; ASY, a bird known to be in its third or later calendar year of life; and AHY, a bird known to be in its second or later year of life—this category is also useful to designate groupings of birds, known to be SY, ASY, and AHY.

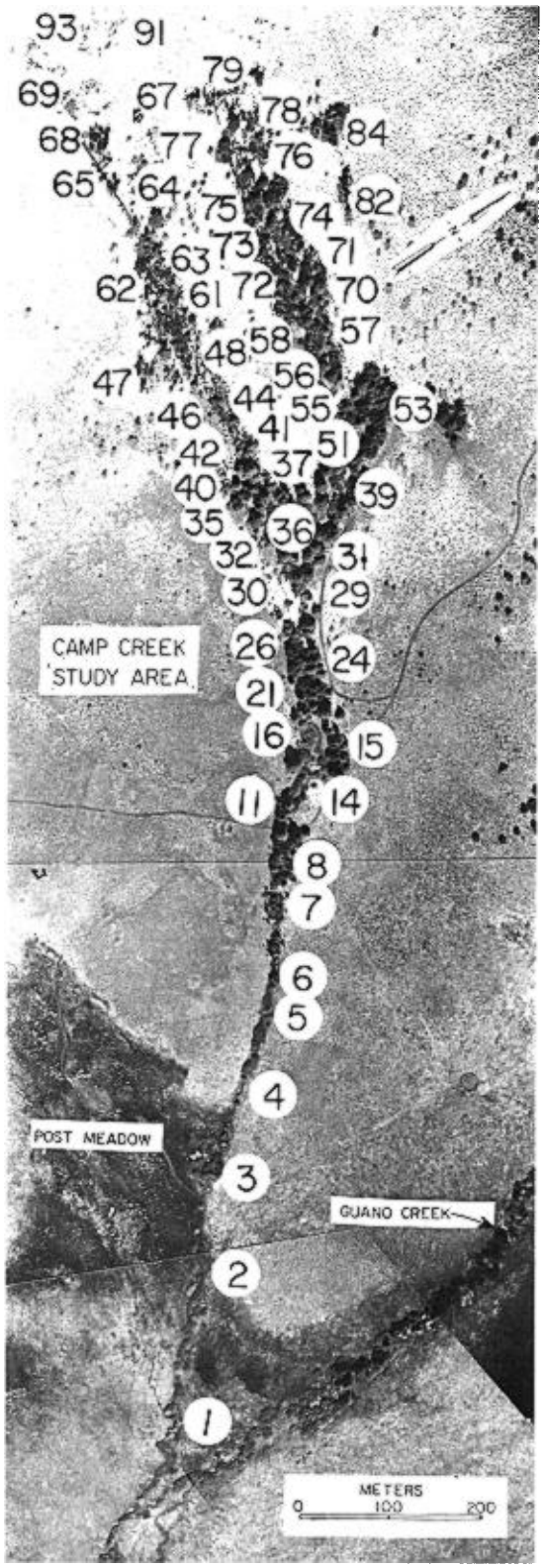

FIGURE 3. Camp Creek, with numbered mist net sites, on 19 June 1979. Upper portion of study area has remnants of heavy snowfall of 16–18 June.

TABLE 1. Summary of Cassin's Finch captures at Camp Creek, 1973–1979.

Month	Number of captures[a]	Net hours[b]	Captures per 1,000 net hours
Apr	4[c]	1,373	3
May	525	7,898	66
Jun	1,090	13,412	81
Jul	140	4,228	33
Aug	13	1,037	13
Sep	1[d]	1,699	1
Oct	0	311	0

[a] New captures, returns, and repeats.
[b] Net hour = one 12 × 2 m net open 1 h.
[c] One on 25 April and three on 30 April (1976).
[d] 12 September 1978.

We distinguished the several age and sex groups as follows: (1) ASY males were streaked with dark grayish brown on smoke gray, with a substantial overwash of vinaceous to ruby, especially on the head, back, and upper breast (colors from Smythe 1975); (2) SY males were streaked dark grayish brown on smoke gray, had a male-type cloacal protuberance, lanceolate decks (=central pair of rectrices), and tended to have longer wings than either SY or ASY females (see Samson 1974, Balph 1977); (3) ASY females were streaked dark grayish brown on smoke gray, had a female-type cloacal enlargement (cone-shaped with apex toward the tail) or incubation patch (or both), tended to have rounded or truncated decks, and had shorter wings than SY males; (4) SY females were streaked dark grayish brown on smoke gray, had a female-type cloacal enlargement or incubation patch (or both), tended to have lanceolate decks, and had shorter wings than either SY males or ASY females. Because we captured most finches more than once, we were able to verify earlier age and sex classifications, frequently with additional criteria.

RESULTS AND DISCUSSION

PERIOD AND NATURE OF RESIDENCY

Our earliest seasonal observations on the study area were on 9 and 10 April 1974, and we first commenced regular daily observations and mist-netting on 15 April 1976. In each of the other years, we did not arrive on the study area until mid-May or later. In mid-April, Camp Creek still retained its winter snow cover and the aspens and alders would not begin to leaf out for another six weeks. A few Cassin's Finches were seen both 9 and 10 April 1974, including one flock of 12 that included four ASY males. In 1976, though sought, none was encountered on 15 or 16 April. On the cool (−8°C), clear, and calm morning of 17 April, however, a flock of 15, including some singing males, was seen in a nearby part of Blue Sky. In that year (1976), as indicated by captures

of returning breeders of both sexes, at least part of the summer resident population arrived at Camp Creek on 30 April and 1 May. This timing is consistent with the observations of Jones and Baylor (1969:64) who reported that "Occasionally a few spring migrants will arrive [at Pocatello, Idaho—about the same latitude as Hart Mountain] in late March, but the distinctive Cassin's Finch migration begins the first week of April, with numbers increasing in mid-April through early May."

As quickly as the young fledged, they left the nesting area, apparently in the company of their parents. In this respect, they are similar to the Common Rosefinch (*Carpodacus erythrinus*) of western Finland, as described by Stjernberg (1979), who found (p. 55) ". . . the nesting place is deserted rather quickly and they leave the breeding area within 2–3 weeks." By mid-July, numbers of Cassin's Finches on the study area were greatly reduced (Table 1). Their presence there after the first week of July until fall migration, probably in September, is apparently in no greater numbers than elsewhere in the riparian and juniper woodlands on the south end of Hart Mountain. Thus, the breeding population actually occupies its nesting grounds in the Blue Sky ponderosa pine grove for about 2½ months.

During the May–June period of nesting in 1973–1979, when Cassin's Finches were abundant at Blue Sky, we encountered comparatively few of them elsewhere on Hart Mountain. In May and June of 1982, we sought to test this trend by observation and netting in nearby riparian areas. The few individual finches that we observed did not appear to be engaged in nesting activites. In 217 net hours in nearby riparian areas we caught one (five per 1,000 net hours), an HY male whose flaccid cloacal protuberance suggested that he was not actively breeding. On alternate days at Camp Creek in 300 net hours, we caught 40 (133 per 1,000 net hours), all in breeding condition appropriate to the date of capture. That some nesting does occur on Hart Mountain outside of Blue Sky, however, has been reported by B. Pyle (pers. comm., 2 July 1984), who found several pairs nesting in sagebrush near Robinson Draw Spring about 8 km NE of Blue Sky.

Beginning in early July, the finches, including some known to nest at Camp Creek, formed into widely ranging flocks of 10 to 30 or more birds. Of 25 captures from these flocks (21 in August, two in September, and two in October), 14 were captured at peripheral sites (e.g., CC-53 and CC-79—Fig. 3) on Camp Creek and the other 11 on other parts of Hart Mountain, but within 10 km of Camp Creek. Of these 25, seven were ASY males, six were AHY females, two were SY males, eight were HY finches of unknown sex, one was an HY male, and one was an HY female. (Sex of these last two HY birds, captured on Guano Creek 3 km from Camp Creek, was ascertained upon subsequent capture at Camp Creek in a later season.) Three of the AHY females and one ASY male, caught several kilometers from Camp Creek, were also captured at Camp Creek in another season.

Six (24%) of these 25 finches, captured peripheral to the central study area, were captured in a later season. Camp Creek comprises about 17% of the pine-dominated riparian habitat of Blue Sky. Hence, we believe that the remaining 19 birds (76%) could well have nested somewhere in the remaining 83% of the pine-dominated riparian habitat of Blue Sky. If, from July to October, Cassin's Finches from areas other than Blue Sky were present, it is unlikely that 24% of the finches that we encountered during those months (including significant netting in parts of Hart Mountain away from Blue Sky) would have been banded during the breeding season on the Camp Creek study area. These comparative numbers tend to confirm the isolation of the Blue Sky population and suggest to us a lack of evidence of recruitment to the Hart Mountain colony from breeding populations in the Warner Mountains or elsewhere.

We have no information about the wintering place of the Hart Mountain breeding population. None of our Cassin's Finches banded there has been recovered elsewhere. It is likely that they are erratic in winter, in common with most other cardueline finches (e.g., Newton 1972, Yunick 1983). During a Christmas Bird Count on 30 December 1973, we found ten Cassin's Finches at Blue Sky, but none has been found in the count area during six counts since 1973, each of which included Blue Sky.

THE REPRODUCTIVE SEASON

Cassin's Finches were the most abundant breeding birds on the study area during at least the period 1975–1979 (Mewaldt, unpubl. data). Although the finches' nesting activities were clearly associated with the pines, they foraged extensively on the ground in the adjacent sage, and congregated several at a time in the scattered junipers. We did not study their nesting habits systematically, but our casual observations agree with Orr's (1968:281), who wrote that the "nests are almost invariably situated in large conifers and usually near the terminal ends of limbs at a considerable height above the ground."

As evidenced by cloacal swelling and for-

TABLE 2. Timing and duration of egg-laying by Cassin's Finches 1975–1979.

Year	Laying period for 96% of first clutches				Type of season
	Beginning	Ending	Duration	*n*	
1975	26 May	11 Jun	16 days	14	Cool, wet
1976	19 May	6 Jun	18 days	62[a]	Mild, dry
1977	26 May	13 Jun	18 days	39	Average
1978	24 May	10 Jun	17 days	57	Average
1979	20 May	9 Jun	20 days	26	Mild

[a] Includes an interpolation adding 12 *n*, estimated on basis of data from the other four years, near end of period to compensate for no field work 1–7 June 1976.

mation of incubation patches in females, egg-laying in the Camp Creek population was well synchronized. Ninety-six percent of the females laid their eggs over a period of 18 days, usually starting about 25 May (Table 2). These estimates are based on 186 records of mist-netted females (AHY) that were found to be about to lay, laying, or having just laid between 21 May and 12 June. The least squares regressions of rectified cumulative percentages of first-clutch laying dates, as displayed on a probability scale in a linear relation to time (Fig. 4), show that egg-laying was earliest in 1976 and latest in 1975 and 1977. The 7-day span in timing of mean egg-laying among years and the position of each of the five seasons within this span show a weak positive relationship to seasonal phenology. Our notes on the leafing-out time of the aspens on the study area, and on the timing of the disappearance of the last snow drifts on the slope immediately above the study area, show that 1976 had the mildest and driest spring, and 1975 had the coldest and wettest (also snowiest) spring during 1975–1979. The spring season of 1979 was relatively mild, approaching 1976 as an early season.

Reproduction in 1976, 1977, and 1978 was limited to a single brood, with most egg-laying in the last week of May and the first week of June (Fig. 5). The temporal extension of the curve into mid- or late June in those years suggests that a few second nestings were attempted, probably after initial failures. In contrast, severe mid-June (17–19 and 24–25 June 1975, and 16–17 June 1979) snow storms and subzero temperatures probably destroyed many first-clutch eggs and young in both 1975 and 1979. Such summer storms are not uncommon in the higher mountains of interior western North America and their detrimental effects on passerine reproduction have been noted (e.g., Ehrlich et al. 1972, Eckhardt 1977) and studied (Morton 1976, 1978). In 1975 and 1979, many Cassin's Finches began a second nesting, as evidenced by a second peak in egg-laying during the last week of June (Fig. 5).

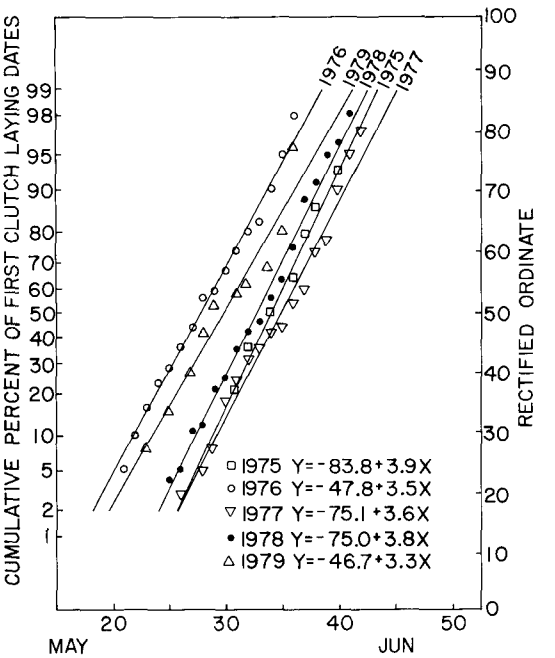

FIGURE 4. Temporal course (cumulative percentages) of first-clutch egg-laying, plotted on a probability scale by years 1975 to 1979. The lines are fitted to each year's data by a least squares regression of the rectified data. An interpolation (adding 12 *n* estimated on the basis of data from the other four years), to compensate for no field operations 1–7 June 1976, brings the slope of the 1976 regression into approximate conformity with the other four years.

Even though there apparently were many second nesting attempts in 1975 and 1979, most finches apparently abandoned those late nests when they left the study area in early to mid-July. This was about the same time that they left in the three years when most first broods were apparently carried to completion. The capture of single fledglings on 16 August 1975 and on 22 July 1979 indicates that some did complete their second nesting attempts after the June storms in those two years. No fledglings were encountered that late in 1974, 1976, 1977, or 1978.

Beginning in 1976, we distinguished yearling females (SY) from older females (ASY). Excluding data from the exceptional years 1975 and 1979, we found that females two years old and older (ASY) tended to lay earlier and were better synchronized in their egg-laying times than were yearlings (Fig. 6).

In male Cassin's Finches at Camp Creek, the cloacal protuberance enlarged in the second half of May (Fig. 7). Males two years old and older (ASY), reached peak development in the period 21–25 May and stayed at that level through the end of June, by which time any second breeding attempts were well underway. Davis (1971) has shown that the size

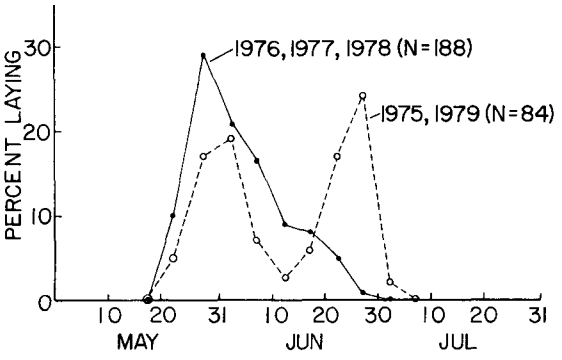

FIGURE 5. Laying times of yearling and older female Cassin's Finches in three "normal" seasons without June snow storms (1976, 1977, and 1978), and in two seasons with severe mid-June snow storms (1975 and 1979).

of the cloacal protuberance is a useful indicator of testicular size in male Rufous-collared Sparrows (*Zonotrichia capensis*) in Peru. Yearling (SY) male Cassin's Finches showed later enlargement of their cloacal protuberance and a lesser mean maximum development than older males. The mean cloacal protuberance index of 2.18 for 131 ASY males (Fig. 7) is significantly larger (Mann-Whitney U Test, $P < 0.001$) than the mean index of 1.63 for 106 SY males during the first ten days of June. These observations are consistent with Samson's (1976a) measurements of testicular volume in ASY and SY males. He found that testicular recrudescence was earlier in ASY males and that their ultimate testes' volumes were greater than in SY males. These laboratory measurements of the testes, and his field tests involving removal of ASY males from established pairs with subsequent replacement by SY males, led him to conclude that testicular development in SY males was adequate to allow them to breed. Certainly our data (see our later section on Sex Ratio) suggest that SY males on Hart Mountain do indeed breed in significant numbers.

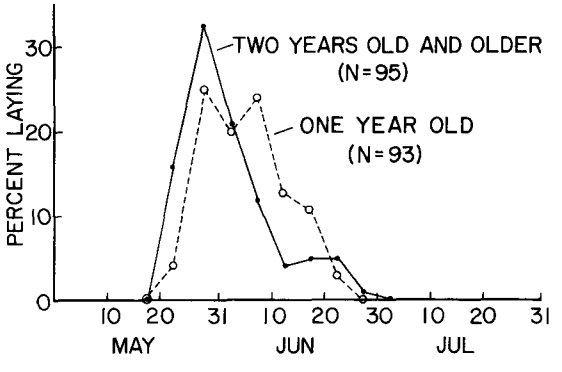

FIGURE 6. Laying times of Cassin's Finch females two years old and older (ASY), and of yearling females (SY) for the "normal" seasons 1976, 1977, and 1978.

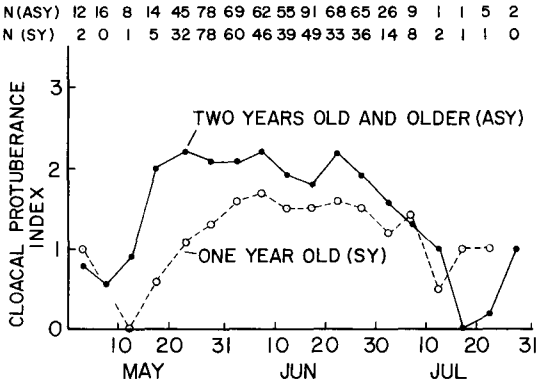

FIGURE 7. Index to mean size of cloacal protuberance (using a scale of 0 = none, 1 = small and flaccid, 2 = medium and firm, and 3 = large and globular) in yearling (SY) and older (ASY) Cassin's Finch males 1973–1979.

Because our method of evaluation showed no significant variation in the cloacal protuberance index from year to year, we believe that these male Cassin's Finches were relatively less sensitive to differences in seasonal phenology than were females. Females responded to destruction of their first nesting attempts in both 1975 and 1979 by a general second recrudescence of their reproductive apparatus in the second half of June (Fig. 5).

MOLT

Data from 158 adults (AHY) captured in July (142), August (14), and September (two) at Camp Creek and elsewhere on Hart Mountain included 56 in prebasic (postnuptial) molt. We scored the molt of each of these 56 finches by using nine primaries and secondary number six on a scale from one to five (one = missing feather, to five = full grown) after Newton (1967). Regression of resulting scores against time in days from 1 July (Fig. 8) indicates that the mean starting date of prebasic (postnuptial) molt of the Hart Mountain population was about 9 July, with mean completion about 27 September (mean duration in the population = 80 days). Because we have so few data from August and September, the mean completion date and mean duration (80 days) are less reliable than in the mean starting date (9 July); consequently, we suggest that the prebasic (postnuptial) molt lasts less than 80 days in the population. Indeed, Samson (1976b) found, with a similar regression technique, that adult Cassin's Finches in Utah, as a population, typically commenced the molt 8 to 11 July and had a mean molt period of 68.8 days, with completion in mid-September.

The capture of relatively few juveniles (HY) in July and August suggests that they, in company with their parents, leave Camp Creek while still in the final stages of prejuvenal

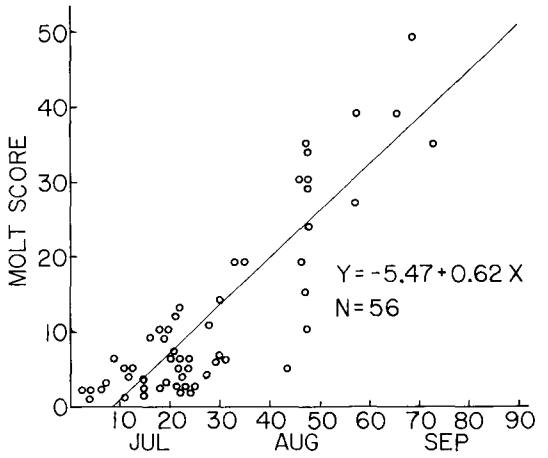

FIGURE 8. Postnuptial molt score (Y-axis), plotted against day of scoring beginning with 1 July, for yearling and older Cassin's Finches (male and female) 1973–1979. The regression intercepts the base line on day 9 (9 July) and the line indicating completion of molt on the 89th day (27 September).

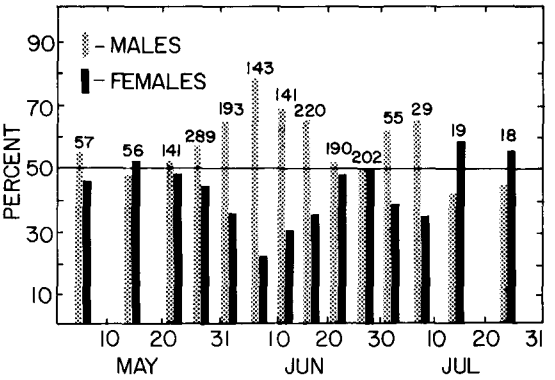

FIGURE 9. Comparative percentages of capture of AHY male and female Cassin's Finches on the Camp Creek study area in May, June, and July of 1973–1979.

(postnatal) molt. Of only 15 fledglings captured on the study area, all with rectrices still in sheaths, 13 clustered around 2 July (23 June to 6 July) were likely issue from first broods from 1974, 1976, and 1978. The two fledglings taken later (22 July 1979 and 16 August 1975) probably came from second breeding attempts, each from a year (1975 and 1979) when severe June snow storms destroyed most first broods.

Our observations and captures of finches on other parts of Hart Mountain and vicinity suggest that, upon leaving Camp Creek in early to mid-July, they moved widely among the riparian strips and juniper woodland on the south end of Hart Mountain (i.e., within 10 to 15 km). There, from mid-July to September, they apparently completed their prebasic (postnuptial and postjuvenal) molts before leaving Hart Mountain. This is consistent with Samson's (1976b) findings for Cassin's Finches in northern Utah. They apparently do not respond to the compressed period for prebasic (postnuptial) molt, however, by migrating first and molting later, as do at least some populations of the long-distance migrant Common Rosefinch of northern Europe (Stresemann and Stresemann 1966, Newton 1972, Peiponen 1974). Completion of the prebasic (postnuptial) molt on the breeding grounds is apparently the norm in most Asian species of *Carpodacus* (Dement'ev et al. 1954).

SEX RATIO

The sex ratio was approximately 50/50 in the Camp Creek population. The apparent sex ratio varied substantially through the spring and

TABLE 3. Sex ratios of Cassin's Finches, based on mist net captures when both males and females were free-ranging, compared to periods when most females were incubating or brooding.

Periods when males and females were free-ranging				Periods when most females were incubating or brooding			
	Percent				Percent		
Dates	Male	Female	*n*	Dates	Male	Female	*n*
May 1–10	54.4	45.6	57	May 26–31	56.4	43.6	289
11–20	48.2	51.8	56	June 1–5	65.3	34.7	193
21–25	51.8	48.2	141	6–10	78.3	21.7	143
Jun 21–25	52.6	47.4	190	11–15	69.5	30.5	141
26–30	50.0	50.0	202	16–20	65.5	34.5	220
Jul 11–20	42.1	57.9	19	Jul 1–5	61.8	38.2	21
21–31	44.4	55.6	18	6–10	65.5	34.5	29
Mean[a]	49.1	50.9	(683)	Mean[b]	66.0	34.0	(1,070)
SE	1.5	1.5			2.4	2.4	

	Male	Female	*n*
Grand mean[c]	57.6	42.4	(1,753)
Standard error	10.0	10.0	

[a] Probability that the two means are not different is 0.45 by two-tailed *t*-test.
[b] Probability that the two means are not different is <0.001 by two-tailed *t*-test.
[c] Probability that the two means are not different is <0.003 by two-tailed *t*-test.

TABLE 4. Summary by sex of Cassin's Finches captured and recaptured at Camp Creek 1973–1979.

No. of captures	Males	Females	Both	Percent male
1[a]	211	145	356	59.3
2	101	64	165	61.2
3–4	85	67	152	55.9
5–19	53	31	84	63.1
All	450	307	757	59.4
Captures/bird[b]	2.36	2.27	2.32	60.4[e]
Percent captured two or more times	53.1	52.7	53.0	—
Captures/bird[c]	3.56	3.40	3.49	60.7[e]
Percent captured in two or more years	29.3	26.1	28.0	—
Captures/bird[d]	4.22	4.16	4.20	62.6[e]

[a] Captured and banded, but not recaptured.
[b] Mean of 1–19 captures of the same individuals.
[c] Mean of 2–19 captures of the same individuals.
[d] Mean of 2–19 captures of the same individuals encountered in two or more years.
[e] Of total captures in that category.

summer (Fig. 9), since females were captured less frequently during periods of incubation or brooding (compare Figs. 6 and 9). During incubation and early brooding, the male feeds the female on or near the nest (Samson 1976a). In mist net captures during periods when females were not incubating or brooding (Table 3), however, the mean male/female ratio was 49/51 ($\chi^2 = 1.66$, 6 df, $P = 0.95$). When most females were incubating or brooding, the sex ratio varied considerably around a central tendency of 66/34 ($\chi^2 = 22.09$, 6 df, $P = 0.001$). The lesser susceptibility of females to capture is also seen in their less frequent recapture (Table 4). Whereas we captured 450 individual male finches in seven years at Camp Creek, we captured only 307 individual females (ratio 59:41, males to females). The difference of 143 fewer individual females captured in those seven seasons is due probably, in the main, to the females' nearly continuous attachment to the nest. Samson (1976a) found an even greater male/female imbalance in captures (520/109) in his Utah study, and attributed much of it to relative inactivity of females during nesting and early brooding.

At Camp Creek, the pooled mean male/female ratio for 14 periods, from May to July (1973–1979 combined), was 58/42 (Table 3); the mean by years (1974–1979) was 61/39 (Table 5); and the actual male/female ratio for the 757 individual adults captured was 59/41 (Table 4). It is not worthwhile to discuss these full-season male/female ratios, usually in the order of 60/40, because our sample periods varied substantially among years (e.g., no field work in May in two years, and beginning on 24 May, 15 April, 15 May, 24 May, and 22 May in the other five years). That there may have been a surplus of males in the greater Hart Mountain population, however, is suggested by our May and June, 1982, observations when we searched for and found small numbers of Cassin's Finches, usually males, at locations on Hart Mountain other than Blue Sky. Although some of these were probably members of nesting pairs, most, by virtue of their observed mobility, seemed unmated.

TABLE 5. Numbers of Cassin's Finches in each of six sex and age groups at Camp Creek by years 1974–1979.

Year	Males			Females		
	SY	ASY	AHY	SY	ASY	AHY
1974	16	25	41	—	—	30
1975	49	48	97	—	—	54
1976	32	91	123	37	51	93[a]
1977	44	73	117	36	46	82
1978	68	111	179	51	56	107
1979	68	89	157	35	44	81[b]
1974–1979	277	437	714	—	—	447
1976–1979	212	364	576	159	197	363[c]

[a] Includes five females known only as AHY.
[b] Includes two females known only as AHY.
[c] Includes seven females known only as AHY.

AGE RATIO

Because the nesting schedules of SY and ASY females were nearly alike (Fig. 6), any distortion in female age ratios, based on mist net captures related to time, should be small. Numbers of females in each annual sample, however, were substantially smaller than numbers of males (Table 5), even though the sexes were present in the Camp Creek population in approximately the same numbers (see section on Sex Ratio).

In the Camp Creek population, ASY males outnumbered SY males except in 1975 (Table 5). Proportionate numbers of SY males encountered were highest in 1975 (102%) and 1979 (76%), the years with June snow storms. This suggests that, in those two stressful seasons, the SY males were more mobile and were thus captured in proportionately greater numbers than during Junes without snow storms. The lowest proportion of SY males was in 1976

TABLE 6. Simultaneous captures of one male and one female Cassin's Finch (of Cassin's Finches, those two only), a probable pair, in mist nets in late May and June, 1976–1979.

Couplets	Number of simultaneous captures				
	1976	1977	1978	1979	Total
ASY M & ASY F	15	2	12	8	37
ASY M & SY F	8	1	8	4	21
SY M & ASY F	3	1	4	2	10
SY M & SY F	6	7	14	8	35
Total	32	11	38	22	103

(35%), perhaps reflecting the low productivity in 1975 due to the June storms. There was, however, no proportionately smaller number of SY females in 1976. This could be because of a higher than usual mortality of nesting females in the June, 1975 snow storms coupled with greater recruitment of SY females in 1976 (see next paragraph). Because our effort was more intense in 1976 (especially in May) than in any other year, we probably did a more thorough job of catching females. ASY females made up 55.3% of all known SY + ASY (N = 356) females in 1976–1979 and outnumbered SY females in every year (Table 5).

Because of reproductive failure at Camp Creek in June of 1975, proportionately fewer SY finches were present in 1976 (31.9%) than in 1977, 1978, and 1979 (40.2%, 41.6%, and 43.3%, respectively). Capture of 69 SY finches (recruits) in 1976, however, was significant. It seems likely that some, perhaps most, of these recruits came from second broods in 1975 at Blue Sky and from scattered breeding pairs on other parts of Hart Mountain. Better survival of male than female Cassin's Finches is suggested (Table 5) by the greater proportion of ASY males (364/576 = 63.2) to SY males (212/576 = 36.8) than of ASY females (197/356 = 55.3) to SY females (159/356 = 44.7) for the years 1976–1979 (χ^2 on actual data = 5.31, 1 df, P = 0.02). Better survival of males is also suggested by the increase in the annual encounter sex ratio of males from 57:43 :: male : female in SY finches (N = 371) to 65:35 :: male : female in ASY finches (N = 561) for the years 1976–1979 (χ^2 = 5.32, 1 df, P = 0.02). These ratios must be interpreted cautiously, however, because they are distorted in favor of males by our failure to capture as many females while they were incubating and brooding (see section on Sex Ratio). We have insufficient data on HY finches to extend a probable trend back toward a likely 50:50 sex ratio at ovulation.

Whereas Samson (1976a) found little breeding by SY males in his Utah population, we have evidence that SY males bred regularly at Hart Mountain (Table 6). There, among 103 captures (1976–1979) of heterosexual pairs (two Cassin's Finches together in the same net at the same time, usually within a meter of each other) 56% involved ASY males and 44% SY males, this in a male population 63% ASY and 37% SY (N = 576). SY males were caught simultaneously with females more frequently than would be expected from their proportion of the male population. The difference between ASY and SY males is not significant, however (χ^2 = 1.76, 1 df, P = 0.18). The 35 "pairs" including SY males and SY females comprised 34% of all pairs netted and 78% of all pairs that involved SY males. Our records indicate that these SY males, as well as ASY males that were caught simultaneously with females, were nearly always accompanied by females who were about to lay, who were laying, or who had recently laid eggs.

POPULATION SIZE AND STABILITY

Because the pine grove at Blue Sky is, like an island, isolated in an expanse of sagebrush (Fig. 1), the Cassin's Finches breeding there constitute an essentially closed population. It con-

TABLE 7. Estimates of Cassin's Finch recruits, transients, and residents by sex at Camp Creek 1975–1978.

Year	New captures this year 1	New captures surviving next year 2	Estimate of recruits (col. 2 × 1/S) 3	Estimate of transients (col. 1 − col. 3) 4	Known survivors from previous years 5	Estimate of residents (col. 3 + col. 5) 6
Males			(Col. 2 × 1.639)[a]			
1975	68	35	57	11	24	81
1976	66	22	36	30	51	87
1977	56	24	39	17	47	86
1978	116	26	43	73	57	100
Females			(Col. 2 × 1.721)[b]			
1975	43	16	28	15	11	39
1976	69	21	36	33	23	59
1977	48	16	28	20	34	62
1978	69	17	29	40	38	67

[a] This year's new captures known surviving next year (Col. 2) multiplied by the reciprocal of AHY male annual survival rate (1/0.610 = 1.639).
[b] This year's new captures known surviving next year (Col. 2) multiplied by the reciprocal of AHY female annual survival rate (1/0.581 = 1.721).

TABLE 8. Summary of Schnabel population estimates of Cassin's Finches at Camp Creek, excluding estimated transients 1975–1978.

Year	Sample days	Captures	Captures and recaptures	Estimated numbers of transients	Captures less estimated transients	Caps and recaps less estimated transients	Population estimates excluding transients ±SE
	(1)	(2)	(3)	(4)	(5)	(6)	(7)
Males							
1975	34	81	117	11	70	106	112 ± 12
1976	54	103	204	30	73	174	76 ± 2
1977	29	83	118	17	66	101	91 ± 8
1978	32	155	265	73	82	192	98 ± 4
1979	47	155	233	—	—	—	—
Females							
1975	34	46	72	15	31	57	39 ± 4
1976	54	83	156	33	50	123	49 ± 1
1977	29	70	108	20	50	88	56 ± 2
1978	32	95	167	40	55	127	60 ± 3
1979	47	79	110	—	—	—	—

forms reasonably well with the major assumptions of the Schnabel method for estimating population size by capture and recapture of marked individuals (Schnabel 1938, Seber 1973, Brower and Zar 1977, Otis et al. 1978, Nichols et al. 1981, Pollock 1981). There are at least four sources of bias in our estimates by this method: (1) the tendency of birds to avoid nets after initial capture or even after striking the net without being captured; (2) incomplete temporal and spatial coverage of the study area (Because this was empirically obvious in 1973 and 1974, we have not included those two years in these estimates.); (3) reduced mobility of females, relative to males, during incubation and early brooding (Table 3, Fig. 9; we have made separate population estimates for females and males.); and, (4) because our population estimates are made on only a portion of the Blue Sky population—that portion which nests on Camp Creek—transients from other portions of Blue Sky occasionally visit Camp Creek. These transients seem to include at least (a) non-territorial females, (b) unmated surplus males, and (c) foragers nesting in nearby portions of the Blue Sky grove. These transients inflate estimates of the breeding population on Camp Creek. We have estimated the number of transients (Table 7) for each of the years 1975 to 1978. We may include all captures or we may exclude estimated transients in making the Schnabel population estimates for those four years.

By removing transients from the Schnabel procedure, we obtained estimates of each year's resident population (Table 8). In the calculation, we randomly subtracted those transients, one or more at a time from daily capture totals, as such subtractions could be absorbed. We used these lowered daily captures and recaptures (totaled by season in columns 5 and 6) to estimate the numbers of breeders encountered (column 7). This yielded estimates of from 76 to 112 resident males (mean = 94 ± 13) and 39 to 60 resident females (mean = 51 ± 8) for the years 1975 to 1978. Because of female attachment to the immediate vicinity of the nest during incubation and brooding (see section on Sex Ratio), we regard the population estimate for females as too low. The mean number of 94 males, however, compares well with several other estimators (see beyond).

To add credibility to estimates by the Schnabel method, we counted the number of known male survivors at Camp Creek in each of 1975 to 1978 (Table 7, column 5). To these we added the estimated numbers of male recruits (column 3) for each year. This very conservative method yielded a mean of 88 ± 7 males (from column 6), only six males fewer than by the Schnabel method.

In contrast, application of the Schnabel population estimator to all captures and recaptures (Table 8, columns 2 and 3), thus **including transients**, for the same four years (1975–1978) yields a mean of 150 ± 30 males (range 123–201) and 96 ± 21 females (range 66–124). The substantially larger numbers of males thus estimated certainly reflects numbers present in the study area during May and June of those years. This clearly includes transients, however, and is not a measure of the breeding population.

Accepting the mean of the Schnabel estimates of 94 ± 13 breeding males at Camp Creek as realistic, and assuming monogamy (Samson 1976a), our best conservative estimate is that the breeding population varied only moderately around a mean of 94 pairs. In its stability in numbers and in the high degree of breeding site faithfulness (see beyond), the Hart Mountain population of Cassin's

Finches differs conspicuously from the large year-to-year variations of breeding populations of Cassin's Finches in northern Utah (Samson 1976a). Samson concluded (p. 495) that in extensive tracts of apparently suitable habitat, Cassin's Finches "nested in colonies and habitat did not appear limiting for colony size or location." He found, as did Farner (1952) at Crater Lake in Oregon, substantial fluctuations in finch numbers in specific areas from summer to summer. Because the colonies that Samson (1976a) studied nested in different areas in successive years, he obtained little information on possible constancy of colony membership from year to year. He documented breeding area fidelity in two successive years among only 18 of 231 ASY males and one of 186 SY males, but found no case among 104 banded females. He concluded that breeding-site fidelity was greater in ASY males than in SY males or in females. This very low rate of breeding site fidelity is in sharp contrast to the situation that we found on Hart Mountain.

Also in contrast to Samson's findings in extensive stands of timber, Balph (1978) working with a nearby population in suburban Logan, Utah, found that some colonies of Cassin's Finches showed somewhat greater year-to-year stability than in Samson's study area. In a breeding population that apparently became established in Logan in 1975, she found that nearly half of 35 ASY and SY males and females that were banded in the summer of 1976 returned for the 1977 nesting season.

We believe that the Camp Creek breeding population saturated the suitable portions of the study area. About 4.5 ha of the 5.4 ha of riparian habitat was suitable nesting habitat for Cassin's Finches, i.e., with pines of suitable size and number. The suitable habitat was essentially continuous and, for modeling purposes, it approximated a riparian strip about 1,000 m long and about 45 m wide. The number of pairs (and, therefore, presumably nests) on this 4.5 ha could have been as low as 88, but probably usually numbered about 100 or even 120 in some years. If we assume a 5-m average inset from the edge of the canopy and evenly spaced nests, mean distances between nests would vary from 25 m for 90 nests to 21 m for 120 nests. Such inter-nest distances compare favorably with those reported by Samson (1976a). He found that male Cassin's Finches in Utah defended a zone around the female with radii varying from about 5 to 15 m in the early part of the nesting cycle. These defense radii perhaps accounted for the means of 22 to 40 m that he found between nests in five colonies consisting of 6, 8, 9, 14, and 20 nests.

Thus, the Camp Creek population probably approached the maximum possible during 1975–1978, with a density of 20 to 25 nests per hectare. Such a high density is likely only when (1) the breeding habitat is insular and sufficiently remote to inhibit long-distance postbreeding dispersal; (2) the insular habitat is conifer-dominated but otherwise diverse and providing optimal breeding conditions; (3) the habitat is linear—ideally riparian in an otherwise shrubsteppe universe; and (4) the insular habitat is relatively small, certainly less than 100 ha.

The breeding assemblage on Camp Creek contrasts with Samson's (1976a, p. 495) findings in the generally unlimited habitat on his study area in Utah, where male behavior did "not limit total breeding numbers . . ." and did "not appear limiting for colony size or location." Male defense of a zone around the female during nest building, as described by Samson (1976a), is apparently responsible for limiting breeding numbers at Camp Creek, and thus colony size, because of the limited insular nature of the habitat.

Our estimates of breeding Cassin's Finches on Camp Creek extrapolate to from 2,000 pairs to perhaps as many as 2,500 pairs per square kilometer. This compares favorably with breeding densities of all species combined in some other structurally similar western linear wooded habitats in otherwise open country. Gaines (1974) found 1,016 males (27 species) and 1,140 males (32 species) per square kilometer in "clumped cottonwood-willow" riparian situations in the Sacramento Valley of California. R. H. Yahner (in Van Velzen 1980) reported from 2,780 to 9,799 territorial males or females (six to 11 species) per square kilometer in mature three- to eight-row shelter belts in Minnesota. In fact, the breeding density for the more than 35 breeding species on the Camp Creek study area exceeded 9,000 pairs per square kilometer during the years of our study (Mewaldt, unpubl. data). Such breeding densities are possible because of the linear nature of such insular riparian strips or shelter belts where some of the breeding species are dependent on adjacent or nearby habitats for food (e.g., Carothers and Johnson 1974). That such high numbers censused on relatively small plots are inversely related to increasing plot size and related to the shape of the plot was demonstrated by Verner (1981). Martin (1981) found that the breeding density of passerines nesting in shelter belts of eastern South Dakota depended not on the land area in the shelter belt, but on the adjacent land where most species foraged. We found that Cassin's Finches at Camp Creek foraged mostly in the shrubsteppe habitat on either side of the riparian study area.

TABLE 9. Mean (and median) distances between year-to-year ranging centers in Cassin's Finches at Camp Creek.

Pair of seasons	Males				Females				Probability means are not different (2-tailed *t*)
	Mean ± SE (m)	Range (m)	*n*	(Med) (m)	Mean ± SE (m)	Range (m)	*n*	(Med) (m)	
1st to 2nd	153 ± 10.0	0–525	146	(125)	118 ± 9.8	0–490	99	(100)	0.013
1st to 3rd	168 ± 13.9	0–460	67	(155)	140 ± 19.3	0–490	40	(108)	0.240
1st to 4th	158 ± 17.1	45–400	32	(145)	131 ± 28.1	0–480	18	(95)	0.400
1st to 5th	169 ± 30.4	30–390	11	(135)	93 ± 13.1	50–150	6	(90)	0.060
Total	158 ± 7.2	0–525	256	(136)	124 ± 8.3	0–490	163	(101)	0.0018

We therefore agree with Samson (1976a) that Cassin's Finches be considered semi-colonial in breeding habit.

BREEDING SITE FAITHFULNESS

Many, perhaps most, species of birds tend to breed where they have bred before. If they are migratory, they tend to return to that place to nest in each following breeding season (Nice 1937, Farner 1945, Lack 1954). Among the relatively few species of passerine birds reported to shift their breeding sites from year to year are several of the cardueline finches, including the Red Crossbill (*Loxia curvirostra*), Pine Siskin (*Carduelis pinus*), Lawrence's Goldfinch (*C. lawrencei*) and the Cassin's Finch (Austin 1968, Wittenberger 1979). In the Bear River Mountains of northeastern Utah, Samson (1976a) found Cassin's Finches to be nomadic as breeders and in winter. He proposed that breeding locale depends at least partially on the availability of food. Balph (1978) suggested that local food abundance in a semi-urban portion of Logan, Utah, may have accounted for the presence of individual finches in the same general locality in successive breeding seasons.

Cassin's Finches at Hart Mountain were not nomadic as breeders. They returned each spring to the grove of ponderosa pines at Camp Creek with a faithfulness that approached 100% of surviving breeders. That is, the number returning each season closely approximated the number we expected to survive from year to year (see beyond). Although the quantities of specific foods, especially nuts of the ponderosa pine, tended to fluctuate from year to year, the overall food availability in and adjacent to the Camp Creek riparian strip appeared to be consistently good. It is apparently reliable food plus the isolation and comparatively small size of the Blue Sky pine grove which entrain this breeding site faithfulness.

For each Cassin's Finch present on the study area for more than one season, we plotted its ranging center for each season on a scale map of Camp Creek. This ranging center was the same as the net site of a single capture in a season, or the mid-point of two or more captures in that season. Distances between these ranging centers were determined for pairs of breeding seasons one year apart, as well as pairs of seasons two, three, and four years apart (Table 9). Note here that the tendency for female and male finches to return close to previous breeding sites was undiminished for pairs of years up to at least four. In each category, females returned closer to their previous year's ranging center than did males. This contrasts with the more common finding in passerines that males show greater attachment to a prior breeding site than females (e.g., Harvey et al. 1979). It also contrasts with Stjernberg's (1979) finding in the Common Rosefinch that 23 males nested a mean distance of 320 m and 37 females 570 m from their previous year's nest.

Male Cassin's Finches, rather than defend a land area or a nest, defend a zone around their mate, and then only during nest-site selection, nest building, and egg-laying (Samson 1976a). This male behavior is common among both Old and New World cardueline finches (Weston 1947, French 1959, Thompson 1960, Johnson 1965, Clement 1968, and Wittenberger 1979). Thus, it appears that female Cassin's Finches have a greater attachment than males to a specific breeding site.

Although our data cannot be used to confirm specific pair bonds from season to season, the high degree of breeding site faithfulness in both sexes suggests that the pair bond must be durable. Among the alternative mating systems described by Wittenberger (1979), the Hart Mountain Cassin's Finches appear to fit, or at least approach, his "Female-Defense, Permanent Monogamy" classification. Either the pair bonds are maintained during the 9+ months away from the Camp Creek breeding area or they are more readily, than by chance, re-established upon return. Our findings in this section are inferential and could be tested with direct observations of individually marked birds over a period of years.

RANGING PATTERNS

For adult Cassin's Finches that were known to be present at Camp Creek two or more years

TABLE 10. Single-season ranging, as revealed by two or more captures per season of Cassin's Finches present at Camp Creek in two or more seasons.

Captures per season	Males			Females			Probability means are not significantly different (*t*-test)
	Mean ± SE (m)	Range (m)	*n*	Mean ± SE (m)	Range (m)	*n*	
2	112 ± 11.9	0–350	78	81 ± 16.0	0–520	47	0.130
3	192 ± 22.4	0–560	45	106 ± 19.3	0–250	18	0.005
4	148 ± 26.0	0–330	13	74 ± 25.8	0–200	8	0.066
5+	157 ± 40.8	0–340	7	85 ± 33.1	0–220	6	0.240
2 to 5+	143 ± 10.4	0–560	143	87 ± 11.0	0–520	79	0.001

and with two or more captures in at least one of those years, we plotted capture sites on individual work maps of the study area. For each season that a finch was captured twice or more, we measured the greatest dimension of its range of activity, as determined by its captures, in that season. Our capture records are for locations only within the canopy of the Camp Creek riparian habitat (Fig. 3). We know from daily casual observation that the finches spent substantial time foraging and in social activities in the adjacent sagebrush steppe and scattered junipers. Thus, our linear measures of the finches' known ranging within the canopy provide imperfect indices to their daily movements and do not warrant more than direct linear comparisons (Table 10).

Within the canopy of pines and aspens on Camp Creek, males ranged more widely than females (Table 10). Because mated males defend a zone around females as they moved about, especially in the final stages of nest construction (Samson 1976a), they should be intercepted by nets more widely placed than the female about which they range. Once incubation by the female began, however, Samson found no further evidence of male defense of a zone around the female or of an area around the nest. The male was then free to range more widely while he foraged to bring food to the female during incubation and in the early stages of brooding.

ANNUAL ADULT SURVIVAL

Most estimates of survival by capture/recapture methods assume (Seber 1973, Johnson 1974, Cavé 1977) that: (1) death is random in time, so that variable dates of recapture do not bias the results; (2) the probability of death from factors other than senescence is independent of age beyond an arbitrary date (usually 1 January) after birth, so that variations of age ratios among samples do not bias the results; (3) breeding site faithfulness is perfect if a single sampling site is used (i.e., all survivors return to the sampling site); (4) all survivors are recaptured or known by recapture in a later year to have been alive in an earlier year; and (5) there is no time-related loss of bands, generally due to wear.

Assumption 1 (that death is random in time) is obviated by sampling in the same brief period (May to July) each year, as in our program at Camp Creek.

We cannot directly test assumption 2 (age-independent mortality) because we captured only 15 HY finches at Camp Creek during the entire 1973–1979 period. Thus, we are unable to make any direct judgement of philopatry. The HY birds and their parents left Camp Creek as the young fledged. Adult males with an estimated 36% annual mortality, however, have an average life expectancy of 2.3 years (calculation after Soikkeli 1970). Because several individuals known to have been six or seven years old appeared to be in good health, they apparently have typical passerine life spans. Camp Creek Cassin's Finches thus appear to fit the common pattern described by Farner (1955) for songbirds of the mid- and high north latitudes and, for demographic purposes, their mortality (beyond their first January 1st) is probably independent of age.

The validity of assumption 3 (perfect breeding site faithfulness) is indeterminate for our samples, as in all other investigations using methods such as ours. Nevertheless, we have already presented evidence that breeding site tenacity is high in the Cassin's Finches at Camp Creek. This encourages us to believe that violation of assumption 3 is minor, even if indeterminate and perhaps not negligible.

Assumption 4, that all returning survivors are detected, is not met in our data set. Our data are of sufficient quality, however, to estimate the full magnitude of return by using the "t" factor in Salvadori's computer program (The Evaluation of the Maximum Likelihood of S by a Newton-Raphson Method) for determination of annual survival rate as in Roberts (1971). We caution, however, that Salvadori's program should be used for complete sets of data only and should not be applied to incomplete sets of data, as was done by Roberts in his 1971 paper. Because our data on Cassin's Finch cover a span of only six years,

TABLE 11. Annual survival rates of Cassin's Finches that were banded and recovered at Camp Creek 1973–1979 (after Roberts 1971, but see text for details and modifications).

Sex and age group	Annual survival rate (S) ± SE	Bird recovery years (*n*)	
		Actual	Plus extrapolated
AHY males	0.641 ± 0.021	191	271
Sub-sets			
ASY[a]	0.702 ± 0.020	128	220
SY[b]	0.573 ± 0.037	98	124
SY[c]	0.351	72/205[d]	—
AHY females	0.602 ± 0.027	117	161
Sub-sets			
ASY[a]	0.588 ± 0.045	56	74
SY[b]	0.502 ± 0.069	44	56
SY[c]	0.306	37/121[d]	—

[a] Included in sub-set when known to be at least two years old, thus includes some banded as SY birds, but only beginning with the season when each became an ASY bird.
[b] Includes only birds one year old on first encounter.
[c] Includes known one-year survival of all yearlings banded at Camp Creek, thus includes transients as well as residents.
[d] Finches known to survive at least one year, divided by the number banded as SY birds.

and are thus incomplete, we determined and applied an extrapolation factor to mimic a full data set. (We will provide detail on determination of the extrapolation factor and its application upon request to the senior author.)

Assumption 5 (band loss from wear) was met. The amount of wear remaining in the bands on finches banded five and six years earlier was sufficient for at least three or four more years. Thus, the useful life of the bands that we used exceeded the duration of the project.

There were two related biases which we have been unable to measure: (1) lowered capture, especially in a given season, because of escape upon initial encounter with a net, and (2) lowered recapture, especially in a given season, because of a probable tendency toward net avoidance following initial capture and handling.

Cassin's Finch males lived longer than females in the relatively stable Camp Creek population (Table 11). This finding is consistent with the increasing ratio of males to females with increasing age, noted in our earlier section on sex ratio. Greater mortality of SY finches is unlikely to account for most of their apparent lower survivorship when compared (Table 11) to that of ASY finches. Some yearlings may have occupied less favorable nest sites at Camp Creek and moved to other parts of the pine grove for their second breeding season.

We found substantial year-to-year variation in survivorship of the Camp Creek population of Cassin's Finches (Table 12). Conditions were comparatively advantageous to survival in the winters of 1974–1975, 1975–1976, and 1977–1978. Conditions were apparently less favorable in the winters of 1976–1977 and 1978–1979. Because we do not know where Hart Mountain Cassin's Finches spend the winter, we will not speculate on the proximate factors accounting for these variations. Because survivorship figures, in the several age and sex groups, vary in a parallel fashion, it is likely that the Hart Mountain population does not fragment into age or sex groupings over the winter months.

TABLE 12. Known survival of Cassin's Finches from year to year by age and sex.

Year class to following year	ASY males		ASY females		SY males	SY females
	Incl. year of banding	Excl.[a] year of banding	Incl. year of banding	Excl. year of banding		
1973–1974	0.667	—	—	—	0.000	—
(KS/*n*)[b]	(2/3)	—	—	—	(0/1)	—
1974–1975	0.625	0.500	1.000	—	0.533	—
(KS/*n*)	(15/24)	(1/2)	(1/1)	—	(8/15)	—
1975–1976	0.622	0.733	0.636	0.000	0.500	—
(KS/*n*)	(28/45)	(11/15)	(7/11)	(0/1)	(24/48)	—
1976–1977	0.430	0.571	0.367	0.429	0.290	0.314
(KS/*n*)	(37/86)	(16/28)	(18/49)	(3/7)	(9/31)	(11/35)
1977–1978	0.617	0.676	0.578	0.667	0.444	0.286
(KS/*n*)	(37/60)	(25/37)	(26/45)	(12/18)	(20/45)	(10/35)
1978–1979	0.406	0.514	0.296	0.462	0.169	0.314
(KS/*n*)	(43/106)	(19/37)	(16/54)	(12/26)	(11/65)	(16/51)
1973–1978 to 1974–1979[c]	0.500	0.605	0.425	0.519	0.351	0.306
(KS/*n*)	(162/324)	(72/119)	(68/160)	(27/72)	(72/205)	(37/121)

[a] By excluding finches in their year of banding, most (hopefully all) transients are excluded from the sample.
[b] Number known surviving (KS) second year divided by the number known alive (*n*) the first year.
[c] Summation of annual data.

CONCLUSIONS

The population of Cassin's Finches, essentially a colony, summering at Camp Creek in the pine grove at Blue Sky on Hart Mountain is unusual, perhaps unique. Instead of conforming to the usual nomadic pattern described for the species (Samson 1976a), the colony returned each spring and nested in the same finite area. From 1974 to 1979, individual finches returned and occupied the same few trees each season. Because rate of return and survival rate are interlocked, and because survival rates (Table 11) are within normal limits for a passerine, it is reasonable to conclude that returning finches approached 100% of those surviving from one year to the next. It is especially noteworthy (Table 9) that the precision of return to site by females, and by males, was as good the second, third, and fourth years, as it was from year to year.

Male Cassin's Finches showed less precise site faithfulness than females (Table 9). The male, rather than select and defend a typical passerine territory, defends a moving zone around his mate during nest building and egg-laying (Samson 1976a). In this scenario, the nest site selected by the female becomes the center of a temporary territory defended by her mate during periods when she is at the nest. Because the nesting activities were nearly synchronous (Figs. 5 and 6), the zone defense activities of the males during nest building apparently spaced nests so that there were no more than about 25 nests per hectare.

Our finding that site faithfulness was almost as high in males as in females strongly suggests that the pair bond persisted from year to year. It is possible the pair bond was renewed each year upon reassembly of the colony at Camp Creek. It seems to us more likely, however, that further investigation will show that the colony-flock remains essentially intact through the winter months and that pair bonds also persist.

ACKNOWLEDGMENTS

We thank the many people who assisted in our field work on Hart Mountain, including especially N. Cobb, H. L. Cogswell, P. Delevoryas, T. Hart, S. Kaiser, R. King, S. A. Mahoney, C. S. Maxwell, F. L. Mewaldt, W. T. Mewaldt, T. Pogson, M. Rigney, J. Shiomoto, D. Starks, and R. Webb. Over the years of the study, Hart Mountain National Wildlife Refuge personnel, and frequently their spouses, were supportive, including especially R. Blacker, W. D. Carter, T. Gladwin, J. Good, M. R. Kaschke, E. Kisler, R. Paxton, J. Rieger, J. Sarvis, P. Tubbs, and K. W. Voget. We received the full cooperation of the Bird Banding Laboratory of the U.S. Fish and Wildlife Service, Laurel, Maryland. R. Johnson adapted a computer program written in FORTRAN to MBASIC. J. Verner, C. J. Ralph, and F. B. Samson reviewed the manuscript and made many helpful suggestions. This investigation was supported in part by the Avian Biology Laboratory, San Jose State University, and by National Science Foundation grants to King, including DEB 7909806.

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Received 20 September 1984. Final acceptance 22 June 1985.

The Condor 87:510

RECENT PUBLICATIONS

Roberts' birds of southern Africa.—Gordon Lindsay Maclean. 1985. Trustees of the John Voelcker Bird Book Fund, Cape Town. 848 p. No price given. This is the fifth edition of a well-known work, first published in 1940 and last revised in 1978. For the nearly 900 species of birds in Africa roughly south of latitude 15°S, it gives their size, identification, voice, distribution, status, habitat, habits, food, and breeding. In addition to incorporating much new information, this edition features many new color plates (by Kenneth Newman and Geoff Lockwood) that show all the species, new enlarged distribution maps in color, sonograms of most vocalizations, revised and corrected bird names, dichotomous keys for identification, and abbreviated references. This is not a field guide (though some thorough birders may put it in their packs) but a comprehensive and authoritative handbook.

Field guide to the birds of southern Africa.—Ian Sinclair. 1984. C. Struik, Cape Town. 361 p. $17.95 hardcover, $13.00 softcover. Source: S.A. Reader's Choice, P.O. Box 1144, Cape Town 8000, Republic of South Africa. This book covers the same geographic region and virtually the same list of birds as that by Maclean. It is designed, however, as an identification manual, so the species accounts are confined to field marks, habitat, and voice. Although these entries are much briefer than Maclean's, they seem to characterize the birds and distinguish between confusing species more clearly. Distribution maps are provided for every species; although smaller and less detailed than Maclean's, they are still easily legible and similar in pattern. All of the birds are shown in color plates facing the text and maps; photographs are used for the great majority of species, drawings for the rest. While it is impressive that so many photographs could be found, this mode of illustration results in uneven treatment and lack of pictures of females or immatures. Birders in southern Africa who want a handy, quick field guide should favor this book, while those who want to know more about the birds will prefer Maclean's. Indices.