PTERYLOSIS AND MOLT IN CASSIN'S FINCH

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Migratory birds which breed in the strongly seasonal high montane environment of middle and high latitudes must carefully integrate their limited time and energy to successfully reproduce, molt, and prepare for fall migration while environmental conditions are favorable. Generally these events are temporally segregated on the breeding area although some populations, including *Carpodacus e. erythrinus*, delay the postnuptial molt until arrival on the winter area (Stresemann and Stresemann 1966), thereby separating these energy-demanding processes.

The nomadism of Cassin's Finch (*Carpodacus cassinii*) and inaccessibility of montane breeding populations to investigators presumably have precluded intensive field studies of this species. The few details known are from observations by resident naturalists or by those engaged in faunistic surveys (Ridgway 1877, Henshaw 1879, Grinnell 1908, Taylor 1912, Bailey 1928 and others). From the summer of 1971 through early summer 1974, I studied Cassin's Finches in an environment where conditions for them are favorable only from late May until early October. I report here on their phasing of breeding, molt, and fall departure, and on details of pterylosis and molt.

Cassin's Finches breed in high mountain forests from southern British Columbia, Alberta, and Manitoba to northern Arizona (A.O.U. 1957). Nesting locations may change from year to year, apparently influenced by availability of food (Bailey and Niedrach 1965). The colonial nesting in Cassin's Finch (Lack 1968) may enhance the exploitation of a varying summer food supply (Samson 1976). In late summer, flocks move to adjacent lower elevations and winter from southern British Columbia to the highlands of Mexico (Orr 1968) wherever an abundance of food exists (Bailey and Niedrach 1965, Buckley 1973). Congregations as large as 5,000 have been reported in winter (Chapin 1958).

MATERIALS AND METHODS

I examined 58 free-living finches in postnuptial molt in 1971, 105 in 1972, and 57 in 1973. Birds were mist-netted from late spring through summer at the Beaver Mountain Ski Area, Cache National Forest, 45 km NE of Logan, Utah, at an elevation of 2250 m. Every bird was given a USFWS band and 290 of them were also marked with unique combinations of celluloid colored leg bands permitting individual recognition without recapture. I measured the chord of the longest unflattened wing feather to the nearest 0.1 mm with a Helios vernier caliper. Plumage color was described for all birds captured, and presence or absence of incubation patch noted. In addition, 12 birds collected at random in 1971, 17 in 1972, and 6 in 1973 are included in the analysis. These birds were collected to verify sex ratios in non-breeding flocks and of those remaining at Beaver Mountain each summer or early fall after the departure of other flocks of Cassin's Finch. In each instance the flocks consisted entirely of yearling males. Four nearly distinct finch populations were studied since only 6 of 71 banded in 1971 returned in 1972, 6 of 451 banded in 1972 were recaptured or seen in 1973, and none of 108 banded in 1973 were noted in 1974.

I recorded the extent of molt by assigning a numerical score to each individual following a system similar to that of Newton (1966). Remiges and rectrices received a 0 for an old feather, 1 for a missing feather, 2 for a small pin to ¼ grown, 3 if ¼ to ½ grown, 4 if ½ to ¾ grown, and 5 if ¾ to full length. A sum of 0 for a bird indicates that molt of the remiges had not started, whereas a sum of 45 indicates that it was complete. Scores were recorded only for the right side and for secondaries or rectrices on only 47 birds of the 255 examined. The timing and duration of primary molt were estimated by regression analysis (Hurst 1972). Limitations on the use of linear regression for analysis of molt were discussed by Evans (1966), Newton (1966), and Niles (1972). Numerical scores were not applied to body molt.

Three adult males, two females, and two yearling males collected in 1973 were used for the study of pterylosis. These birds were prepared as dried flat skins to study patterns of calami projecting from the inner skin. In spring 1974, 13 nestlings were collected 4 km SE of Beaver Mountain, injected with formalin, and preserved in alcohol to determine distribution and number of natal down feathers.

All females and first-year males have a streaked gray-brown plumage, but females can be distinguished by winglength and possession of a brood patch during the breeding season (Samson 1974). Older males are mainly reddish-pink and are easily identifiable.

RESULTS AND DISCUSSION

NATAL DOWN

Natal down in Cassin's Finch is sooty-gray compared to the pure white reported for eight other cardueline finches (Wetherbee 1957). The number of down feathers per nestling averaged 140.5 (R = 134–158; n = 11), slightly exceeding the mean of 136 for 51 species of Fringillidae examined by Wetherbee.

The capital tract bears a row of 3 to 7 down feathers dorsal to both eyes. Two additional lines of 9 to 12 feathers extend from

The Condor 78:505–511, 1976

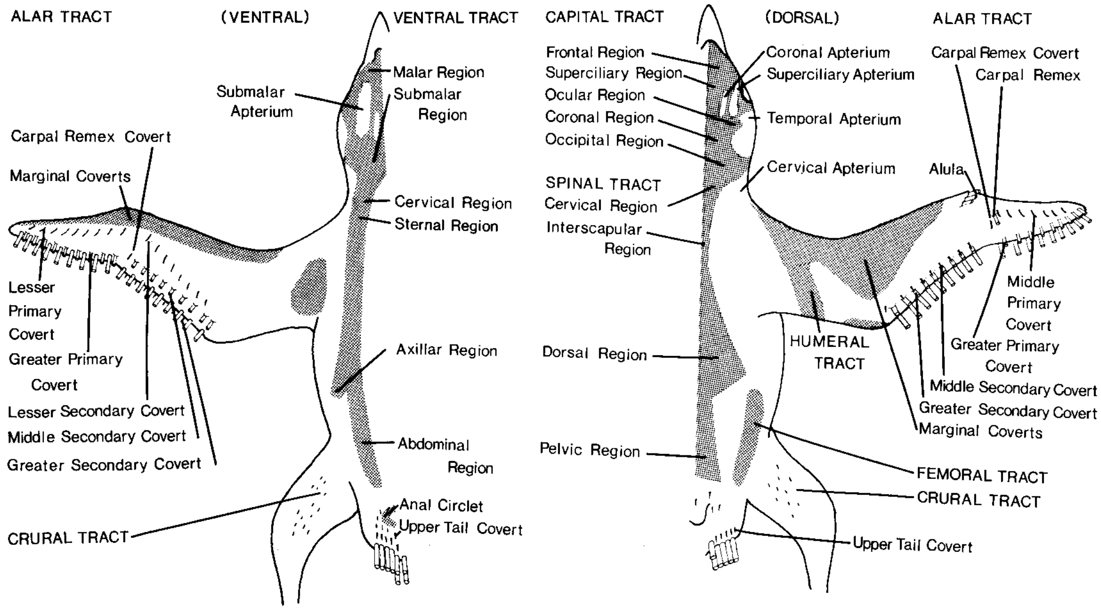

FIGURE 1. Arrangement of feather tracts of Cassin's Finch.

near the culmen to the occipital region, and a third of 5 to 7 feathers reaches laterally across the occipital area. A fourth row across the occipital area was noted in four specimens. In eight nestlings, the dorsal and pelvic regions of the spinal tract were continuous, including two rows of 8 to 14 down feathers near the midline in the dorsal region and a single row of 8 to 13 in the pelvic area. These regions were separated in three nestlings, a tendency observed in other fringillids (Wetherbee 1957). The number and position of feathers in the pelvic region of all 11 varied considerably. Single rows of down feathers were present in the scapulohumeral, femoral, and abdominal tracts, with most variability noted in the abdominal tract. Two down feathers anterior and dorsal to the protruding S_7 and S_8, a line of six anterior to S_1 to S_6, and a row of nine in the region of the developing greater secondary coverts may represent a typical alar tract but specimens varied. These observations concur with the variability noted in natal plumages of other passerines (Clark 1967, Foster 1967, Verbeek 1973).

GENERAL PTERYLOSIS

Alar tract. There are nine well-developed primaries, the seventh being the longest. A 5–8 mm feather situated distal to P_9, but lacking a covert, is considered the vestigial tenth primary and is molted in sequence with the other primaries. Distal and dorso-lateral to the first nine primaries are the nine greater primary coverts (fig. 1). The ninth greater primary covert is dorsal to the vestigial tenth primary and conceals it. The seven or eight middle primary coverts are dorsal and anterior to their corresponding primaries. The first and often second and third are missing. The site of the first covert is occupied by the carpal remex. As interpreted by others (Boulton 1927, Pitelka 1945), the small down feather adjacent to the base of P_1 is considered to be the carpal remex covert. The small feather proximal and anterior to the first under greater covert is considered the under covert of the carpal remex. Lying slightly proximal to each of the nine primaries is a greater under primary covert. On the under side of the wing from the greater upper primary coverts are nine under lesser primary coverts.

The first of the nine secondaries is the longest and the ninth the shortest. Each of nine greater upper secondary coverts extends above its corresponding remex and originates proximal and adjacent to its base (fig. 1). Upper middle secondary coverts, numbers 1 to 8, lie dorsal to the base of their corresponding greater upper secondary coverts. Proximal and slightly anterior to the ninth middle secondary covert is the ninth upper middle covert. Arising proximal to secondaries 1 through 7 are greater under secondary coverts. The nine middle and eight lesser under secondary coverts are arranged with decreasing intervals from distal to proximal and originate anterior to the greater under secondary coverts. The location of small down feathers at the dorso-lateral bases of S_1 through S_8 and P_1 resembles a pattern reported in other passerines (Miller 1931, Pitelka 1945, Foster 1967).

The distal alular remex and two progressively smaller alular remiges (fig. 1) obscure a subalular apterium. Extending outward from the anterior end of the humeral tract, marginal coverts of the patagium merge with those of the alula. A compact band of marginal coverts extends along the anterior wing edge distal to the alula. The underside of the wing is sparsely covered with under marginal coverts.

Ventral tract. Anterior to the breast, the ventral tract in *C. cassinii* is typically passerine in pattern (fig. 1). Clench (1970:664) suggested a "redefinition of the ventral branch beginning on the heart." In three nestling Cassin's Finches with discernible feather tracts, the pattern is identical to *Passer domesticus* (Clench 1970:665). The main element (terminology of Clench) in the nestling *C. cassinii* begins as the single medial row adjacent and similar to the flank rows. Beginning at approximately row 17, the median-most two feathers are separated from those of the flank element. This point of separation of the main and flank elements was detectable in older birds only when examined with a microscope. Posterior to the division, the axillary branch is eight feathers wide. The abdominal branch narrows from four or two or three feathers near the vent.

Spinal tract. The spinal tract, four to five feathers wide in the posterior occipital region, narrows to two feathers in the interscapular region (fig. 1). The dorsal region of nestling Cassin's Finches was narrow and more lanceolate as in *P. domesticus* (Clench 1970). Feathers in this region form chevron-shaped rows 13 feathers wide, similar to those in *P. domesticus* and *Anthus spinoletta* (Verbeek 1973). Beyond this region, which lacks an apterium, the tract narrows to six feathers and then expands again to eight or nine extending laterally over the oil gland.

Caudal tract. The innermost pair of the 12 rectrices is dorsal to the remaining 10 and adjacent to the second pair of upper tail coverts (fig. 1). There are 10 upper tail coverts with the first pair absent. Twelve under tail coverts form a row under the rectrices, the central pair being dorso-lateral to the second pair. Other under tail coverts form a partial second row and scattered feathers extend toward the anal circlet. Two rows of feathers arranged into two semicircles form the anal circlet.

Humeral, femoral, and crural tracts. These tracts (fig. 1) were similar to those in other passerines. The gap between the sternal region of the ventral tract and the beginning of the humeral tract in two nestling *C. cassinii* was not evident in juvenile or adult birds.

CHRONOLOGY OF MOLT IN NON-BREEDING AND BREEDING BIRDS

Non-breeding birds. Grinnell (1908) found an excess of adult and first-year males in the San Bernardino Mountains during the breeding season. During each of three breeding seasons, I noted more males than females, but flocks of non-breeding birds included only yearling males (Samson 1976). Yearling males participated in the construction of only three of 57 (5.3%) nests observed during this study, although first-year males did replace seven paired older males that disappeared. Thus, very few yearling males, which represented 14 of 71 (19.7%) of the birds banded in 1971, 172 of 451 (38.1%) in 1972, and 28 of 108 (26.0%) in 1973, breed. The total energy demands for unmated males presumably are less than for breeders, permitting a more relaxed molt schedule (table 1). Within each year, rates of molt are statistically similar. Molt was completed well before each fall departure (table 1).

Breeding birds. In 1972, molt and reproduction occurred at different times except in the late nesters (fig. 2). Although the last pair feeding fledglings was observed on 19 July, molt began on 10 July for older males and females (table 1). Weather conditions were mild throughout the spring and early summer of 1972 even though the last but unseasonable snow fell 23 June. Suitable weather conditions were late in 1973. Construction of the first nest began 28 May compared to 13 May 1972 and of the last 18 June versus 1 June 1972. This delay of nearly two weeks in nesting did not correspondingly defer onset of molt for all finches (table 1). As compared to 1972, older males began molt two days earlier and females five days later. Figure 3 depicts the overlap of nesting and molt in 1973 influenced by the late spring. I last saw fledglings being fed on 31 July.

Dates of fall departure from Beaver Mountain and the adjacent high mountain terrain were nearly as consistent as onset of molt in three summers. Flocks of breeding birds and young departed before flocks of yearling males (table 1). Magee (1924) described a presumably similar differential fall migration

TABLE 1. Timing of postnuptial molts in Cassin's Finch in relation to fall departures.

	Yearling Males	Older Males	Females
1971			
Sample size	17	46	7
Regression equation	$y = 3.64 + .665x$	$y = .13 + .684x$	$y = .65 + .72x$
Calculated duration of molt (days)	67.7	65.8	62.5
Calculated molt interval	4 July–9 Sept.	10 July–3 Sept.	11 July–11 Sept.
Correlation coefficient, r(P)	0.94 ($P < .01$)	0.87 ($P < .01$)	0.96 ($P < .01$)
Date last observed	2 Oct.	17 Sept.	17 Sept.
1972			
Sample size	53	43	26
Regression equation	$y = -5.01 + .615x$	$y = -7.71 + .677x$	$y = -7.84 + .691x$
Calculated duration of molt (days)	73.2	66.5	65.1
Calculated molt interval	6 July–17 Sept.	10 July–14 Sept.	10 July–12 Sept.
Correlation coefficient, r(P)	0.96 ($P < .01$)	0.93 ($P < .01$)	0.81 ($P < .01$)
Date last observed	29 Sept.	16 Sept.	16 Sept.
1973			
Sample size	25	31	7
Regression equation	$y = 2.57 + .612x$	$y = -1.75 + .637x$	$y = -6.92 + .689x$
Calculated duration of molt (days)	73.5	70.9	65.3
Calculated molt interval	1 July–12 Sept.	8 July–16 Sept.	15 July–7 Sept.
Correlation coefficient, r(P)	0.95 ($P < .01$)	0.95 ($P < .01$)	0.75
Date last observed	30 Sept.	17–22 Sept.	17–22 Sept.[1]

[1] A single small flock was seen on 17 Sept. and no finches were noted on 22 Sept. Study area was not censused between 17 and 22 Sept.

from northern Michigan in *C. purpureus*, and the patterns of *C. cassinii* and *C. purpureus* are somewhat similar to that of *C. e. erythrinus* in southern Finland (Peiponen 1974). Thus, the temporal separation of molt and migration versus that of molt and reproduction and the consistent dates of fall departure suggest that the impending fall limits the chronology of summer events including onset of molt.

Payne (1972) pointed out that many variations exist in the breeding-molt chronology. Gonadal inhibition of molt may partially account for the separation of these events as observed at Beaver Mountain in 1972 and, to a lesser extent, in 1973. Ligon and White (1974) described a similar phenology in adult Piñon Jays (*Gymnorhinus cyanocephalus*) and suggested photoperiod as a proximate factor in onset of molt. Similarly, photoperiod is the most constant aspect of Cassin's Finch environment and could determine the regular onset of molt and serve as the cue for the subsequent fall migration.

In two other montane breeders, *Zonotrichia leucophrys oriantha* (Morton and Welton 1973) and *A. spinoletta* (Verbeek 1973), males initiate molt before females. This was evident in Cassin's Finch only in 1973. All females attempted to breed each summer, and I consider the number of females a limiting factor for reproduction in this species (Samson 1976). Behavioral adaptations within the Cassin's Finch social system tend to reduce the energy requirements of females. Examples include female social dominance throughout the annual cycle, the mated-female distance form of territorial behavior, and the feeding of fledglings by males for 10–14 days. These traits may equalize energy requirements between mates in Cassin's Finch and thus influence the similar onset of molt unless substantial overlap of breeding and molt is evident, as in 1973.

POSTNUPTIAL MOLT

Molt of flight feathers. Postnuptial molt is first shown by the loss of P$_1$. The primaries are replaced sequentially and the pattern is symmetrical in both wings. Secondary 8 generally is shed first, followed by S$_9$ or S$_7$ and S$_9$ simultaneously and then S$_1$ through S$_6$ in sequence. Loss of S$_8$ usually occurs when P$_3$ or P$_4$ is shed, but considerable variation was noted. Secondary 1 most often is shed when P$_5$ is dropped and P$_1$ through P$_3$ are full length. Figure 4 depicts the relationship of secondary and primary molt scores.

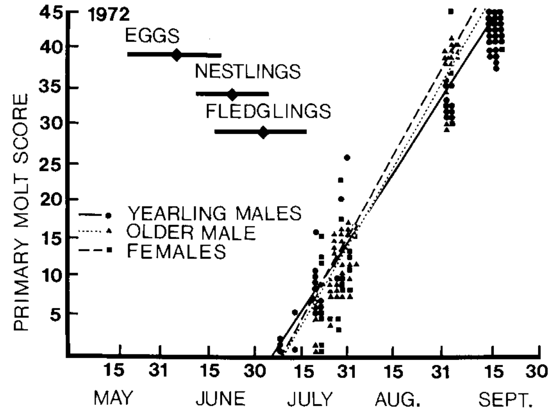

FIGURE 2. Timing of reproductive events and postnuptial molt in Cassin's Finch in 1972. Regression equations listed in Table 1.

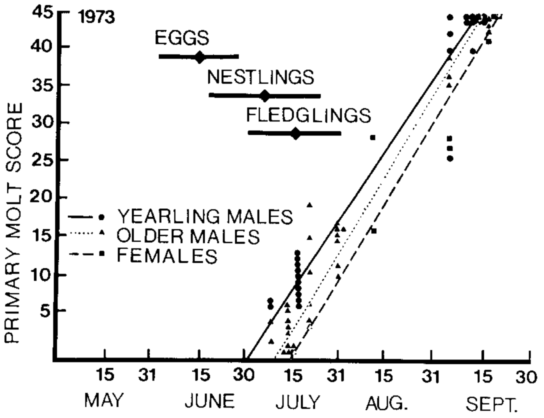

FIGURE 3. Timing of reproductive events and postnuptial molt in Cassin's Finch in 1973. Regression equations listed in Table 1.

The rectrices molt centrifugally and usually symmetrically. Several birds were recaptured with the inner two or three pairs missing. Tail molt normally begins when P_4 is shed and is completed before the outermost primaries are full length (fig. 4).

Molt of the body feathers. Renewal of body plumage begins in the ventral tract. As in *C. mexicanus* (Michener and Michener 1940), molt in the interramal and submalar areas is most evident when primary molt nears completion. Molt in the interramal area of three individuals was still evident after primary molt was complete. The molt of the capital tract is similar to that in *C. mexicanus*, molt in the occipital area not beginning until the molt of the primaries is nearly complete. Molt in the spinal tract begins nearly simultaneously or shortly after that in the ventral tract. Patterns of feather replacement in the scapulohumeral, femoral, and crural tracts are similar to those in *C. mexicanus* (Michener and Michener 1940).

Adult plumage appeared complete in the yearling males I examined at Beaver Mountain. Several males captured during the winter of 1972–73 in Cache Valley in northern Utah showed partial feather replacement particularly in the ventral tract.

POSTJUVENAL MOLT

In young Cassin's Finches as in *C. purpureus* (Dwight 1900), remiges and rectrices but not body feathers are retained until approximately 14 months of age. I saw no sign of replacement of flight feathers or acquisition of the reddish-pink plumage of adults, as has been noted in *C. mexicanus* (Michener and Michener 1940). First-year birds can be distinguished from adults primarily by the shape of the rectrices (Samson 1974). Adult rectrices are more rounded or blunt than those of juveniles or first-year birds, and rectrices of first-year birds often show considerable wear, appearing frayed at the tips. Particularly in early fall, juvenile feathers are more pointed than those of adults, wing edgings generally appearing "more or less ochraceous and buffy" (Ridgway 1901:127).

COMPARISON OF MOLT AMONG NORTH AMERICAN *CARPODACUS* AND OTHER SONGBIRDS

Stresemann and Stresemann (1966) and others (Newton 1966, 1972, Evans et al. 1967, Morton et al. 1969) have reported a briefer postnuptial molt within a species or between species breeding at high latitudes in comparison to others breeding at lower latitudes. This inverse relationship of latitude and duration of molt is only partially evident in North American *Carpodacus*. The 105 days required by *C. mexicanus* to complete the postnuptial molt in California (38° N) exceeds the duration of molt for both *C. purpureus* in Michigan (46° 30′ N) and *C. cassinii* in northern Utah (41° N). However, the mean duration of molt ($\bar{x} = 68.8$ days, all data combined) in Cassin's Finch is less than the 72 days estimated for *C. purpureus* even though separated by a latitude of 5° 30′. I interpret the abbreviated postnuptial molt of Cassin's Finch as an adaptation to the high altitude-montane environment similar to the compression of postnuptial molt observed in some species breeding at high latitudes.

Newton (1968:91) in a review of molt relative to other events of the annual cycle in finches and buntings has suggested that molt "is more closely related to their breeding

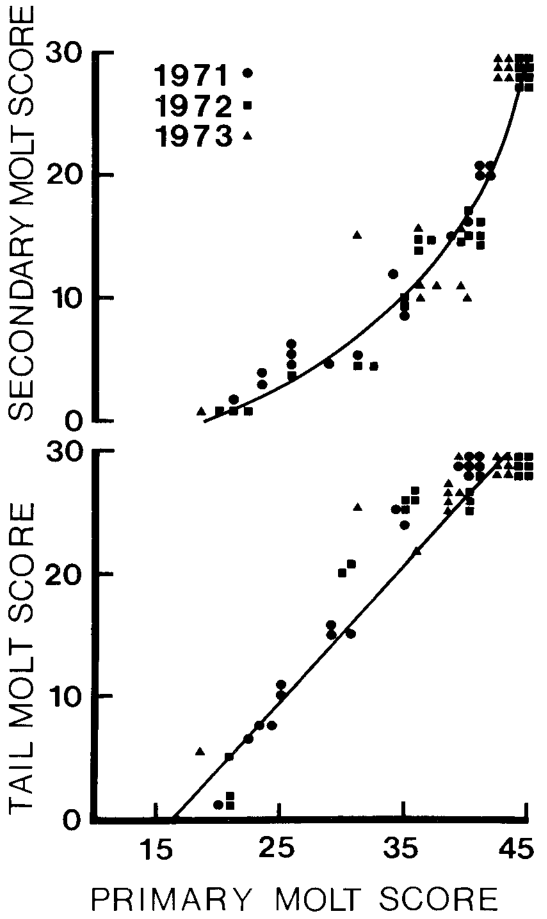

FIGURE 4. Secondary molt scores and tail molt scores in relation to primary molt scores for Cassin's Finch. Sex and age classes combined in each year.

and migratory habitat than to their feeding ecology." In Cassin's Finch, migration prior to impending unfavorable conditions is important. Additionally, to avoid severe mortality in the non-breeding season, it may be advantageous to have completed the molt before fall departure in order that energy can be fully devoted to locating the spatially varying food supply. Winter food resources are reported important in determining patterns of survival and population levels in several other finches (Newton 1964, Pulliam and Enders 1971, Fretwell 1972, Davis 1973).

SUMMARY

Arrangement, but not color, of natal down of Cassin's Finch is similar to that in other fringillids. Pterylosis is similar to that in other fringillids but the main and flank elements of the ventral tract are separated.

In a three-year study of a montane population of Cassin's Finches in Utah, non-breeding yearling males began molt each summer before older males and all females. The similarity in onset of molt in breeding older males and females in two years may reflect a social system that tends to equalize energy requirements among mates. Reproduction and molt overlapped when favorable conditions for breeding were late in 1973 but not molt and migration.

The duration of molt as estimated by linear regression analysis is considered an adaption to the high altitude-montane environment wherein Cassin's Finch must reproduce, molt, and prepare for fall migration in a period of four months.

ACKNOWLEDGMENTS

Appreciation is extended to K. L. Dixon for advice throughout this study. K. L. Dixon, R. P. Balda, and C. F. Thompson improved an earlier draft with helpful suggestions. I thank S. Samson for assistance in the field, J. Sidelinger for assistance in preparing figure 1, and S. McLane for typing the manuscript. This research was partially funded by grants from the Society of Sigma Xi and the Frank M. Chapman Memorial Fund, American Museum of Natural History, New York.

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Accepted for publication 2 March 1976.