POSTFLEDGING DISPERSAL OF GREEN-TAILED TOWHEES TO A SUBALPINE MEADOW¹

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The first months of life are fraught with difficulties for young birds. During that time, for example, they must make the transition to independence from parental care and soon thereafter also cope with new surroundings as they begin to disperse from their natal areas. In migratory passerines of many species there are additional dietary and metabolic demands imposed by feather replacement (the postjuvenal molt) and by the deposition of fat required to fuel the impending migration to wintering areas. The time interval between their achievement of independence and migration departure is usually on the order of two or three months. Obviously, this is an important phase of avian life history, but it has scarcely been studied in any migrant species.

Green-tailed Towhees (Pipilo chlorura) are migrants that winter in the southwestern United States and in Mexico and summer in montane and high plateau regions of the western United States (Norris 1968). On their breeding range they occur in shrubsteppe habitat, showing a preference for sagebrush (Artemisia) ecotones rather than monotypic stands (Knopf et al. 1990). Nesting is known to occur in the eastern Sierra Nevada in May and June (Rowley 1939) up to elevations of 3,000 m or more (Grinnell and Miller 1944) and fall migration occurs in September and October. Herein I report data obtained during the period of postfledging dispersal in juvenile Green-tailed Towhees that traveled to a subalpine meadow that may have been located well away from their birth sites. On this meadow they often completed the postjuvenal molt, fattened quickly, then disappeared, presumably on migration. The number of individuals involved was greatest in dry years which suggests that normal postfledging movements may have been magnified by food shortages on the natal areas.

STUDY AREA AND METHODS

The study area was a large subalpine meadow of about 50 ha located at Tioga Pass, Mono County, California between Tioga Lake and the boundary of Yosemite National Park. I call this Tioga Pass Meadow (TPM) and on it my students and I routinely tended a trapline from July through early October for 10 years (1978– 1987) for the purposes of capturing and banding birds. Traps were maintained at 24 stations, baited with seed, and operated four or five days a week in the morning hours only. On the occasion of their first capture, individual birds were banded with fish and Wildlife Service bands and sexed by laparotomy. They were also weighed to the nearest 0.1 g with a Pesola scale, examined for molt and subcutaneous fat stores, and wing chord of the right wing was measured with a mm ruler. These four measurements were repeated at all subsequent recaptures. Fat scores, based on visual inspection of subcutaneous depots, ranged from 0 to 5 (see Morton et al. 1973 for additional details).

RESULTS

During the 10 seasons of this study, 104 Green-tailed Towhees were captured. All were juveniles and none returned again as adults except for one male that was caught both as a juvenile and as a one-year-old. The number of towhees captured each season was highly variable, ranging from 0 to 26. They seemed most numerous to us in dry years, that is, in years when snowpack was light on TPM. Since snow depth data are available to us from State of California snow surveys taken on TPM every year on or about 1 April, we were able to plot the number of towhees captured there each season versus available moisture as indexed by snow depth. This shows clearly that Green-tailed Towhees appeared most often in years when snowpack was less than 250 cm. In the four years when packs were above that depth, only two individuals were captured (Fig. 1).

Most individuals arrived in August with the mean date of arrival (=mean date of all first captures) being 22 August. The earliest date that we caught a Green-tailed Towhee was 20 July and the latest (including recaptures) was 9 October. There were more females than males, 58 vs. 46, but this ratio was not different from 1:1 ($\chi^2 = 1.38$, P > 0.20).

Males were larger than females at initial capture as measured both by wing length and body mass (Table 1). The sexes did not differ significantly in their fat scores at the time of initial capture nor did they differ in the number of times that individuals were recaptured or in the number of days they were known to be on the study area (days on study area = interval between dates of initial and last captures, Table 1). Nearly every bird handled in July and August was undergoing postjuvenal molt; the molt being completed in late August or early September. An interesting feature of this molt was that it resulted in the young birds acquiring the rufous crown typical of adults. In a few

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FIGURE 1. Number of immature Green-tailed Towhees captured on TPM during 10 seasons (1978–1987); seasons characterized by 1 April snow depth on TPM.

females (but not all, as suggested by Chapman 1914), the new crown feathers had grayish tips.

Within a few days after completion of postjuvenal molt, members of both sexes exhibited a rapid increase in body mass that was accompanied by increased fat scores. These scores sometimes reached class 5, the maximum in our system, wherein subcutaneous fat depots were bulging. This period of rapid fat deposition lasted for only about seven to 10 days but it resulted in birds attaining weights that sometimes exceeded 35 g in females and 40 g in males (Fig. 2). Individuals were rarely trapped again once they had reached peak body weights.

DISCUSSION

The study area lies at the upper end of Lee Vining Canyon, a glacially carved canyon which starts at the eastern edge of the Sierran crest at about 3,000 m elevation and which then descends by about 1,000 m



FIGURE 2. Seasonal changes in body mass of six immature Green-tailed Towhees frequently recaptured on TPM. Data are for two males, curves 1 and 2, and four females, curves 3-6. Data points are solid when the individual was molting and open when it was not.

over a distance of 15–20 km until it terminates at the western edge of the Great Basin near Mono Lake. Greentailed Towhees are abundant in the sagebrush-dominated shrubby vegetation in the lower parts of Lee Vining Canyon where they probably nest in May and June (see Rowley 1939). Each year we also see one to three breeding pairs in sagebrush patches that occur on steep, dry slopes in the upper parts of the canyon within 1–3 km of TPM. I conclude that juvenile towhees could be moving from these slopes and/or up-canyon from breeding areas found at lower elevations. Clearly these postfledging movements were greatest in the driest years, suggesting that the response may be stimulated by low food resources on the xeric natal areas as compared to subalpine meadows nearby or above which stay green

TABLE 1. Data obtained from 46 male and 58 female Green-tailed Towhees captured on TPM from 1978 to 1987. NS indicates P > 0.05 (*t*-test).

	Males				Females				
	x	SD	Min	Max	х.	SD	Min	Max	Р
Wing length (mm) at initial capture	78.2	1.5	76	82	74.8	1.5	71	79	< 0.001
Body mass (g) at initial capture	29.1	3.1	23.5	39.4	27.6	2.1	22.5	33.2	< 0.01
Fat class at initial capture	1.2	0.9	0	4	1.3	0.8	0	4	NS
Number of captures per individual	4.2	3.1	1	11	4.6	3.2	1	17	NS
Days on study area	15.5	12.4	1	41	14.8	10.4	1	44	NS

through July even in drought years. Uphill movements by several species, including Green-tailed Towhees, have been noted in montane areas in Utah by Hayward (1945), but he did not report if there were interannual variations related to environmental conditions. If the dispersal movements we observed were indeed in response to deteriorating trophic conditions, and meant to counteract food shortages, the evidence is that they were highly effective. The birds we handled were invariably in good condition. They appeared to proceed through molt without faltering and their ability to fatten quickly while on TPM, prior to departure, was impressive.

Natal dispersal, usually described as being the movement of immature birds from their site of birth to their first breeding area, is poorly understood in passerine migrants. It is frequently assumed that selection of breeding sites occurs when the birds first arrive on their breeding range as adults. There is a body of evidence and thought, however, which suggests that postfledging movements in immatures prior to their first migration may be an important part of the natal dispersal process, serving several important functions. For example, during this time immatures may be: (1) selecting habitat suitable for future nesting efforts (Brewer and Harrison 1975, Seastedt and Maclean 1979, Gluck 1984, Pärt 1990, Morton et al. 1991), (2) becoming imprinted on or familiarized with local landmarks that would facilitate eventually their ability to home to the natal area, for breeding purposes, from wintering areas (Löhrl 1959, Wiltschko and Wiltschko 1978, Able and Bingman 1987), and/or (3) locating areas that are favorable for food acquisition and perhaps for social contacts important to the onset of migration behavior (Morton et al. 1991). In Green-tailed Towhees, it appears that these movements, as we have observed them, may serve primarily as a mechanism for securing the food needed for maintenance and premigratory fattening, i.e., as in hypothesis (3), above.

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