FOOD, PREDATION, AND REPRODUCTIVE ECOLOGY OF THE DARK-EYED JUNCO IN NORTHERN UTAH

KIMBERLY G. SMITH[1] AND DOUGLAS C. ANDERSEN[2]
Department of Biology and Ecology Center, UMC 53, Utah State University,
Logan, Utah 84322 USA

ABSTRACT.—During 1976, 1977, and 1978, 26, 29, and 19 nests, respectively, of the ground-nesting, "Pink-sided" Dark-eyed Junco (*Junco hyemalis mearnsi*) were monitored in a spruce-fir ecosystem in northern Utah. In 1976 and 1977, 4-egg clutches, found mainly in June through mid-July, produced more young than did 3-egg clutches, found after mid-July. In these two years, nestlings from 4-egg clutches in which all eggs hatched gained significantly more weight than did nestlings from 3-egg clutches. In 1978, only 5- and 4-egg clutches were found, and these nestlings were intermediate in weight between nestlings from the 4- and 3-egg clutches of the previous years but not significantly different from nestlings of either clutch size. Growth rates (*K*) of body weight were not significantly different among nestlings from all clutch sizes, so that the rate of weight gain seems independent of clutch size in the Pink-sided Junco. Final tarsal length upon leaving the nest also did not differ significantly among clutch sizes, but the rate of tarsal growth did. The length of tarsi was independent of clutch size, and the length upon leaving the nest was equal to that of adult juncos. We interpret this as support for the adaptive-growth hypothesis, as tarsal length should have high functional importance in passerines that run rather than fly from the nest.

Populations of major food items and potential nest predators were monitored. Although climatic conditions varied dramatically during the three seasons we studied these juncos, the dry biomass of food items in junco diets peaked 1 week after the mean hatching date of 4-egg clutches in all three years. We suspect that nestlings from late 3-egg clutches experienced reduced food availability, which explains the difference in weight between nestlings from 3- and 4-egg clutches. Total rodent predation pressure remained at or above 10 individuals/ha, although populations of the species involved fluctuated between years. Increased predation was noted in 1977, when weasel populations were unusually high. Late-spring snowstorms and late-summer thunderstorms also probably influence nesting success. We hypothesize that predation pressure and short periods of both food abundance and favorable weather influence the initiation of breeding, clutch size, and nestling-growth patterns and lead to a decline in clutch size as the breeding season progresses. *Received 14 November 1979, resubmitted 9 November 1981, accepted 11 April 1982.*

NUMEROUS models have been proposed to account for variation in avian clutch size in terms of both proximate and ultimate factors (reviewed by Klomp 1970). Lack's (1954: 22) suggestion that food supply directly affects mean clutch size has been supported by field observations (Bryant 1975 and references therein), natural experiments (Anderson 1977), and controlled field experiments (Hussell 1972, Crossner 1977). In a recent review of experimental evidence, however, Högstedt (1981) concluded that factors other than food must also be important. Such factors would include predation, competition, and territoriality (e.g. Cody 1966, Brockelman 1975, Dhondt 1977, Perrins 1977, Högstedt 1980). Undoubtedly, many factors act in concert to produce variation in clutch size within and among species; hence, simple explanations encompassing only one factor should not be expected to explain variation in clutch size over broad areas or among diverse avian taxa. Ultimately, natural selection should promote the clutch size that results in the greatest parental fitness (e.g. Charnov and Krebs 1974, Perrins and Moss 1975; but see De Steven 1980).

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[1] Present Address: Department of Zoology, University of Arkansas, Fayetteville, Arkansas 72701 USA.

[2] Present Address: Department of Forestry and Natural Resources, Purdue University, West Lafayette, Indiana 47907 USA.

Research on avian reproductive ecology has expanded to include an examination of selective factors affecting growth and development of nestlings (Ricklefs 1967, 1968a, 1976; Austin and Ricklefs 1977; O'Connor 1977a, and references therein). The "adaptive-growth hypothesis" states that a nestling's resources are allocated to the growth of those body components with the highest current functional priority but also with regard to future needs (for review see O'Connor 1977a). Because functional priorities (e.g. development of flight muscles, feathers, or digestive organs) are different among species having different nesting habits, the adaptive-growth hypothesis predicts differences in the growth patterns of different species (e.g. Austin and Ricklefs 1977, O'Connor 1977a).

In this report, we examine the breeding ecology of the Pink-sided Junco (*Junco hyemalis mearnsi*), a member of the Dark-eyed Junco complex. We correlate several direct determinants of fitness (clutch size, nesting success, and growth rates) with environmental features (available food supply, predator populations, and weather conditions) and suggest causal relationships among them. We contend that selection has operated to produce a suite of interdependent characteristics allowing the Pink-sided Junco to occupy a relatively harsh and unpredictable environment, and, based on our observations, we suggest an adaptive strategy, which we present as hypotheses to be tested by other independent studies.

Study Area and Methods

The Pink-sided Junco is the most common ground-nesting, ground-feeding, insectivorous bird found above 2,000 m in northern Utah. Females were flushed from nests incidental to extensive foot travel by ourselves and co-workers throughout about 2 km^2 of mixed subalpine meadows, aspen (*Populus tremuloides*) forest, and spruce-fir (*Picea engelmannii-Abies lasiocarpa*) forest in or near the Utah State University School Forest (elevation = 2,600 m), Cache and Rich counties, Utah (41°52′N, 111°30′W). Although no systematic search for nests was made, most of the area was repeatably visited by us and cooperating workers advised in our techniques for locating nests. A more thorough description of the study site is presented in Schimpf et al. (1980).

Data were collected during the summers of 1976, 1977, and 1978. Upon discovery, nests were visited almost daily, but no set visitation time was followed. Nestlings were weighed to the nearest 0.25 g using a 30-g Pesola spring scale. In 1977 and 1978, the right tarsus was measured to the nearest 0.1 mm with dial calipers, and individual nestlings were identified by marking tarsi with indelible black ink. Average weighing times of nestlings ranged between 1200 and 1600, and most were between 1300 and 1500. Nestlings were banded with USFWS aluminum bands on about Day 8; a few chicks banded at earlier ages were removed from the nest by parents. Nest losses due to banding were not included in the analysis. Weights and measurements of adult and juvenile juncos were obtained from birds mist-netted on the study site during summers of 1976 and 1977.

Females that laid 4-egg clutches initiated incubation after the 3rd egg was laid. The first 3 eggs hatched synchronously 11–12 days after incubation was initiated, while the 4th egg hatched later the same day or the next morning. For each individual nestling, the day of hatching was considered Day 0 in all analyses, so that in some nests one nestling was a day younger than its siblings (two nestlings in a few five-egg nests). Eggs hatched more or less synchronously in three-egg clutches. Only nests in which all eggs hatched are included in the analyses of weight gain and tarsi growth. Of the 73 nestlings used in the analysis of weight gain, 44 were first measured on Day 0 or Day 1, 21 on Day 2, and 8 on Day 3. Based on our observations, we assumed in the analysis that all nestlings weighed 1.75 g on Day 0 if they were not measured on that day.

We analyzed the increase in body weight and length of tarsus by fitting logistic growth curves to the data points of individual nestlings (see Ricklefs 1979). The logistic curve has the form:

$$M(t) = A/[1 + \exp(-K[t - t_i])]$$

where $M(t)$ is the weight (g) at age t (days), A is the asymptote (g) of the growth curve, K is the growth rate constant (days^{-1}), and t_i is the age at the inflection point. The curves were fitted using the nonlinear least-squares regression procedure (NLIN) available in the SAS statistical package. Only individuals with four or more data points were included in the analysis. Also, individuals were deleted from further analysis if the standard error of the asymptotic estimate was greater than 10% of the estimated asymptote. Differences in asymptotes (final weights) and rates of growth (K) among clutch sizes and years were then examined using t-tests.

The stomach contents of three adult juncos shot while actively feeding within the study area (1 each on 20 June, 13 July, and 21 July 1977) were examined to determine major food items. The stomach-content data corroborated results of other studies (see below) and supported our field observations that seeds are not important in junco diets during breeding on our study site. Estimates of abundance and biomass of known and suspected food items (arthropods) were made available to us by James A. MacMahon (Utah State University). These data were collected concurrently with ours in two meadows within which several nests were found. Random locations within

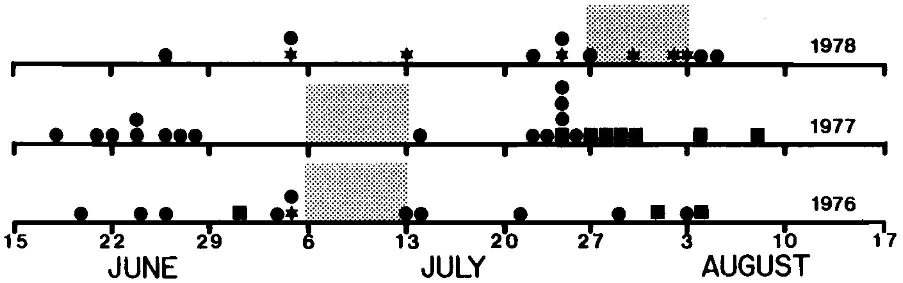

Fig. 1. Distribution of known hatching dates for 3-egg (squares), 4-egg (circles), and 5-egg (stars) clutches in 1976, 1977, and 1978. Shaded areas highlight the weeks of peak dry biomass of food items in junco diets.

meadows were sampled by vacuum (Dietrick 1961) at approximately weekly intervals inside a 1.0-m^3 sampling cage in 1976 and a 0.125-m^3 sampling cage in 1977 and 1978. During late morning and early afternoon on each sampling date, 20–47 ($\bar{x}$ = 30) localities were sampled in 1976 and 20 localities were sampled in 1977 and 1978. No samples were collected on windy or rainy days. Although these data represent insects collected from all parts of the vegetation sampled, most meadow vegetation is <0.5 m in height. We feel that these estimates accurately reflect insects available to juncos, as juncos obtain insects from both the ground and lower parts of vegetation (White 1973, Smith 1982a).

Insect biomass estimates for all three years are based on mean oven-dried (60°C) weights of at least 10 individuals from each of the dominant operational taxonomic units (OTU's) within the major taxa we considered. Ratios of OTU's and/or age classes that varied in size were used to determine a weighted mean as appropriate for each sampling date. Relative abundances of spiders were taken from Waagen (1979).

The only vertebrate nest predators on the study site are mammals. Three rodent species and two weasel species were sufficiently abundant to be considered important potential nest predators (Andersen et al. 1980). Density estimates for these species were based on live-trapping conducted in and adjacent to the School Forest in open meadow and in nearby subalpine fir-dominated forest during the summers of 1976 through 1978 [see Andersen et al. (1980) for details]. Because aspen is found on our study area as thin ribbons separating meadow and coniferous forest and because junco nests were not found in Engelmann spruce-dominated climax forest, neither of these areas was considered in quantitative analyses of predation pressure.

RESULTS

Clutch size and fledging success.—Twenty-six, 29, and 19 nests were discovered during 1976, 1977, and 1978, respectively. In 1976 and 1977, 4-egg nests were prevalent through mid-July, after which most 3-egg nests were found (Fig. 1). Mean hatching date for four-egg nests was 9 July in 1976 and 6 July in 1977, but the variation was great in both years (SD = ±15 days in both years). In 1977, mean hatching date for three-egg nests was 30 July. Our observations suggest that late three-egg clutches represent renesting following successful fledging of a first clutch or renesting after predation. For example, in 1977 a female junco abandoned her four nestlings after we trapped and banded her at the nest. Three weeks later she was found within the same territory incubating a three-egg clutch about 30 m from the original nest (see also Tanner 1958, Hostetter 1961, White 1973). Early three-egg clutches may be due to primiparous birds, which in some species commonly produce smaller clutches (e.g. Ross 1980a, Baker et al. 1981). We have no data on the age of breeders; none of the 102 nestlings banded in 1976, 1977, and 1978 has returned to our study area (through 1981). The early three-egg clutch in 1976 was deleted from analysis.

In 1978, five-egg clutches were relatively common, although they are rarely reported for most junco races (Austin 1968). No three-egg clutches were found, even in early August (Fig. 1). Elsewhere, we (Smith and Andersen MS) have suggested that this pattern was due to a late-lying snowpack prohibiting female juncos from initiating nesting until mid-June. Mean hatching date for 4-egg clutches in this year was 21 July (±15 days) and 23 July (±12 days) for 5-egg clutches.

Differences in hatching and fledging success among clutch sizes were determined by comparing 62 nests that contained either eggs or hatchlings when discovered. Four- and 5-egg clutches had poorer average hatching success than did 3-egg nests (Table 1); 4- and 5-egg clutches produced more fledglings from those

TABLE 1. Hatching and fledging success for 3-, 4-, and 5-egg clutches of the Pink-sided Junco during 1976, 1977, and 1978.

Clutch size	Year	n	Eggs hatched	Eggs hatched/ eggs laid	Chicks fledged	Chicks fledged/ eggs laid	Chicks fledged/ eggs hatched	Chicks fledged/ nest (SD)
3	1976	3	8	0.89	5	0.56	0.63	1.67 (1.53)
	1977	8	19	0.79	13	0.54	0.68	1.63 (1.30)
	1978	0	—	—	—	—	—	— —
	ALL	11	27	0.82	18	0.55	0.67	1.64 (1.29)
4	1976	16	36	0.56	27	0.42	0.75	1.69 (1.62)
	1977	17	45	0.66	34	0.50	0.76	2.00 (2.00)
	1978	8	25	0.78	22	0.69	0.88	2.75 (1.83)
	ALL	41	106	0.64	83	0.51	0.78	2.02 (1.82)
5	1976	2	5	0.50	4	0.40	0.80	2.00 (2.83)
	1977	1	0	0.00	0	0.00	0.00	0.00 —
	1978	7	26	0.74	20	0.57	0.77	2.86 (2.12)
	ALL	10	31	0.62	24	0.48	0.77	2.40 (2.17)

eggs that did hatch, however, than did 3-egg clutches. Overall, 5-egg clutches tended to produce more young than did 4-egg clutches, but 4-egg clutches were much more common. Three-egg clutches produced the least average number of young. None of these differences was statistically significant (Wilcoxon rank sum, one-tailed test, $P > 0.30$), however, as most clutches either fledged or lost all nestlings, with few instances of brood reduction.

Growth of nestlings.—We monitored body weight as a general index of developmental stage and tarsus length as a specific morphological feature that we felt would receive functional priority. Our rationale was that tarsi development should be important in ground-nesting birds such as juncos, in which young walk or run from the nest and are flightless for several days thereafter.

Nestlings in 4-egg clutches in which all eggs hatched were heavier than nestlings of the same age from 3-egg clutches after Day 1 (Table 2). With the exception of Day 5, nestlings from 4-egg clutches were significantly heavier (t-test, one-tailed test, $P < 0.05$) from Day 4 through Day 9, the usual day that young leave the nest. The estimated asymptotes for 3-egg clutches (15.2 g ± 2.4 SD, $n = 18$) and 4-egg clutches (16.9 g ± 2.1, $n = 33$) were also significantly different ($t = 2.68$, $P = 0.01$). Growth rates of the nestlings from 3-egg clutches ($K = 0.538 \pm 0.07$) were slower than those from 4-egg clutches ($K = 0.554 \pm 0.09$) but not significantly so ($t = 0.65$, $P = 0.50$). These relationships indicate that nestlings from larger earlier nests were consistently heavier than nestlings from later smaller nests, but nestlings in both clutch sizes grew at the same rates.

In 1978, no significant differences were found between 4- and 5-egg clutches in either weight or growth rate, so they were combined for comparison with the 1976–1977 patterns. Nestlings in 1978 were lighter than nestlings in four-egg clutches the previous years (Table 2), consistently lagging, on the average, by about 0.5 g each day. There was no significant difference between the estimated asymptote in 1978 (16.0 g ± 1.3, $n = 22$), however, and the one estimated for four-egg clutches the previous two years ($t = 1.83$, $P = 0.07$). Nestlings in 1978 were heavier than nestlings from three-egg clutches (Table 2), but the differences are not significant ($t = 1.40$, $P = 0.15$). Nor was the growth rate for nestlings in 1978 ($K = 0.557 \pm 0.06$) significantly different from either 4-egg clutches ($t = 0.13$, $P \gg 0.50$) or 3-egg clutches ($t = 0.97$, $P = 0.35$) the previous two years. Thus, growth rate of body weight is independent of clutch size in juncos.

Nestlings in 4- and 5-egg clutches left the nest at about 80% of adult weight ($\bar{x} = 19.04$ g ± 1.2, $n = 22$ adults). Most nestlings from all nests left on Day 9, although "handling effect" (Burtt 1977) occasionally resulted in birds leaving the nest a day earlier. A similar pattern has been reported for the ground-nesting Rufous-

TABLE 2. Average daily measurements of body weight and tarsal length of nestlings from 3-, 4-, and 5-egg clutches in which all eggs hatched during 1976, 1977, and 1978.

	Body weight						Tarsus length					
	1976–1977				1978		1976–1977				1978	
	3-egg		4-egg		4- + 5-egg		3-egg		4-egg		4- + 5-egg	
Day	n	$\bar{x}$ (SD)	n	$\bar{x}$ (SD)	n	$\bar{x}$ (SD)	n	$\bar{x}$ (SD)	n	$\bar{x}$ (SD)	n	$\bar{x}$ (SD)
0	—	— —	5	1.68 (0.2)	18	1.94 (0.4)	—	— —	—	— —	8	8.4 (0.6)
1	13	2.98 (0.6)	18	2.86 (0.5)	20	2.64 (0.5)	7	9.3 (1.4)	—	— —	5	9.8 (0.7)
2	9	3.67 (0.5)	20	4.68 (0.8)	20	3.92 (0.5)	3	10.2 (0.7)	16	11.4 (0.5)	12	11.0 (0.9)
3	8	5.73 (1.2)	19	6.61 (0.7)	14	6.43 (1.2)	8	13.3 (1.0)	12	14.0 (0.7)	9	14.4 (1.5)
4	7	7.40 (1.0)	20	8.97 (0.9)	14	8.81 (1.1)	4	15.5 (1.0)	16	16.7 (0.9)	12	16.0 (1.4)
5	11	9.50 (1.0)	15	10.65 (0.8)	20	9.95 (1.4)	8	17.6 (0.9)	15	18.3 (0.6)	14	17.7 (1.5)
6	9	11.22 (1.5)	21	12.65 (1.3)	13	12.18 (0.9)	3	18.5 (0.6)	8	20.5 (0.5)	13	20.0 (0.8)
7	9	12.60 (1.8)	15	14.03 (0.7)	14	13.64 (1.4)	—	— —	4	21.2 (0.6)	14	21.1 (1.2)
8	11	13.62 (2.0)	12	14.97 (0.5)	8	14.10 (1.1)	5	22.6 (1.0)	5	22.0 (0.5)	10	21.6 (0.7)
9	3	13.27 (1.3)	8	15.54 (0.9)	6	15.43 (0.5)	3	22.4 (1.5)	3	23.3 (0.6)	2	23.1 (0.2)
10	3	16.53 (0.9)	13	15.98 (1.7)	1	15.50 —	—	— —	9	23.1 (1.0)	—	— —
11	3	13.47 (1.2)	6	15.56 (1.2)	4	15.48 (0.4)	3	21.9 (2.2)	5	23.2 (0.7)	5	23.3 (0.6)

winged Sparrow (*Aimophila carpalis*) (Austin and Ricklefs 1977) and the Ipswich Sparrow (*Passerculus sandwichensis princeps*) (Ross 1980b). Nestling juncos that remained in the nest after Day 10 lost weight ($n = 10$). Banded birds captured by hand 1–2 days after leaving the nest weighed less than they did at fledging ($n = 8$). The average weight of juveniles capable of flight ($\bar{x} = 18.9$ g ± 1.3, $n = 32$) that were caught in mist-nets in July and early August, however, was close to the average adult weight (t-test, $P > 0.50$).

An effect of clutch size on the rate of tarsus growth was evident. Unlike growth rate of body weight, significant differences in the rate of tarsus growth were found between 4-egg clutches ($K = 0.485 \pm 0.11$, $n = 13$) in 1977 and both individuals from 3-egg clutches ($K = 0.363 \pm 0.07$, $n = 7$) in 1977 ($t = 2.67$, $P = 0.02$) and those from 1978 clutches ($K = 0.359 \pm 0.05$, $n = 8$) ($t = 3.09$, $P = 0.008$). Growth rates of tarsi were not significantly different between three-egg clutches in 1977 and 1978 clutches ($t = 0.12$, $P \gg 0.50$).

The greatest differences in tarsus length occurred in the first 7 days (Table 2). After Day 6 average tarsus lengths of individuals from four-egg clutches and 1978 nestlings were almost identical. (Nestlings from 4- and 5-egg clutches in 1978 were again combined in this analysis, as no significant differences were found in tarsus length or rate of growth.) No significant differences existed among clutch sizes on Days 7, 8, and 9 (one-way ANOVA, $P > 0.10$), indicating that tarsus length at the time that the birds leave the nest is independent of clutch size. By Day 8, nestling tarsi were almost fully developed regardless of clutch size. Further, average estimates of asymptotic tarsi lengths for 3-egg (24.2 mm ± 1.7), 4-egg (23.6 mm ± 1.4), and 1978 (24.6 mm ± 1.1) clutches were not significantly different (3-egg vs. 4-egg: $t = 1.03$, $P = 0.35$; 3-egg vs. 5-egg: $t = 0.59$, $P > 0.50$; 4-egg vs. 5-egg: $t = 1.91$, $P = 0.06$). These results support our hypothesis that tarsal length in the Pink-sided Junco has a high functional priority, presumably to accomodate rapid abandonment of the nest, and that final length is a relatively conservative characteristic.

Food availability.—Ants (Formicidae), beetles (Coleoptera, six families identified), leafhoppers (Cicadellidae), and spiders (Arandeida) were the major food components in the three stomachs examined. Lacewings (Hemerobiidae), leaf bugs (Miridae), and several wasps (mostly Ichneumonidae) were also identified. A single Coleoptera larva was found in the stomach samples, but many larvae (including lepidopterans) were observed being fed to nestlings, as were orthopteran nymphs. These stomach contents were almost identical to those reported for juncos on the basis of much larger samples (Martin et al. 1951, Gashwiler and Ward 1968, White 1973), and our observations of larvae and nymphs being fed to nestlings

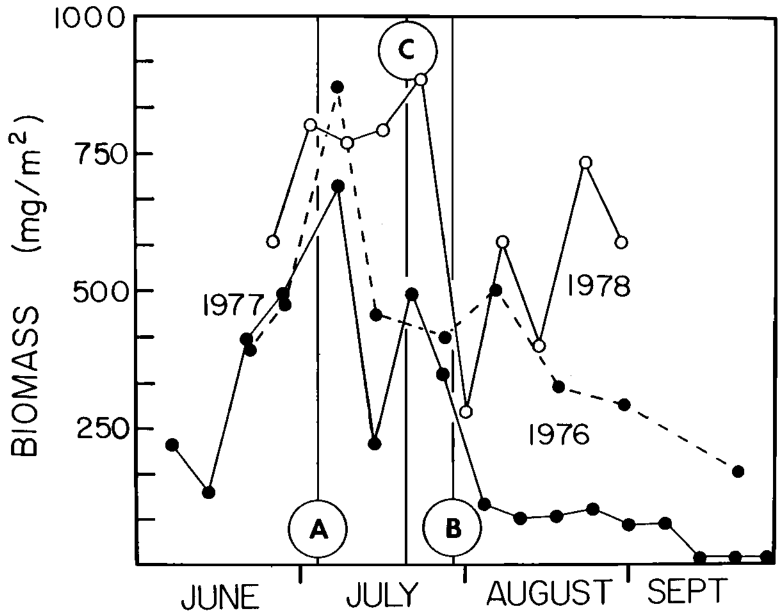

Fig. 2. Changes in biomass of meadow insects known to be captured by breeding Pink-sided Juncos during 1976, 1977, and 1978. Values plotted represent the summation of individual biomass estimates for each major taxa considered (Appendix). Line A is the approximate hatching date for four-egg clutches in both 1976 and 1977. Line B is the mean hatching date for three-egg clutches in 1977. Line C is the mean hatching date for 4- and 5-egg clutches in 1978. In all three years, the mean hatching date of the four-egg clutches is approximately one week before the peak biomass estimate.

match closely the food of nestling juncos sampled by restrictive neck collars in Michigan (Allan 1978). Because of the differential digestibility of hard- and soft-bodied insects (Custer and Pitelka 1975), no attempt was made to assign proportions to various components of the diet.

Densities of food items varied greatly during the three summers, both seasonally and among taxa considered (Appendix). Cicadellids were common in all three years, while lepidopteran and coleopteran larvae and orthopteran nymphs were consistently rare. During the summers of 1976 and 1977, biomass estimates of food items were similar (Mann-Whitney *U*-test, $P > 0.10$), and in both summers biomass dropped substantially during the second week of July, one week after the mean hatching date of four-egg clutches (Fig. 2, line A). A small increase in insect biomass occurred in 1976 just after the mean hatching date for three-egg clutches (Fig. 2, line B), but in 1977 insect biomass steadily declined from mid-July through September (Fig. 2), probably as a result of severe drought conditions that summer (Smith 1982b). Significantly more biomass was present in 1978 (Mann-Whitney *U*-test, $P < 0.001$) than in either 1976 or 1977, but the temporal patterns of insect biomass did not differ between any two years (Kolmogorov-Smirnov two-sample test). As in the two previous years, 1978 insect biomass declined markedly a week after the mean hatching date of 4- and 5-egg clutches (Fig. 2, line C), although about three weeks later than in previous years. The abundance of ground spiders generally paralleled insect abundance changes between 1978 and 1977 (Waagen 1979).

Predator populations and nest predation.—Information on potential predators of junco nests is largely limited to anecdotal accounts, inferences based on studies of other western montane ground-nesting passerines, or on consideration of the food habits of predators themselves (see Williams 1900; Twining 1940; Verbeek 1967, 1970; Morton et al. 1972; Maxson and Oring 1978). We considered two species of chipmunks [*Tamias* (= *Eutamias*) *umbrinus* and *T. minimus*], along with deermice (*Peromyscus maniculatus*), and two species of weasels (*Mus-*

TABLE 3. Densities (individuals/ha) of rodents considered to be important predators on Pink-sided Junco nests within the Utah State University School Forest. Data are modified from Andersen et al. (1980); "forest" represents subalpine fir-dominated forest. Sampling periods are (1) early-, (2) middle-, and (3) late-summer.

		Year and sampling period						
		1976			1977			1978[a]
Species	Habitat	1	2	3	1	2	3	2
Chipmunks[b]								
[*Tamias* (= *Eutamias*) spp.]	Meadow	7.3	2.7	3.5	6.3	2.2	6.4	3.6
	Forest	17.3	5.7	6.6	8.4	4.6	2.1	2.3
Deermice								
(*Peromyscus maniculatus*)	Meadow	8.7	15.8	16.1	6.0	6.1	6.3	4.1
	Forest	2.3	2.9	8.1	4.6	3.6	3.6	2.5
Total mean density		17.8	13.6	17.2	12.6	8.2	9.2	6.2

[a] The trapping program was not initiated until July, several weeks after meadows became snowfree.

[b] Includes *T. umbrinus* and *T. minimus*.

tela frenata and *M. erminea*) as the dominant predators affecting junco reproductive success in our study area. Other potential predators were either locally absent [e.g. other carnivores, snakes, ground squirrels (*Spermophilus armatus*)] or of such low abundances as to be considered insignificant [e.g. corvids (Smith and MacMahon 1981: Appendix].

Individual rodent species showed variation in numbers both seasonally and annually (Table 3). The combined average for all three species remained above about 10 individuals/ha (Table 3) in 1976 and 1977. The lower combined numbers of rodents noted in 1977 was probably the result of an increase in weasels present within the study area that year. No weasels were caught incidental to small rodent trapping in 1976, and only one was captured in 1978, and sightings were rare in both years. In 1977, 11 weasels (9 *M. frenata* and 2 *M. erminea*) were captured in live traps (baited with peanut butter), and sightings were common throughout the School Forest. Seven of the long-tailed weasels caught were young, suggesting an unusually successful breeding year rather than an influx of adults. Density estimates of rodents were lower still in 1978, possibly due to the effects of the late-lying snowpack or to weasel predation the previous year.

Seven of the 26 nests (27%) found in 1976 were eventually preyed upon. A minimum of 38% (11/29) of the nests found in 1977 were eventually preyed upon. Of these, 5 nests contained eggs (or possibly newborn chicks), while 6 contained nestlings. In 1978, 31% (6/19) of the nests found were eventually preyed upon. We attribute the greater predation levels in 1977 to increased numbers of weasels that year. Scattered feathers around two nests in 1977 lead us to suspect weasel predation of brooding females. No evidence of predation on adults was associated with nests during 1976 and 1978, and it is unlikely that adult juncos are susceptible to predation from chipmunks or mice. Several times we have observed adult juncos chasing chipmunks from the vicinity of a nest.

DISCUSSION

Role of food availability.—Early clutches generally hatched in late June or early July before or near the week of peak insect biomass (Fig. 1), at which time insect biomass was nearly double (1976) or triple (1977) the level when adults first arrived (Fig. 2). Young in these nests left the nest in early to mid-July and became independent during a period when insects were still relatively abundant (Appendix, Fig. 2). Thus, the timing of breeding appears to be adapted to insure that periods of maximum energy demand (nestling and fledgling stages) coincide with maximal energy availability (Lack 1968, Dyrcz 1974). The facts that 3 of 4 chicks hatch synchronously and brood reduction is rare or absent both support the argument that the junco's food supply is usually high during mid-summer (see Ricklefs 1967, Lack 1968; cf. O'Connor 1977b, 1978). In those cases in which the first clutch is lost quickly, renests would still produce young at a time when insect biomass is high, in mid- to late-July (Fig. 2). Fledglings from these nests, however, would encounter the late-summer reduction in food supply at a younger age.

Late-summer nests, most probably initiated after either successful fledging of a clutch or a nest loss, usually contained three eggs. This reduction in clutch size may be the result of selection adapting later clutch size to a predictable reduction in food supply (Ricklefs 1967). The decline in insect abundance with the progression of summer drought in the western United States has long been recognized (Cooper 1879). By August 1977, and to a lesser extent in August 1976, our study area experienced a large decrease in insect numbers (Appendix) and biomass (Fig. 2). Also, reductions in day length decreased daily foraging time during the second nesting period (15.2, 14.7, and 14.0 h on 22 June, 22 July, and 22 August on our study sites).

Insect biomass was much greater in 1978, and the peak in biomass occurred about three weeks later than in the two previous years, yet the average hatching date of clutches was again about one week before the peak in insect biomass (Figs. 1 and 2). If insect availability were linked to soil moisture, as suggested by Morton et al. (1972), and junco nesting were controlled by the melting of the snowpack and the exposure of sizable areas of bare ground, as we have suggested (Smith and Andersen MS; see also White 1973), then the nesting cycle of the juncos would be linked to the available insect abundance. Unfortunately, this hypothesis of the mechanism that initiates breeding does not explain how breeding and insect biomass were coordinated in 1977, when the snowpack had melted by the end of April (Smith 1982b). Morton et al. (1972) also suggest that late-lying snowbanks result in insect densities remaining high enough during late summer to insure adequate food for late clutches, and our data demonstrate a maintenance of insect availability well into August in 1978 (Fig. 2).

Growth rates.—Nestlings from 4-egg and 1978 clutches attained greater weight than did nestlings in 3-egg clutches, although all nestings weighed the same on Days 0 and 1 (Table 2). Growth rates of body weight were quite similar among all groups, however. White (1973) also found no difference in growth rate between 3- and 4-egg clutches of juncos in the Sierra Nevada. The difference in weight of nestlings is most pronounced for the period just before leaving the nest (Days 7, 8, and 9, Table 2). This corresponds to the first and second weeks of August for most three-egg clutches, when estimates of insect biomass were lowest. In 1976 and 1977, food availability was highest during the nestling period of most 4-egg clutches (Fig. 2), while numbers (Appendix) and biomass (Fig. 2) of insects were reduced or declining during the nestling period of most all 3-egg clutches. We suggest that this reduction in quantity of available food accounted for much of the reduction in nestling weight in three-egg clutches. We have no data, however, on parental condition (Gibb 1955) or feeding rates, quality of food during the second nestlings, or physiological effect of fewer nestlings begging food (O'Connor 1975a) and, thus, cannot discount these as factors contributing to the differences.

Survival rates as well as family sizes may decrease as the breeding season progresses. Differences in weight at the time young leave the nest (Table 2) may result in differential survivorship favoring the heavier individuals from early nests (Perrins 1965, Perrins and Moss 1975). Ross and McLaren (1981), however, were unable to document any such weight-survivorship correlation with Ipswich Sparrows. Perrins and Moss also argue that optimal clutch size may change during the breeding season. They suggest determining optimal clutch size for a particular time within the breeding season. Ideally, maximum energy requirements of nestlings should match exactly the maximum food-gathering rate of adults (Ricklefs 1968b). If the decrease in insects within our study area is as predictable as we have suggested, then the laying of four-egg clutches and provisioning for the rapid growth of nestlings—both possible in early summer—would become difficult or impossible to achieve in late summer, as environmental conditions and possibly parental quality deteriorate (see Bryant 1978). Thus, two clutch sizes may each be optimal in terms of energy requirements and food availability for the time periods in which they occur.

The proximate factor(s) or mechanism that synchronizes the junco breeding season with insect availability remains obscure. In all three years studied, the mean hatching date of larger clutch sizes was one week before the peak in insect abundance, despite the first year being relatively "normal," the second year including one of the worst droughts this century (Smith

1982b), and the third having unusually late snowmelt (Smith and Andersen MS). We suspect that in most years, as in 1976 and 1978, snowmelt is the important factor, but, as mentioned earlier, other factors must at least occasionally determine breeding dates.

Role of predation and tarsus growth.—We consider the combined abundance of both chipmunks and deermice as a general index of rodent predation pressure. This index (Table 3) remained relatively consistent between years, despite large fluctuations in the contributions of individual species, suggesting that rodent predation pressure may be relatively constant. Although more egg losses occurred early in the breeding season and more nestling losses occurred later on, overall predation generally occurred evenly between egg and nestling periods (13 and 12 clutches, respectively), as predicted for ground-nesting species by Ricklefs (1969). Additional predation loads may be incurred in some years, such as in 1977 when we noted the unusual abundance of weasels (and higher predation rates).

A major means of reducing the risk of predation at the nest is to reduce the amount of time one is vulnerable: natural selection should thus promote rapid growth and nest abandonment. Selective pressures to minimize time spent in the nest are probably intense, as nest predation, in terms of losses of eggs or young, is typically an all-or-none event. The advantage of having a relatively small, fast-growing brood is obvious for small, temperate, ground-nesting birds such as the Pink-sided Junco, Rufous-winged Sparrow (Austin and Ricklefs 1977), and Ipswich Sparrow (Ross 1980b). Rapid tarsal development allows nestlings to run out of the nest before they are able to fly. The fact that nestlings from 3-egg clutches were significantly lighter than nestlings from 4-egg clutches yet attained adult-length tarsi lengths by the time they left the nest (Table 2) supports the adaptive-growth hypothesis (O'Connor 1977a).

Weather.—Adverse weather has much the same influence on nesting birds as predation in that all nestlings are usually lost. Two main climatic events that would influence nesting success in our study area are June snowstorms (1 on 20 June in both 1975 and 1976) and increasingly frequent convectional rainstorms after mid-July. Late-spring snowstorms in western mountains result in nest desertion (Morton et al. 1972), adult mortality, and delayed breeding (Hadley 1969a). We have no direct evidence of the effect of late-spring snowstorms on juncos on our study site, but we suspect that most juncos only raised one brood in 1978 (and 1975) when much of the snowpack remained into late June. One nest was flooded by a thunderstorm in the first week of August 1977, and the three nestlings succumbed. Likewise, Phelps (1968) reported Pink-sided Junco nest losses in late summer due to inclement weather. Locating the nest under protective cover (Hadley 1969b) and rapid fledging of the young would reduce the risk of nest loss due to inclement weather (Ricklefs 1969), although larger clutches may be able to withstand such events better due to nestlings "huddling" together (e.g. O'Connor 1975b).

Selective pressures on junco reproductive biology.—A strategy for increasing reproductive success other than increasing clutch size is to have more than one clutch per breeding season. Reduction in individual clutch size would be selectively advantageous if such reductions contributed to a compensatory increase in the likelihood of successful second broods (for a more detailed treatment, see O'Connor 1978). Individuals with low probabilities of surviving for several years (e.g. small migratory passerines such as juncos) should demonstrate a great commitment to each reproductive cycle (see De Steven 1980), although environmental factors may limit the magnitude of this commitment (Ricklefs 1977). Because selection should promote any adaptations that reduce the negative impact of environmental factors, renesting ability may be favored in nidicolous species. Reducing later clutches by one egg may not significantly affect the number of young fledged compared to four-egg clutches (Table 1). Indeed, fledging a single summer's three extra young may represent a major contribution to individual fitness relative to the average lifespan of a junco (probably <5 yr) and the average reproductive success for single four-egg clutches (Table 1).

We hypothesize that the growth pattern and rapid nest abandonment of nestlings and the possibility of renesting, with associated reduction in the size of the second brood, are a suite of adaptations for maximizing reproductive success in an environment with predictable rodent predation pressure, short periods of food abundance, and weather conditions favorable to nestling survival.

We had intended to test some of these ideas in 1978 by manipulative egg experiments, but Nature provided what we feel is a "natural" egg-switching experiment. In 1978, the snowpack was exceptionally late in melting, and the ground-nesting juncos delayed breeding until sizable patches of bare ground existed. Juncos apparently had little trouble getting the young out of the nest in their five-egg clutches, and average success was higher that year (Table 1), although nestlings weighed somewhat less than in previous years (Table 2) (cf. De Steven 1980). Elsewhere, we (Smith and Andersen MS) develop the argument that in 1978 it was profitable to lay an extra egg, whereas in most years no selective advantage is gained by a delay in breeding. From this we conclude that the initiation of breeding in juncos must also be sensitive to environemntal conditions; it is not clear, however, what factors are controlling the number of eggs a specific female lays.

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APPENDIX. Density (number/m³) of major insect taxa in the diet of the Pink-sided Junco calculated from vacuum samples taken at approximately weekly intervals during the breeding seasons of 1976, 1977, and 1978.

		June				July				August					September			October
Taxa	Year	8	15	22	29	6	13	20	27	3	10	17	24	31	7	14	20	17
Cicadellid adults and nymphs	1976			17	14	48	55		50	81		74	32				16	
	1977	5	15	44	116	75	105	50	60	16	21	25	13	8	15	2	3	2
	1978				95	126	213	311	288	96	212	139	321	290				
Formicidae	1976			15	32	40	13		19	30		11	11				6	
	1977	20	6	42	8	5	1	6	11	1	3	1	3	5	5	0	0	0
	1978				27	19	7	44	26	22	63	20	26	31				
Lepidopteran and coleopteran larvae	1976			1	2	1	2		3	3		1	2				0	
	1977	0	1	0	2	2	1	2	3	1	0	1	0	0	1	1	0	1
	1978				1	1	1	3	6	3	5	2	4	1				
Coleopteran adults	1976			3	6	3	3		5	3		2	4				2	
	1977	12	12	12	11	7	11	4	8	8	13	13	22	15	12	1	2	2
	1978				26	6	1	6	9	5	15	6	11	7				
Orthopteran nymphs	1976			1	1	2	1		1	1		0	1				1	
	1977	1	1	2	2	4	0	3	2	1	0	0	0	0	0	0	0	0
	1978				2	4	3	1	2	1	1	1	1	0				