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GROWTH OF NESTLING MOUNTAIN BLUEBIRDS

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Patterns of nestling growth have been described for many passerine and non-passerine species (e.g., Ricklefs 1968, 1973, 1979, Dunn 1975, Ricklefs et al. 1980), but comparative data are still inadequate for thorough analyses of variation within and among most populations. Although bluebirds (genus *Sialia*) are distributed throughout North America and will readily use nest boxes placed in suitable habitat, little is known about post-hatching growth. Pinkowski (1975) described growth and development of Eastern Bluebirds (*S. sialis*) in southern Michigan. Power (1966, 1974) provided weights for nestling Mountain Bluebirds (*S. currucoides*) in Montana, and McCluskey et al. (1977) listed weights for Western Bluebirds (*S. mexicana*) and Mountain Bluebirds in Oregon. However, neither Power (1966, 1974) nor McCluskey et al. (1977) analyzed the weight data with respect to growth rate or other variables associated with nestling growth.

Here I present an analysis of growth of nestling Mountain Bluebirds with respect to brood size and season in Washington during 1976 and 1977 and compare these data with those of other bluebird populations. I also compare Ricklefs' (1967) graphical method and the Non-Linear Regression (NLIN) procedure of the Statistical Analysis System (SAS) for fitting weight data to growth equations.

STUDY AREA AND METHODS

The study area was located about 4 km south of Bickleton, Klickitat County, in south-central Washington where elevations ranged from 701 to 915 m. The vegetation is sagebrush prairie with big sagebrush (*Artemisia tridentata*), rubber rabbitbrush (*Chrysothamnus nauseosus*), bluebunch wheatgrass (*Agropyron spicatum*), and cheatgrass brome (*Bromus tectorum*). The climate is characterized by hot, dry summers and cool, wet winters with most precipitation falling as snow or rain during winter and early spring. Compared to long-term averages, the breeding season in 1976 was drier and cooler and 1977 was drier yet, but warmer (U.S. Environmental Data and Information Service 1965–1977).

Mountain Bluebirds used nest boxes placed on fence posts bordering county roads (Herlugson 1981). Nestlings of known age (hatching day designated as day 1) were weighed in the early morning to the nearest .1 g on an Ohaus triple-beam balance. Individuals within a brood were weighed from 1 to 5 times ($\bar{x}$ = 2.0 ± .01 SE) throughout the nesting period. Therefore, all observations were not independent, but the large sample sizes obtained in this study (Table 1) should lessen the effects of this lack of independence. All data points were combined for a given brood size, year, or season (see below) rather than attempting to generate growth curves for individual nestlings. The data presented here,

TABLE 1. Number of individual weights and number of broods in parentheses for each brood size of Mountain Bluebird nestlings early and late in the breeding season.

Year	Season	Brood size 3	4	5	6	Total
1976	Early	36 (6)	88 (10)	220 (14)	150 (10)	494 (40)
	Late	30 (3)	88 (7)	105 (7)	60 (3)	283 (20)
1977	Early	33 (9)	44 (8)	100 (16)	60 (8)	237 (41)
	Late	12 (4)	36 (7)	60 (7)	24 (2)	132 (20)

then, represent growth characteristics for the population and not for a given group of chicks throughout the nestling period. Broods were classed as (1) Early—only first brood nestlings, or as (2) Late—renests of first brood attempts that failed, second broods, and late first broods (those hatching after 15 June 1976 or 13 June 1977). Late first broods were placed in the second category because these broods may have represented second brood attempts by birds immigrating to the study area or birds changing nest sites. Because of the dates of hatching, I assumed that adults raising late broods had raised or attempted to raise a previous brood, although some may have been initial attempts by primiparous females that normally nest late (Power pers. comm.).

Logistic equations for Mountain Bluebirds in Washington were fitted to growth curves in two steps. First, equations of the form $W(t) = A/\{1 + \exp[-K(t - t_i)]\}$, where $W(t)$ is the body weight (g) at age t (days), A is the weight asymptote (g), K is the growth rate constant (days^{-1}), and t_i is the age (days) at the inflection point of the growth curve, were fitted to growth curves by the graphical method of Ricklefs (1967). Second, the same data were fitted to a logistic equation model using the NLIN procedure of SAS (Helwig and Council 1979). Regression coefficients (A and K) from NLIN were first tested for homogeneity of variances using an F statistic and then compared using a *t*-test when variances were equal and t' when variances were not equal (Snedecor and Cochran 1967). Variances for the above comparisons and for comparisons among species of bluebirds were based on the number of broods rather than on the number of individual nestling weights to compensate partially for multiple weighings of most nestlings. I used variances from the NLIN procedure and a *t*-test to check for differences between regression coefficients from the NLIN procedure and Ricklefs' (1967) method. I compared the two methods by using weight asymptotes from NLIN to derive growth rate constants by Ricklefs (1967). I fitted weight data from McCluskey et al. (1977) to growth equations following Ricklefs (1967). All data are expressed as $\bar{x} \pm$ SE except where noted otherwise.

RESULTS AND DISCUSSION

Ricklefs' (1967) graphical method for estimating regression coefficients has been used in many comparative studies (e.g., Dunn 1975),

TABLE 2. Weights (g) of nestling Mountain Bluebirds in Washington.

Day	$\bar{x}$	SE	n	Day	$\bar{x}$	SE	n	Day	$\bar{x}$	SE	n
1	3.14	.08	82	8	21.68	.38	40	15	29.56	.51	34
2	4.48	.13	52	9	23.11	.44	50	16	30.53	.27	35
3	6.79	.20	43	10	24.33	.42	68	17	30.91	.28	44
4	8.62	.22	93	11	26.33	.39	82	18	30.71	.38	51
5	9.83	.21	101	12	26.98	.28	90	19	29.86	.45	25
6	11.43	.33	56	13	27.32	.62	36	20	30.72	.43	18
7	15.25	.55	53	14	29.05	.44	63	21	29.61	.24	30

but the NLIN procedure seems to have been used relatively little (Constantz 1980) and the two methods may not be strictly comparable. Ricklefs' (1967) method does not use all the weight data because conversion factors become sensitive to small weight changes as the upper asymptote is approached. Therefore, Ricklefs recommended that unless the data were exceptionally good, the conversion factors "should not be relied on for weights greater than 90% of the asymptote" (1967:981). In the present study, only 13 of 21 (62%) values would be used (Table 2). Also, estimates of K are affected by the asymptote(s) selected (Ricklefs 1967, 1968) and by the number of iterations used when fitting data to growth curves. The NLIN procedure uses the entire data set and produces a best-fit to a given non-linear model (in this case a logistic equation) with least-squares or weighted least-squares estimates of the variables by regressing the residuals on the partial derivatives of the model with respect to the variables, until the iterations converge or convergence is assumed (Helwig and Council 1979). Interspecific, intraspecific, and geographic comparisons of growth among populations are difficult because, unless individual chicks are followed for the entire nestling period, Ricklefs' (1967) graphical method does not yield estimates of variance. The NLIN procedure of SAS provides estimates of standard errors for the regression coefficients for each data set.

None of the regression coefficients A and K produced by NLIN for Mountain Bluebirds in Washington (Table 3) differed ($P > .40$); therefore, all nestling weight data for years, seasons, and brood sizes were combined (Table 2). Growth rate constants from Ricklefs' (1967) method and from the NLIN procedure (Table 3) likewise did not differ ($P > .05$) except that the 1976 growth rate constant from NLIN was greater ($t = 2.25$, df $= 59$, $P < .025$). I could find nothing in the raw data or in the data analysis to explain this disparity.

Both regression procedures (Ricklefs 1967, NLIN-SAS) yielded higher growth rate constants for late broods (Table 3). Ricklefs and Peters (1979), however, noted significantly higher growth rates in early (first) broods of Starlings (*Sturnus vulgaris*) and Ross (1980) reported that nestling Ipswich Sparrows (*Passerculus sandwichensis princeps*) had non-significantly higher growth rates early (June) in the breeding season than late (August). Analysis of weight data using Ricklefs' (1967) method for

TABLE 3. Variation in calculated growth rate constants (K) using Ricklefs' (1967) graphical method and the Non-Linear Regression (NLIN) procedure of the Statistical Analysis System (SAS). Weight asymptotes were estimated by the NLIN procedure.

	Growth rate constant ($days^{-1}$)		Weight asymptote
	Ricklefs (1967)	NLIN (SAS) $\bar{x} \pm SE$	$\bar{x} \pm SE$ (g)
Year			
1976	.379	.414 ± .011	30.99 ± .23
1977	.382	.385 ± .015	29.55 ± .37
Season			
Early	.355	.379 ± .011	30.59 ± .28
Late	.390	.426 ± .014	31.00 ± .25
Brood size			
3	.379	.370 ± .034	30.08 ± .65
4	.389	.390 ± .019	30.80 ± .46
5	.404	.424 ± .013	30.84 ± .26
6	.378	.359 ± .015	31.01 ± .45
Years, seasons, and brood sizes combined	.377	.397 ± .009	30.71 ± .20

broods of equal size compared between seasons with years combined shows that growth rate constants for broods of 4 and 5 were greater (K_4: $P < .01$; K_5: ns) for early ($K_4 = .448$ $days^{-1}$, $K_5 = .431$ $days^{-1}$) than for late broods ($K_4 = .332$ $days^{-1}$, $K_5 = .390$ $days^{-1}$). Data for broods of 3 and 6 were not complete enough for both years to compare early and late broods. Higher late season K values for pooled data (Table 3) resulted from an increasing proportion of brood sizes with the highest growth rates. Broods of 4 and 5 comprised 59.2% of early and 70.0% of late nests. Growth rate increased up to broods of 5, then decreased for broods of 6 (Table 3). Maximum growth rate corresponded to the most frequent brood size for the study population; broods of 5 represented 49.3% (n = 67) and 61.1% (n = 95) of all broods in 1976 and 1977, respectively (Herlugson 1980). Ricklefs (1968, using data from Lack and Silva 1949, and Lees 1949) showed that European Robins (*Erithacus rubecula*) had increasing growth rates as brood size increased from 2 to 5 but then decreased for the largest broods of 6 and 7. Mountain Bluebirds in Washington followed the same pattern.

Ricklefs and Peters (1979) used estimates of variance for A and K from their Starling population to test for differences between their regression coefficients and those from other studies which did not report variances. Using estimates of variance for weight asymptote ($s_A^2 = 4.84$ g^2) and growth rate constant ($s_K^2 = .0098$ $days^{-2}$) from the present study, conservative statistical differences ($P < .01$, n = 20) between bluebird populations would be accepted when differences between means exceeded 1.3 g for A and .085 $days^{-1}$ for K. Mountain Bluebirds from

TABLE 4. Adult weights and growth data for three bluebird species.

Species	Locality	Adult weight (g) $\bar{x} \pm SD$ (n)	R %	Nestlings: n[a]	Weight asymptote (g)	Growth rate constant ($days^{-1}$)	Age in days when leaving nest: $\bar{x} \pm SD$ (n)[b]	Range	Source[c]
Eastern	Michigan	30.0 ± 1.4 (16)	90.7	608	27.2	.488	18.8 ± 1.5 (184)	16–22	1
	New York	30.4	90.5	2	27.5	.484			2
Western	Oregon			265	28.0	.436	19.1 (34)		3
	Washington	28.0 ± 2.2 (21)	96.4	127	27.0	.464	21.0 ± 1.3 (7)	19–23	4
Mountain	Oregon			214	29.9	.462	18.0 (46)		3
	Washington	29.6 ± 3.0 (42)	103.7	1146	30.7	.397	20.9 ± 1.6 (33)	18–24	5

[a] n = number of individuals except for Hamilton (1943) in which only the number of broods was given.
[b] n = number of broods except for Pinkowski (1975) who reported the number of individuals.
[c] 1 = Pinkowski 1975, 2 = Hamilton 1943 (in Ricklefs 1968), 3 = McCluskey et al. 1977, 4 = Herlugson unpubl., 5 = this study.

Washington differed from all other bluebird populations in weight asymptote (Table 4). With respect to growth rate constant, Mountain Bluebirds from Washington differed from Eastern Bluebirds in New York and Michigan, but not from Western Bluebirds in Washington and Oregon or from Mountain Bluebirds in Oregon. Age when the young leave the nest varied little among species and ranges overlapped nearly completely (Table 4).

The ratio (R) of nestling weight asymptote to adult weight varies (Table 4) and may be related to foraging behavior of adults. Ricklefs (1968) has shown that aerial feeders (swallows, swifts, etc.) have the highest R values, foliage feeders (tanagers, vireos, warblers, etc.) are next, and ground feeders (many finches, icterids, and some thrushes) have the lowest R's. The three bluebird species differ in the percentages of aerial and ground foraging and these are reflected in R values. Breeding Eastern Bluebirds use aerial foraging (flycatching, flight-gleaning) only 8.9% (Goldman 1975) and 11.8% (Pinkowski 1977) of the time, values similar to but less than that of 12.8% aerial foraging (flycatching, hover-foraging) for Western Bluebirds (Herlugson 1980). Mountain Bluebirds do much more aerial foraging (hover-foraging, flycatching, hawking, perch-foraging/hover-foraging) both in Washington (22.5%, Herlugson 1980) and Montana (32.3%, Power 1980: data from Table 4). The ranking of bluebirds with respect to amount of aerial foraging, Eastern < Western < Mountain, is the same as for ranking of R values (Table 4).

SUMMARY

Nestling Mountain Bluebirds in Washington exhibited no statistically significant differences in growth rate between years or seasons or among brood sizes. Slight variations in growth rate between seasons and among brood sizes were consistent with analyses of growth for other passerines. Ricklefs' (1967) graphical method and the NLIN procedure of SAS produce similar estimates for growth rate constants.

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