PRODUCTION AND SURVIVAL OF THE VERDIN

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A review of avian demography (Ricklefs 1973) demonstrates the dearth of knowledge on this subject. Although certain demographic parameters are relatively well known for a wide variety of species, data are generally lacking for their seasonal, annual, and geographic variability. These, including population densities, nesting season, clutch size, and nesting success, are straight forward and can be obtained with relative ease. Survival and annual recruitment are also of interest, but are difficult to determine under field conditions.

If first year individuals (*I*) can be distinguished from adults (*A*), the ratio of the 2 can be used to calculate annual mortality and recruitment of first year birds into the breeding population given the assumptions of constant population size and no collecting bias. In many species, the first prebasic molt is incomplete (e.g., Dwight 1900), providing a basis of distinguishing first year birds from adults. Although it has long been recognized that I/A ratios can be used to determine annual survival (Emlen 1940, Snow 1956), this method has not been widely used.

The Verdin (*Auriparus flaviceps*) is an ideal species for a demographic study as first year birds can be distinguished from adults through at least March (Austin and Rea 1971), the species is nonmigratory and relatively sedentary, and general aspects of its life history are known (Moore 1965, Taylor 1967, 1971, Austin 1976). In this paper, I will analyze the demographic data available for the Verdin from the literature and my own studies in Arizona and Nevada. Geographical and/or seasonal trends will be examined and estimates of mortality and annual recruitment will be presented.

METHODS

Clutch size was determined for 144 nests in Pima County, Arizona (1970–71), and 87 nests in Clark County, Nevada (1959–70, 1976). Additional data were obtained through the North American Nest Record Card Program, Cornell University (NANRCP). The clutch was considered complete when the number of eggs remained constant for 2 or more successive days. Verdins lay 1 egg per day on successive days until the clutch is complete (Moore 1955, Taylor 1971, this study). Nesting success was obtained by periodically (1–3 day intervals) inspecting active nests. Hatching success is percent of eggs to hatch, fledging success is percent of eggs to produce young which fledge, nestling success is percent of hatchlings to fledge, and nest success is percent of breeding nests built to fledge at least one young.

I aged museum specimens of Verdins according to the methods of Austin and Rea (1971). Briefly, at fledging, Verdins are grayish-headed and lack the rich chestnut lesser primary coverts characteristic of adults. During the first prebasic molt, the upper greater primary coverts and the proximal 2–5 primaries are retained. These feathers appear more faded and worn than the newer distal primaries. This difference was reliable through at least late March or April of the following spring after which feather wear was too great for reliable determinations. A bird was considered a first year bird if (1) it was gray-headed (before first prebasic molt), (2) it was undergoing first prebasic molt, or (3) it had retained upper greater primary coverts and proximal primaries after molting. After April, yellow-headed birds which had not begun prebasic molt were considered adult. The latter included some birds which were not as yet one year of age but had entered one breeding season since the first prebasic molt.

RESULTS

Relative abundance.—The population density of the Verdin in the United States in winter is greatest in the Big Bend region of Texas, southern Arizona (excluding eastern Arizona), and adjacent southeastern California (Fig. 1). Distribution and relative abundance appears similar during summer (data from U.S. Fish and Wildlife Service breeding bird survey courtesy C. S. Robbins). Population densities during the breeding season in suitable habitat averaged about 8 pairs/40 ha in the San Antonio region of Texas (American Birds breeding bird censuses 1968–1972, 1974), 2–3 pairs/40 ha in the Chihuahuan Desert of western Texas and New Mexico (Dixon 1959, Raitt and Maze 1968), about 8 pairs/40 ha in southern Arizona and southeastern California (range 3–16; American Birds breeding bird censuses 1941, 1942, 1965, 1969–1971, Hensley 1954, Taylor 1967, Anderson and Anderson 1973, Tomoff 1974, this study), and about 4 pairs/40 ha in southern Nevada (Austin 1970, Miller 1974).

Clutch size.—In southern Nevada, modal clutch size remained at 4 throughout the season although mean clutch size decreased (Table 1). In southern Arizona, mean clutch size decreased through the breeding season with a modal size of 4 in March and April and 3 for the remainder of the season. Similarly, Moore (1965) and Taylor (1971) reported a decrease in clutch size through the breeding season in New Mexico and central Arizona, respectively.

There also appears to be an east to west and north to south decrease in clutch size (Table 1). Two sets of eggs from Texas contained 6 eggs each (collection at Oregon State Univ., *in* Taylor 1967), although the usual size in Texas was reported as being 4 (Attwater 1892) or 3 to 6 (Oberholser 1974, NANRCP). The average clutch in Texas and New Mexico contained 3.75 eggs, in Arizona 3.41, and in central Baja California, Mexico, 2.41. Only 1 clutch of 100 examined in the latter location contained 4 eggs (Bancroft 1930). The average southern Nevada and central Arizona clutch was nearly 0.5 egg larger than those in southern Arizona.

Breeding season.—The breeding season extends generally from mid-March

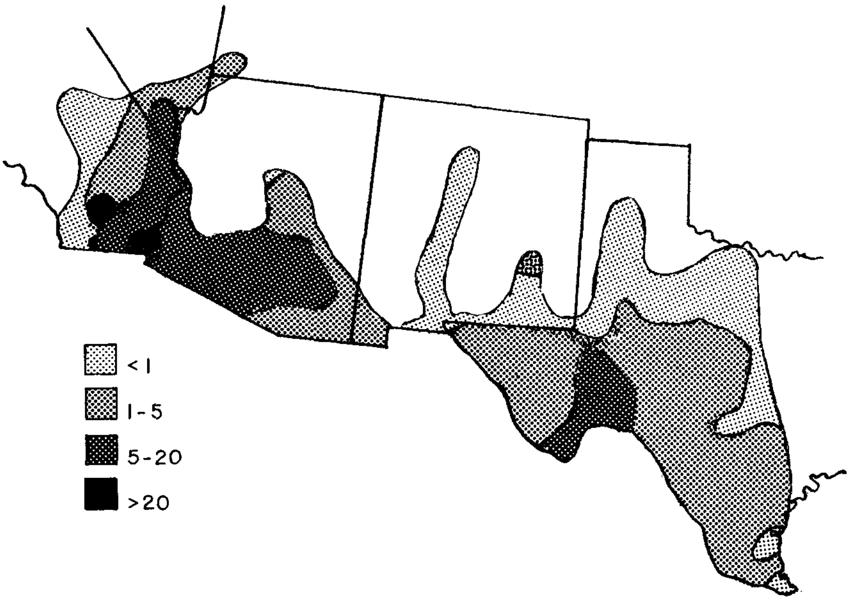

FIG. 1. Relative density of Verdin populations during winter (values are numbers/10 party hours averaged for the years 1965–1974 from American Birds Christmas bird count).

through mid-June over much of the Verdin's range (Bent 1946, Hensley 1959, Moore 1965, Taylor 1971, this study) with the earliest egg date of 4 March (Bent 1946). In desert grassland in southern Arizona, I have found fresh clutches as late as 23 July with young fledging after mid-August. Near Tucson, a fresh clutch was found in early August (P. Gould, pers. comm.).

TABLE 1

CLUTCH SIZE OF THE VERDIN

Locality	Mean clutch size (N)			Source
	Early nests	Late nests	Total	
Texas	–	–	4.06 (16)	Taylor 1967, NANRCP
New Mexico	3.71 (14)	3.00 (6)	3.50 (20)	Moore 1965
Southern Arizona	–	–	4.00 (16)	Hensley 1959
Southern Arizona	3.77 (48)	3.02 (96)	3.27 (144)	this study
Central Arizona	4.13 (16)	3.42 (12)	3.82 (28)	Taylor 1971
Southern Nevada	3.83 (53)	3.68 (34)	3.77 (87)	this study
Baja California	–	–	2.41 (est.)	Bancroft 1930

TABLE 2

LENGTH OF BREEDING SEASON IN THE VERDIN

Location	Number of clutches laid during						Index of season length (months)	Source
	March	April	May	June	July	Aug.		
Texas	1	5	6	7	1	0	3.95	NANRCP
Southern Arizona	1	3	5	5	0	0	3.50	NANRCP
Saguaro-Palo Verde	22	86	80	23	0	1	3.44	this study
Mesquite grassland	0	11	14	18	7	0	3.79	this study
Central Arizona	6	10	8	4	0	0	3.80	Taylor 1971
Southern Nevada	4	102	65	11	0	0	2.58	this study

Texas birds may occasionally breed into September (Oberholser 1974). Further south in Mexico the breeding season was apparently well underway by late March (Short and Crossin 1967) and extended into August (Amadon and Phillips 1947, Short 1974) or later (Brewster 1902, but see Banks 1963). This longer breeding season in Mexico was further suggested by Bancroft (1930) who found many fresh clutches in mid-June.

An estimate of season length adjusted for peaks in breeding activity is derived from the index of "equally probable months for nesting" (MacArthur 1964):

$$\text{months} = e - \Sigma p_i \log p_i$$

where p_i = the number of clutches initiated in each month. These data for the Verdin are presented in Table 2. Season length in southern Nevada was nearly a month shorter than in Arizona. This may be due to the lack of a distinct summer rainy season in the Mojave Desert. Here the peak of the breeding season is in April compared to a peak extending over a 2-month period in southern Arizona (Table 2).

Number of broods.—In Arizona, most pairs had no more than one successful brood per year although some with successful first nests attempted a second nesting. On the average, ½ of the pairs built 2 nests. As many as 4 breeding attempts were made in a season and as many as 2 were successful (Taylor 1967, this study).

The length of one successful cycle was approximately 43 days (6 days building, 3 days laying, 16 days incubation, 18 days nestling period). Second and successive cycles were shorter as the male constructs succeeding nests during the previous nest period. After a successful nesting, an average of 2 days elapsed between fledging and the first egg of the next clutch (r_s); after a failure, an average of 4 days elapsed (r_f) (Taylor 1967, this study).

TABLE 3

SEASONAL CHANGES IN NESTING SUCCESS OF THE VERDIN DURING 1970 AND 1971 IN PIMA COUNTY, ARIZONA

Month	Hatching (%)	Fledging (%)	Nestling (%)	Nest (%)	N eggs	N nests
March	77.8	72.2	92.8	88.8	36	9
April	85.6	71.2	83.2	82.9	146	41
May	80.0	70.5	88.2	80.0	95	30
June	48.5	29.4	60.6	36.0	68	25
July	35.3	35.3	100.0	42.9	17	7

Length of an unsuccessful cycle can be calculated (assuming a constant probability of nest loss during the nest period) with Ricklefs' (1973) equation

$$T_f = \frac{Q - mPT}{mQ}$$

where P is the proportion of successful nests, Q is $1 - P$, T is length of egg laying, incubation, and nestling periods and m is the average daily mortality rate (see below). Length of an unsuccessful attempt averaged 19.3 days in southern Arizona (all data combined) and 17.2 in southern Nevada. With these an average nesting attempt can be calculated by

$$\overset{*}{T} = P(T + r_s) + Q(T_f + r_f)$$

(Ricklefs 1970). This value was 36.9 days in southern Arizona and 31.5 days in Nevada. Thus about 3.7 and 2.1 broods could be attempted, on the average, in the 2 localities given the breeding season length in Table 2.

Nesting success.—Several factors affect nesting success in the Verdin. Nest orientation was shown to be an important variable (Austin 1976) as was found for the Cactus Wren (*Campylorhynchus brunneicapillus*) (Austin 1974). Success also tended to decrease from beginning to end of the breeding season (Table 3). Considerable variation existed in nesting success among the several localities for which data were available (Table 4), possibly a reflection of annual differences, although 2 successive years in southern Arizona were very similar. Overall fledging success for all studies reported in Table 4 was 59% which is within the range given for enclosed nesting species (Nice 1957).

Daily mortality rates calculated by

$$m = \frac{-(\log_e P)}{T}$$

TABLE 4
NESTING SUCCESS OF THE VERDIN

Location	Success (%) Hatching	Fledging	Nestling	Nest	N eggs	N nests	Source
Texas	56.3	34.4	61.1	33.3	32	12	NANRCP
New Mexico	–	56.9	–	–	48	18	Moore 1965
Southern Arizona	96.4	82.1	85.5	80.0	56	15	Hensley 1954
Southern Arizona							
Saguaro-Palo Verde	73.5	65.5	89.2	76.4	264	72	this study
Mesquite grassland	61.5	44.1	71.6	54.2	143	48	this study
Central Arizona	48.8	29.1	59.5	36.0	86	25	Taylor 1971
Southern Nevada	85.9	72.4	84.2	86.5	199	52	this study
Total	72.7	59.1	81.5	67.4	780	224	
Average daily mortality rate (%)	1.67	1.42	1.13	1.06			

(Ricklefs 1969), averaged 1.42% (0.53–3.33) from laying to fledging for eggs and 1.06% (0.39–2.97) for nests. This indicates that within-nest loss exceeded total losses and was true for all samples except for the Texas sample (Table 4) and Hensley's (1954) sample. Within-nest losses exceeded whole nest losses during both the egg (0.57%) and nestling (0.26%) stages for all samples combined. Individual losses during the incubation period averaged greater (by 0.54%) than during the nestling period although 2 of the 6 samples (Hensley, southern Nevada) showed the opposite trend (Table 4). Similarly, whole nest losses averaged greater during incubation (0.23%).

These low values are typical of enclosed nesting species, and the resultant vectors indicate that hatching failure and possibly desertion are major factors of mortality (Ricklefs 1969). I was able to assign probable factors responsible for mortality of 105 individuals (65 eggs, 40 nestlings). Hatching failure accounted for 24.8% and desertion for 21.9% of all mortality. These factors accounted for only 8.2% and 5.2% of total mortality in 6 species summarized by Ricklefs (1969). Predation accounted for 58.4% of nest mortality in these species compared to 19.0% in the Verdin.

Success and productivity comparisons between 3 and 4 egg clutches are presented in Table 5. Four egg clutches produced more young per nest than 3 egg clutches. The difference is greater in early nests than in late nests. In early nests, 4 egg clutches were more efficient in fledging young from eggs which hatched than were 3 egg clutches. In late nests, however, 3 egg clutches were somewhat more efficient in fledging young. The relatively high pro-

TABLE 5

COMPARISON OF PRODUCTION AND NESTING SUCCESS BETWEEN 3 AND 4 EGG CLUTCHES OF THE VERDIN

	Early nests clutch size		Late nests clutch size	
	3	4	3	4
Number of nests	13	69	81	38
% Nests with hatched eggs	85	94	77	87
% Nests with fledged young	69	88	65	74
% Nests hatch. young/fledg. young	82	94	85	85
% Eggs hatching	85	85	68	74
% Eggs producing young which fledged	62	74	55	56
% Eggs hatch./producing yg. which fledged	73	87	81	76
Mean no. of fledglings per nest in which eggs hatched	2.2	3.1	2.2	2.6
Mean no. of fledglings per nest	1.9	3.0	1.7	2.2

portion of 4 egg clutches among late nests may be of value during favorable years.

Post-fledging mortality.—Fledgling Verdins remained dependent on the parents for 2 or more weeks post-fledging. In southern Arizona, I was able to follow 21 fledglings of which 17 survived this period. Mortality rates averaged 0.87% per day (1.05% per day during the first 15 days). The immediate post-fledging period has previously been shown to be the time of heaviest mortality of birds out of the nest (Lack 1966, Ricklefs 1973).

Immature adult ratios.—Immature to adult ratios for 286 specimens from southwestern United States are presented in Table 6. These were high during and immediately after the breeding season, decreased rapidly thereafter and leveled off in November at a value averaging about 0.67. The change reflected a greater mortality rate of first year birds than adults until mid-winter. Thus, the breeding population of Verdins was composed approximately of 60% birds in at least their second season.

TABLE 6

NUMBERS OF IMMATURES (I) AND ADULTS (A) AMONG SPECIMENS EXAMINED AND RATIO OF IMMATURES TO ADULTS

	May–June	July–Aug.	Sept.–Oct.	Nov.–Dec.	Jan.–Feb.	March
I	32	40	31	24	17	4
A	18	22	29	39	24	6
I/A	1.78	1.82	1.07	0.62	0.71	0.67

TABLE 7
NUMBER OF YOUNG FLEDGED BY VERDINS

Location	Number of pairs	$\bar{x}$ no. young fledged per nest	$\bar{x}$ no. young fledged per individual	Source
Nevada-Arizona[1]	–	3.61	1.81	this study
Nevada[2]	9	3.44	1.72	this study
Arizona[2]	20	3.40	1.70	this study
Arizona[3]	8	2.88	1.44	Taylor 1967
New Mexico[4]	14	3.78	1.89	Moore 1965

[1] Data for Clark County, Nevada and Pima County, Arizona (1969–1971) assuming 50% of pairs build late nests (Moore 1965, this study) and means of 2.74 and 1.73 young fledged per early and late nest, respectively (this study).
[2] Known pairs followed throughout season.
[3] Data for 1965 excluding 4 pairs which left study area shortly after laying.
[4] Data for 1965 assuming as stated that 50% of pairs renest and mean of 2.64 young fledged per nest from first nests and 2.27 young fledged per nest from second nests (Moore 1965).

Because first year Verdins before the first prebasic molt are distinguishable from adults in the field, a bias by collectors may result. As a check on the accuracy of the I/A ratio during and just after the breeding season, I compiled data on average production per pair (Table 7). This averaged 1.71 young fledged per adult and was very similar to the I/A ratio (Table 6). Another check was made by multiplying mean clutch size (3.55) by mean fledging success (0.591) and number of broods attempted (1.5) which gave a similar value of 1.57 nestlings per individual (3.15 per pair). Thus, for the Verdin, the I/A ratio (in May–August) appears to be a good indicator of successful production.

For a sample of 54 specimens for October to March from Baja California, Mexico, the I/A ratio was 1.16 (29/25) and for 23 specimens from the main part of Mexico a ratio of 0.92 (11/12). These ratios were considerably higher than for southwestern U.S. populations.

First year and adult mortality.—From the I/A ratio data, mortality and survival rates can be calculated. Assuming breeding populations are stable and adult mortality rates are constant throughout the year, mortality rates of first year birds can be calculated on a seasonal basis. Because I assumed stable populations and that the proportion of first year birds in the breeding population equaled adult losses, annual adult mortality was 40%. Annual mortality for first year birds was 75%. This complements the 24% first year survival predicated from known production (1.7 fledglings per adult) and adult mortality (40%).

Mortality rates of first year birds from 1 July to 1 December averaged 0.81% per day. From 1 December to 1 May, mortality averaged 0.13% per day similar to the adult rate of 0.14% per day. The mortality differential between first year birds and adults can be calculated by:

$$m_A - m_I = \frac{\log_e R(t)/R(o)}{T}$$

(Ricklefs 1973) where $R(o)$ is the I/A ratio at some time o and $R(t)$ is the I/A ratio after some period of time (T). This value for the Verdin was nearly 20% per month until 1 December. The mortality differential from 1 July to 1 May was 9.7% per month.

The samples from Mexico indicated a greater annual adult mortality (approaching or exceeding 50%) than further north.

DISCUSSION

Among passerine birds, mortality rate generally decreases at each stage of the life cycle from egg to adult (e.g., Lack 1966, Ricklefs 1969, 1973). These data for the Verdin are summarized in Table 8. As noted by Ricklefs (1973) post-fledging survival rate appears higher in species with long nestling periods reflecting their greater maturity at fledging. In many species post-fledging mortality rate is lower or about equal to nestling mortality rate. Most species in which post-fledging mortality rate approached or exceeded nestling mortality rate, nest in enclosed nests or cavities. Such species are well-known for their high nesting success (Nice 1957). The first week out of the nest may be the most critical for some species (Snow 1958) and newly fledged young may be especially susceptible to severe weather (Smith 1967). First year survival rate is usually greater than in the nest and lower than annual adult survival rate. As was true for thrushes and tits (Lack 1946, 1966) survival rates of the Verdin approached adult levels after 6 months. The adult survival rate of 60% per year is at the upper end of the range for passerines given by Lack (1954).

In addition, first year survival was about 42% of adult annual survival and considerably higher than the 25% of adult survival suggested for first

TABLE 8

MORTALITY AND SURVIVAL RATE OF THE VERDIN

	Egg stage[1]	Nestling stage	Post-fledging stage	First 6 months[2]	Second 6 months	Adult
Mortality (% per day)	1.69	1.05	0.87	0.81	0.13	0.14
% Eggs to survive to the end of this period	72.5	59.9	46.9	13.9	11.0	—
Number of days	19	18	28	180	180	—

[1] Including laying period.
[2] Including post-fledging stage.

year small land birds (Ricklefs 1973) and may reflect the lower level of productivity in arid temperate regions (Ricklefs 1973).

The increase in I/A ratio with decreasing latitude and clutch size was counter to the trend for Blue Tits (*Parus caeruleus*) (Snow 1956) and Rough-winged Swallows (*Stelgidopteryx ruficollis*) (Ricklefs 1972). The data for the Verdin from Mexico suggest that nesting success or first year survival is greater in Mexico or that the nesting season is substantially longer (as indicated above) and productivity is greater to offset a higher rate of adult mortality.

SUMMARY

Demographic parameters of the Verdin are discussed. Clutch size displayed a decreasing gradient from east to west and north to south. Breeding season length decreased from south to north. Nesting success was greatest during the first 2 months of the breeding season and varied with locality and year. Based on immature/adult ratios, annual adult survival was 60% in southwestern U.S. and 50% in Mexico. Survival increased during the first year of life and approached adult levels at about 6 months.

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