

was estimated as the probability of nesting success times fecundity and was 2.8 fledglings/pair or 1.4 fledglings/individual.

Discussion.—Productivity is influenced by both length of season and timing of onset of reproduction. Early breeding and a long breeding season are advantageous in coping with high nesting mortality, but the factors determining these characteristics are complex. By breeding as early as possible, towhees can increase breeding season length. A long breeding season favors productivity by increasing opportunities to renest, especially after failures. Initiation of breeding requires adequate food supply and nesting sites and materials. In this study, Abert's Towhees had a prolonged nesting season of 4.2 months, compared to an average of 2.17 months for eight Arizona passerine species reported in Ricklefs and Bloom (Auk 94:86–96, 1977). Towhees began breeding shortly after a February peak in rainfall. My data are in apparent agreement with Marshall's (1963) contention that the onset of reproduction is associated with rainfall. Early breeding, possibly initiated by rainfall, was facilitated by flexibility of nest-sites and nest materials (Finch, M.S. thesis, Arizona State Univ., Tempe, Arizona, 1981). However, insect biomass along the lower Colorado River is typically much lower in March than later in the season (Cohan et al., USDA For. Serv. Gen. Tech. Rept. WO-12:371–381, 1978; Anderson et al., Am. Nat. 120:340–352, 1982), and I observed one-egg clutches and nestling starvation at this time. Nonetheless, the combined effects of predation and brood parasitism later in the breeding season lead to the greatest probability of nesting success early in the season (Finch 1983). Thus, early breeding appeared to be favored but may be limited by food availability in March.

Another factor affecting annual productivity is the rapidity of nest replacement. In 1980, the time interval between nesting attempts declined as the season progressed. Increase in the rapidity of nest replacement may be: (1) an adaptation to save time before the favorable period for breeding ends; (2) a response to an environmental change (e.g., increased food supply or nesting material); (3) a behavioral adjustment to a physiological change (e.g., hormonal production); or (4) an improvement because of recent practice. More nests can be attempted during the breeding season if the number of days spent in non-nesting pursuits is minimized.

I have shown in this study that nesting success is not the only factor influencing productivity in Abert's Towhees. Towhees can adjust length of breeding season and rapidity of nest replacement in order to maximize the number of nesting attempts per season. In conclusion, by maximizing the time available for renesting, towhees to some extent can regulate their annual productivity despite low nesting success.

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Aspects of nestling growth in Abert's Towhee.—Among factors selecting for rapid growth rates in avian young are those that cause mortality of whole broods (e.g., predation, weather) (Ricklefs, *Ecology* 50:1031–1039, 1969). Abert's Towhee (*Pipilo aberti*) endures a high rate of nesting mortality caused by predation and brood parasitism (Finch, *Condor* 83:389, 1981; *Condor* 85:355–359, 1983). Predation is the principle factor causing loss of whole broods. Nesting mortality may have an important role in the development of life history traits (e.g.,

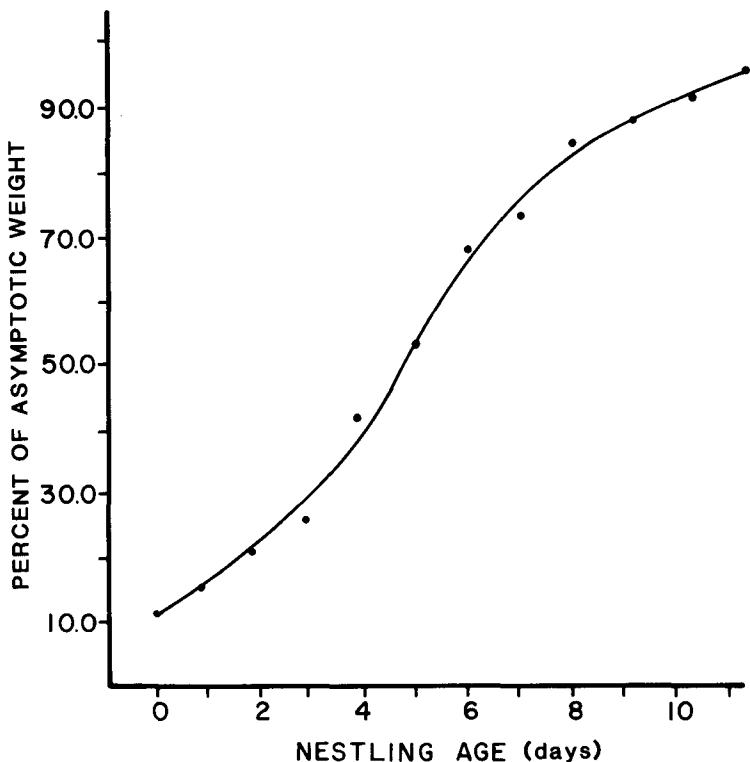


FIG. 1. Growth curve of Abert's Towhee nestling calculated from Ricklefs' (1967) logistic model. Growth equation = $32.8/1 + e^{-0.476(t-4.7)}$. Hatching day = 0.

nestling growth, clutch-size, number of broods/season) in Abert's Towhee, yet little is known about these traits (but see Finch, Wilson Bull. 96:703-707, 1984). In this study, I describe growth rate of nestling Abert's Towhees and discuss its possible adaptive significance. I studied nestlings of Abert's Towhee in honey mesquite (*Prosopis glandulosa*) habitat of the lower Colorado River Valley 10 km N of Ehrenberg, Yuma Co., Arizona.

Methods.—I estimated nestling growth rate by means of Ricklefs' (Ecology 48:978-983, 1967) logistic model, in which the weight of the bird in grams (W) at a certain age in days from hatching (t) is equal to $A/1 + e^{-K(t-t_0)}$, where A = asymptote of the growth curve, K = the growth rate constant $4(dW/dt)$, and t_0 = age at the point of inflection of the growth curve. Weights of nestlings from seven broods were measured with an Ohaus scale accurate to 0.01 g, and wing chord and tarsus length were measured with calipers. Because nestling mortality occurred in some broods, a growth curve was estimated from composite data for each day of the nestling stage. The growth index (G) (Ricklefs 1967; Auk 96:16-30, 1979a) allowed comparison of tarsus and feather growth and was calculated by the formula: $G = 0.445 \ln [W/(1 - W)]$.

Results.—The hatching weight of Abert's Towhee was 3.63 ± 0.075 g ($N = 8$ clutches,

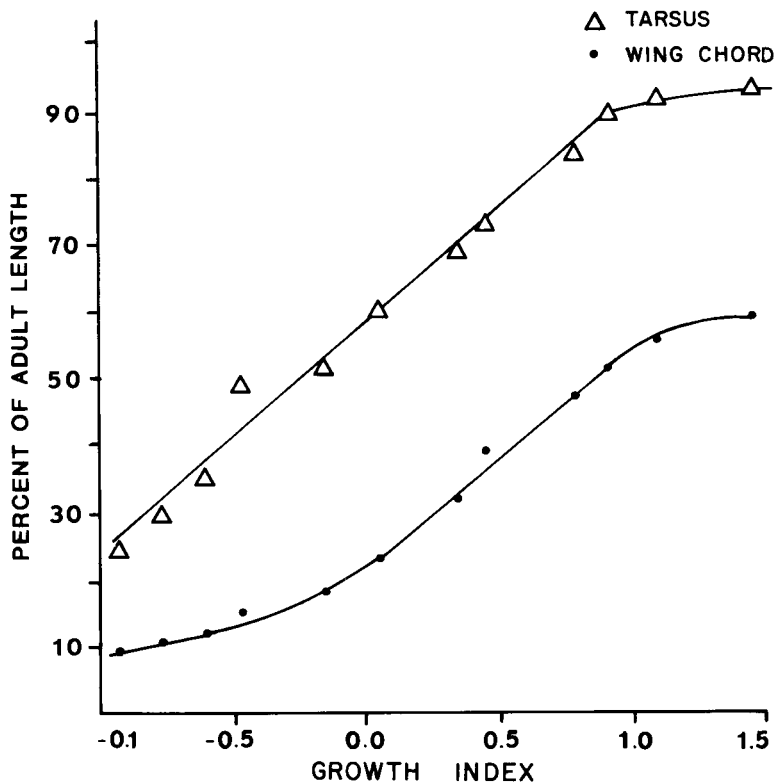


FIG. 2. Development of wing chord and tarsus as percentages of adult length plotted against the growth index ($G = 0.445 \ln [W/(1-W)]$), where W = nestling weight at a given age.

13 eggs) and was 7.8% of adult weight. Towhees fledged at a mean asymptotic weight of 32.8 g. Adults weighed 46.8 g ($N = 13$, sexes combined) so that the ratio (R) of asymptotic weight to adult weight was estimated to be $32.8/46.8 = 0.70$. The instantaneous growth constant (K) was equal to four times the slope (0.122 of the logistic conversion curve) and was estimated to be 0.476. The growth curve of Abert's Towhee was approximated by the logistic equation having the form: $32.8/1 + e^{-0.476(t-4.7)}$. Nestling growth measured as a percentage of the asymptotic weight and plotted against nestling age in days described a sigmoid curve (Fig. 1). The curve did not level out at the end of the nestling period indicating that towhees were still growing rapidly at the time of fledging.

Flight did not appear in Abert's Towhees until a week after fledging, but young could run at 10 days of age. When plotted as a function of the growth index, wing chord can be seen to remain less developed than the tarsus during the nestling period (Fig. 2). Tarsus length was 93% of adult tarsus length at fledging, whereas wing chord at fledging was only 59% of adult wing chord.

Discussion.—The length of the nestling period is related to growth rate. The growth rate

of a species is determined within narrow limits by adult body size and mode of development (Ricklefs, *Ibis* 115:177–209, 1973). Hence, variation in growth rate among species is not directly explained by energy requirements or rate of nestling mortality. Adult Abert's Towhees weigh three times as much as another desert emberizine, the Rufous-winged Sparrow (*Aimophila carpalis*). Adult Rufous-winged Sparrows weigh 15.3 g and their nestlings have high growth rates ($K = 0.57$, Austin and Ricklefs, *Condor* 79:37–50, 1977). When the growth rate (0.476) of Abert's Towhee is scaled to an adult body weight of 15.3 g by use of the relationship $K_2 = K_1 (W_2/W_1)^b$ and $b = -0.26$ (Ricklefs 1979), K for the towhee becomes 0.637. Thus, adult body weight partially explains differences in growth rates of Abert's Towhees and Rufous-winged Sparrows.

Abert's Towhee is a large emberizine with a short nestling period relative to adult body size. Abert's Towhees have completed only about 70% of their growth when they leave the nest, and parents continue feeding them long after fledging. Sparrows, in general, are still growing and accumulating energy in their tissues at fledging (Austin and Ricklefs 1977).

The ratio of fledgling weight to adult weight (R) of Abert's Towhees is somewhat lower than the R value for smaller species of *Pipilo* such as the Rufous-sided Towhee (*P. erythrophthalmus*) in Pennsylvania (Ricklefs, *Ibis* 110:419–451, 1968). Compared with the R values for other temperate emberizine species (Ricklefs 1968), offspring of the genus *Pipilo* fledge at light weights relative to adults. A regression of R against adult weight for emberizines ($r = -0.54$, $N = 18$, data from Ricklefs 1968, Austin and Ricklefs 1977, this study) indicated that R is inversely related to adult weight. Because the regression is significant ($P < 0.05$), low R values in large emberizines like towhees are not unexpected.

The difference in maturity at fledging between the wing chord and the tarsus may be dependent on the importance of the structure after the nestling leaves the nest (Ricklefs 1968). An adult Abert's Towhee spends much of its foraging time scratching on the ground with its feet (Marshall, *Condor* 62:49–64, 1960; Finch, *Auk*, 101:473–486, 1984). At fledging, its legs must be well-developed for the bird to learn the locomotory skills of feeding. On the other hand, an aerial forager like a swallow (*Hirundo* sp.) depends primarily on its wings for hunting, and it leaves the nest fully grown (Ricklefs 1968). In addition, towhee young tend to run from danger rather than fly, and thus, escape may be an important reason for advanced tarsal development.

Nestling mortality may be the major selective factor driving growth rate to its physiological maximum (Ricklefs 1969). The rate of nestling mortality is high in Abert's Towhee (Finch, *Auk* 99:719–724, 1982; 1983), and therefore it is adaptive to complete the nest cycle as quickly as possible, particularly because the probability of predation increases over time. The short nestling period of Abert's Towhees may be an adaptive compromise between high nestling mortality and internal developmental constraints (e.g., the slowest-growing-tissue hypothesis (see review, Ricklefs, *Biol. Rev.* 54:269–290, 1979b). Cryptic ground coloration and early ground mobility aid a fledgling's chance for success.

In conclusion, mobility in the face of predators and, hence, maturity of locomotory function, may ultimately set the limit to length of the nestling period. Success of Abert's Towhee in a difficult environment may be partially explained by its rapid development and short nest period.

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