be substantial (Pattee and Hennes, Trans. N. Am. Wildl. Nat. Resour. Conf. 48:230–237, 1983). Golden Eagles regularly feed on waterfowl and carrion (Sherrod, Raptor Resear. 12: 49–121), and individuals that winter at waterfowl concentration areas where lead shot is used probably feed on moribund and dead ducks and geese. Secondary lead poisoning may be a significant cause of mortality for this species as well.

Acknowledgments.—The NWF midwinter eagle survey was coordinated from 1979–1981 by M. E. Pramstaller, and the survey data used in this analysis resulted from his efforts on this project as well as the efforts of the regional coordinators and several thousand dedicated volunteers. R. W. Fyfe, J. W. Grier, and W. R. Spofford graciously permitted the use of information on band recoveries, and M. R. Fuller was instrumental in making this information available. We would like to thank K. W. Ballard, G. R. Bortolotti, W. S. Clark, K. W. Cline, M. W. Collopy, M. R. Fuller, R. S. Kennedy, M. N. LeFranc, Jr., S. D. Miller, and W. A. Wentz for critically reviewing the manuscript, as well as R. Hudson for typing the manuscript.—BRIAN A. MILLSAP AND SANDRA L. VANA, *Raptor Information Center, Institute for Wildlife Research, National Wildlife Federation, 1412 Sixteenth Street, N.W., Washington, D.C. 20036.* *Accepted 27 Aug. 1984.*

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Some factors affecting productivity in Abert's Towhee.—Abert's Towhee (*Pipilo aberti*) is restricted to desert riparian zones of Arizona and bordering states (Phillips et al., The Birds of Arizona, Univ. Arizona Press, Tucson, Arizona, 1964). Its breeding behavior, communication, and physiological responses have been detailed by Marshall (Condor 62:49–64, 1960; pp. 620–622 *in* Proc. XIII Int. Ornithol. Congr., Ithaca, New York, 1962; Condor 66:345–356, 1964), and Dawson (Univ. Calif. Publ. Zool. 59:81–124, 1954), but no information is available on annual productivity. Abert's Towhee is multibrooded, and therefore, the number of broods per season as well as nesting success and clutch-size contribute to productivity. My objectives were to describe the productivity of Abert's Towhee in 1980 and to quantify seasonal variation in length of nesting, a factor that affects productivity. I have documented elsewhere (Finch, Condor 85:355–359, 1983) the effects of changing rates of brood parasitism on the nesting success of Abert's Towhee.

Methods.—During the summer of 1979, I established a 20-ha grid in honey mesquite (*Prosopis glandulosa*) habitat 10 km N of Ehrenberg, Yuma Co., Arizona. From January–July 1980, 15 h each week were spent looking for nests on, or near, the study grid. Nests were inspected between 10:00 and 12:00 every 2 or 3 days. Fieldwork terminated in July when no new nests were initiated.

From May–August 1979, I mist-netted and color-banded Abert's Towhees, of which eight were adults. Five banded adult females were present in the breeding population the following year. In 1980, I color-banded 12 more females.

Annual productivity, which is the number of fledglings produced in one year, can be estimated from the expression (Ricklefs, pp. 336–435 *in* Breeding Biology of Birds, D. S. Farner, ed., Natl. Acad. Sci., Washington, D.C., 1973): (no. eggs/clutch·no. nesting attempts·% success)/2 adults/pair. The number of nesting attempts was measured directly by following marked females throughout their breeding cycle. To increase sample size, I also used nesting data for unmarked birds and estimated the number of attempts indirectly by dividing the length of the season by the time required for each nesting attempt (Ricklefs 1973). The length of a nesting attempt is approximated by the equation (Ricklefs 1973): $T = P(t + r_s) + Q(t_f + r_f)$, where T = average length of a nesting attempt, P = proportion of nestings that succeed, $Q = 1 - P$, proportion of nestings that fail, t = combined average

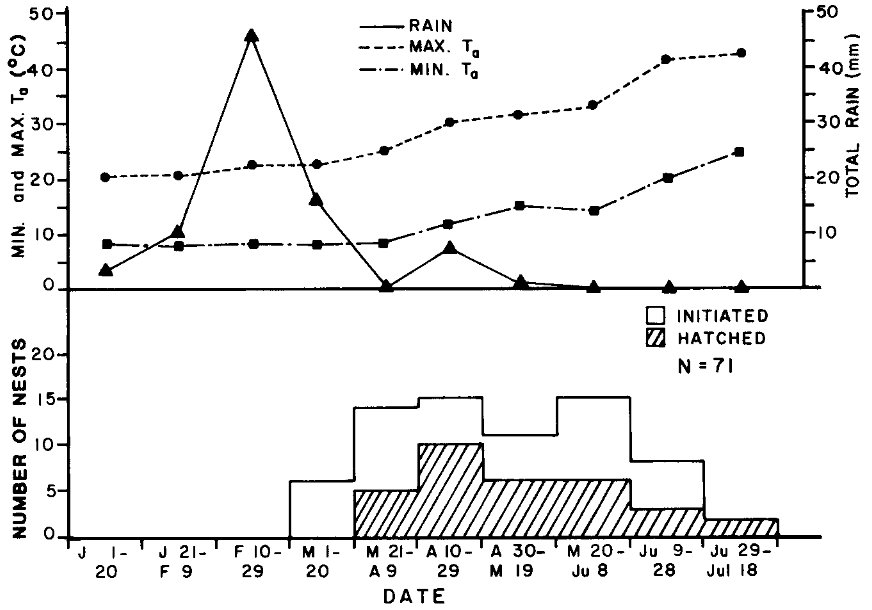

FIG. 1. Nest initiation in relation to patterns of air temperature (T_a) and total rainfall.

length of laying, incubation, and nestling periods, t_f = average time to failure in an unsuccessful nest, and r_s, r_f = time before initiation of a new nest after a success and a failure, respectively (estimated from marked birds). The number of attempts during the year was calculated as length of season divided by T. Using Ricklefs (1973) methods, season length was estimated from MacArthur's (Am. Nat. 98:387–397, 1964) index: $e^{-\Sigma p_i \ln p_i}$, where p_i is the proportion of all nests that are started during the time interval i. Multiplying the index by the time interval (in this case 20) converted it into days.

The success of nest contents was calculated by Mayfield's (Wilson Bull. 73:255–261, 1961; Wilson Bull. 87:456–466, 1975) method. Johnson's (Auk 96:651–661, 1979) statistic was used to test for differences between daily success rates ($\hat{s}$) of incubation and nestling phases.

Maximum and minimum air temperature and precipitation data that approximate conditions in the study area were obtained from the Palo Verde Irrigation District weather station, Blythe, Yuma Co., California, located about 25 km SW from the study area.

Results.—Abert's Towhees began building nests on the study area in early March 1980. Air temperatures during this period averaged 23.9°C maximum and 8.3°C minimum (Fig. 1). Air temperatures averaged 42.9°C maximum and 24.8°C minimum in July when towhees terminated breeding. Over a 20-year period, the greatest monthly precipitation usually occurred in July, and the average rainfall in February was 8.1 mm (Anderson et al., USDA For. Serv. Gen. Tech. Rept. RM-43:183–192, 1977). However, 1980 was atypical, with no precipitation in June and July and with the peak rain falling in February (46.2 mm) (Fig. 1).

Abert's Towhees began breeding approximately 2 weeks after the peak in February rains (Fig. 1). The earliest clutch was initiated (i.e., first egg laid) on 13 March. Because it takes

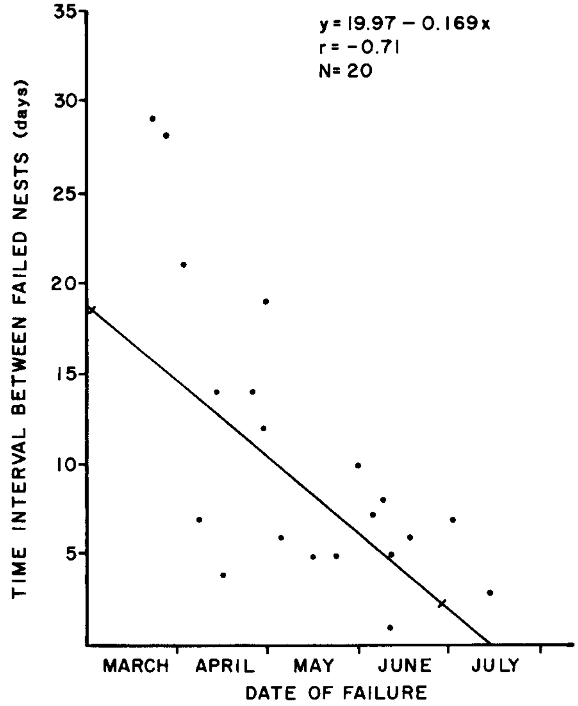

FIG. 2. Time intervals between nest failure and first egg laid in new nest of banded females.

towhees at least a week to construct their first nest, nest building was probably initiated in the first week of March. Mean clutch-size was 2.85 eggs (N = 65, SE = ±0.35, range 1–4, mode = 3). Females began incubating shortly after the first egg was laid. Hatching was asynchronous (up to a day apart) after an incubation period of 14 days. Nestlings fledged at 12–13 days of age. The total length of a successful nesting cycle (t_s), excluding time involved in nest building and post-fledging stages, was approximately 30 days.

Fledglings were attended by both parents 4–5 weeks before they attained independence. The time interval between fledging of young and laying of the first egg in a new nest (r_s) was approximately 42 days (i.e., 5 weeks of fledgling dependency plus 1 week to build a new nest). The time interval required by a female before she laid the first egg of a new clutch after a failed clutch, significantly decreased with time of season ($r = -0.71$, $P < 0.01$, N = 20) (Fig. 2). There was also a decrease in the time interval between new nest construction and first egg laid in a new nest ($r = -0.9$, $P < 0.01$, N = 10). The average time before initiation of a new nest after a failure (r_f) was 10.06 days (N = 18, two nests excluded from computation because new clutches were laid in old nests). A decline in r_s (time before nest initiation after a success) over the breeding season, if present, (e.g., Kluyver et al., pp. 153–169 *in* Evolutionary Ecology, B. Stonehouse and C. M. Perrins, eds., Univ. Park Press, London, England, 1977) could not be detected because of insufficient data.

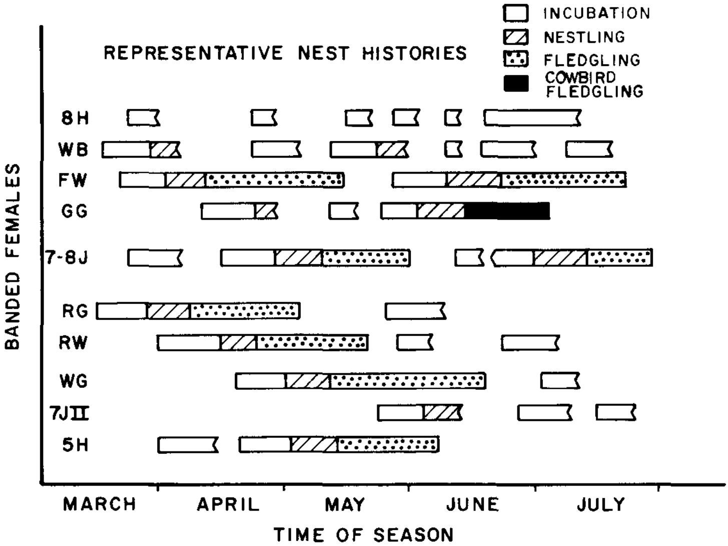

FIG. 3. Representative nesting histories of banded female Abert's Towhees. Bars with squared-off ends signify successful completion of nest cycle. Bars with indented ends represent failed nests. Female identifications are given in column on left side of figure.

The length of time a nest was active declined with season, so that nests failing in March and April were active significantly longer than those failing in June or July ($r = -0.4$, $P < 0.01$, N = 64). The average time before a nest failed (t_f) was 11.67 days.

The probability of nesting success was low (0.2) in 1980. Nesting success was lower during the incubation period (0.368) than during the nestling period (0.571), although the differences in daily success rates between incubation and nestling phases were not significant for either whole nests (Johnson's statistic = 1.088, $P = 0.28$) or partial losses alone (Johnson's statistic = 1.414, $P = 0.16$).

Studies of 10 banded females (Fig. 3) showed that Abert's Towhees built numerous replacement nests and raised at least two broods when possible. The maximum number of clutches, laid by two females, was six (each laid five replacement clutches). Females that did not succeed in fledging offspring extended their breeding season into July. Thus, the length of the reproductive cycle was, in part, dependent on breeding success.

A direct estimate of the number of nesting attempts gave a value of 3.79 nests/female in 1980 (N = 8, two females were excluded because of incomplete data). This is a rough estimate, however, because sample size was limited and females were difficult to follow within their large territories (mean territory size was 1.22 ha, N = 7, measured in 1979). Replacement nests that were active for only a few days may have been missed.

An expected number of nesting attempts was estimated with Ricklefs' (1973) indirect method. The length of an average nesting attempt by towhees was 31.73 days. Average season length (Ricklefs 1973) was equal to 124.65 days. The number of nesting attempts was equal to 124. 65/31.73 + 1 = 4.93. Fecundity, estimated by multiplying average clutch-size by the number of nesting attempts, was 14.05 eggs/female. Annual productivity in 1980 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.,