

THE RELATION OF BREEDING SCHEDULE AND CLUTCH SIZE TO FOOD SUPPLY IN THE RUFOUS-SIDED TOWHEE

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Food is important as an ultimate factor in the timing of breeding (Moreau 1950, Lack 1954, 1966, 1968) and in the evolution of clutch size (Lack 1954, 1966, 1968, Cody 1966, 1971, Klomp 1970, von Haartman 1971) in birds. Although early studies emphasized the significance of food for dependent young (see Lack 1954), it now appears that the food available to the laying female may have a proximate effect as well on the date of first egg deposition and on clutch size, at least in some species (Pitelka et al. 1955, Mebs 1964, Perrins 1965, 1970, Cody 1966: Table 1, Lack 1966, Bengtson 1971, Moss et al. 1971). In this paper, I examine the relation of breeding schedule and clutch size to food in populations of Rufous-sided Towhees (*Pipilo erythrophthalmus*) inhabiting two different habitats along the northeastern Atlantic seaboard.

STUDY AREAS AND METHODS

One population occupied a mesic site which was the William L. Hutcheson Memorial Forest (HMF) near East Millstone, Somerset Co., New Jersey. This is a high-canopied oak-hickory forest, much of which is considered virgin, characterized by rich soils, distinct plant stratification, and a thick layer of litter-duff. It is surrounded by abandoned and cultivated fields. The forest and its vegetation were described by Buell (1957) and Monk (1961).

Two populations occupied xeric woodlands of pine barrens. One of these sites was near Cooper Branch in Lebanon State Forest (LSF), Burlington Co., New Jersey. The moderately open pine-oak woodland here corresponds most closely to the Pine-Oak-Shrub type defined by Stephenson (1965). It is characterized by sterile, sandy soils, two shrub zones (high shrub and low shrub), a low tree canopy, and a patchy and often thin layer of litter. In contrast to HMF, herbaceous vegetation is scarce.

The second pine barrens site was on eastern Long Island at Brookhaven National Laboratory (BNL) near Upton, Suffolk Co., New York. Like the pine barrens in southern New Jersey, this site is on a sandy outwash plain near the coast. The flora, avifauna, soil type, litter structure, and general physiognomy of the LSF and BNL study areas are similar although the latter woodland is somewhat more mesic with more oaks and fewer pines. The towhee is the most abundant bird at both sites.

CLUTCH SIZE AND TIMING OF BREEDING

Data on clutch size were collected routinely as nests were discovered in 1961 and 1962 at BNL and from 1966 to 1968 in New Jersey. Clutch sizes were determined from nests visited at least twice (usually every other day) during the egg-laying or incubation

stages. In a large sample of towhee nests (including those reported here) studied from 1961 to 1975, I found no evidence that predation affecting only part of a clutch early in the nest cycle was a significant problem.

In this paper, timing of breeding refers to the dates when clutches were started. In the absence of first-hand information, I estimated these dates using the criteria described by Peakall (1970). Behavioral data diagnostic of the earliest stages of the nesting cycle (e.g. precopulatory behavior, copulation, carrying nest material) were available for nearly all the pairs studied in the HMF and LSF populations (see Greenlaw 1969). These data verify the nest-based estimates of first laying and support the conclusion that breeding started earlier in the mesic area (HMF) than in the xeric ones (see later).

FOOD SUPPLIES

I tested methods of sampling invertebrates in the normal feeding zones of towhees in HMF and LSF in June 1966. These preliminary samples indicated that the mesic and xeric areas differed markedly in food accessible to towhees. Considering the similarities of LSF and BNL, I feel that the same kind (not necessarily the same magnitude) of difference in food supplies also occurred between HMF and BNL. I systematically sampled HMF and LSF in 1967 and 1968.

Sampling of the food supplies available to foraging towhees in LSF and HMF was guided by information (observations, stomach specimens) on the feeding habits of these birds. By mid-May, 90% or more of the food items taken by towhees in these forest habitats consisted of invertebrates (mostly arthropods). Also invertebrates are brought almost exclusively to nestlings and fledglings (Barbour 1951, pers. observ.). The invertebrate diet was supplemented with ripe fruit from early July on, especially in LSF where blueberries (*Vaccinium* spp.) and huckleberry (*Gaylussacia* sp.) were prevalent. Depending on date and stage of breeding, towhees in HMF spent between 87-98% of their foraging time from May to July searching for food on or just above the ground. In LSF, the proportion was 89-94% (Greenlaw 1969). When defoliating caterpillars became abundant in late March-early June, particularly in HMF, towhees also foraged high above the ground in trees.

The invertebrate stocks in the litter were measured by collecting litter samples to be examined in the laboratory, and inspecting in the field strips of litter 30 mm wide and 5 m long. The first method involved collecting 15 (1968) or 30 (1967) random samples of litter in each study area (HMF, LSF) at several times during the breeding season. The size and depth (maximum of 4 cm, see Davis 1957) of the samples were standardized by using a coring device (0.05 m² in cross-section). In 1967, I collected one core at each sample site while in 1968 I took two cores (0.10 m²/sample) at each site and placed them together in a plastic bag. Later, the

TABLE 1. Food supply (mg dry wt/m²) in the litter in HMF and LSF, 1967 and 1968^a.

Time ^b	W. L. Hutcheson Memorial Forest (HMF)			Lebanon State Forest (LSF)			Probability ^c
	N	Geometric mean	95% confidence limits	N	Geometric mean	95% confidence limits	
1967							
Early May	30	39.5	19.2-85.6	-	-	-	-
Mid-May	30	89.8	44.6-179.7	30	19.0	10.5-32.3	$P < 0.02^d$
Late May- early June	30	169.8	92.9-310.2	30	22.4	7.4-40.8	$P < 0.001$
Mid-July	30	121.5	71.2-241.4	30	21.5	6.8-39.5	$P < 0.02$
1968							
Mid-May	15	155.9	73.2-331.4	15	30.2	5.6-164.0	$P < 0.05$
Early June	15	247.1	116.7-523.6	15	21.3	2.8-55.3	$P < 0.001$
Early July	15	315.0	185.5-828.8	15	88.1	39.3-197.6	$P < 0.01$

^a Data from collected litter samples.

^b Samples were collected in the two study areas from 1 to 7 days apart, averaging about four days.

^c *t*-tests (one-tailed) performed on $\log_{10}(x + 1)$ transformed data; see text.

^d Approximate *t*-test used.

samples were screened and each fraction (according to particle size) was inspected in a white enamel pan. All conspicuous intact seeds (very few) and invertebrates ≥ 2 mm long were placed in alcohol-filled vials for further study. In the second method, I carefully and systematically inspected strips of litter in each study area approximately every two weeks. Flushed invertebrates were counted and assigned to size categories. This method yielded values (numbers/m² or mg/m²) assumed to be proportional to the density of invertebrates in the litter.

Invertebrates on low herb-shrub foliage up to 0.6 m above the ground were sampled in HMF and LSF in June and July 1968, by sweeping 2.2 m-wide strips of such vegetation with a net. Each sample consisted of 50 sweeps taken at the rate of one sweep/pace while walking at a constant speed. Since the density of the low foliage varied within each study area, I minimized variation between samples in the amount of foliage intercepted, and thus in the number of invertebrates obtained per sample, by spacing five sets of 10 sweeps about 10 m apart along a randomly selected compass heading for each 50-sweep sample. This made each sample more representative of the invertebrates in the general area. All samples were collected in the early afternoon on sunny days when wind velocity was low. At this time of day, towhees are chiefly foraging (Greenlaw 1969). Data on numbers of invertebrates/sample in several length categories were converted to dry weight biomass using predetermined mean dry weight values.

The relative levels and occurrence of defoliating caterpillars in HMF and LSF in 1967 and 1968 were estimated by subjectively evaluating the intensity of frass-fall (insect debris) into four categories: none, light, moderate and heavy.

STATISTICS

Parametric statistical tests employed in this paper follow Sokal and Rohlf (1969). Nonparametric tests are described in Siegel (1956). Statistical significance is accepted at the 0.05 level.

RESULTS

FOOD IN HMF AND LSF

Because frequency distributions of the dry weight biomass data on invertebrates in the

litter were strongly skewed (rankit analysis) in both study areas, and since mean biomass values tended to be positively correlated with variance in different sets of litter samples, the data were transformed using $\log_{10}(x + 1)$. This transformation made the distributions more symmetrical and produced variances independent of the means. F-tests on the transformed data showed that most paired samples (samples collected about the same time in the two areas) had homogeneous variances.

The estimates of invertebrate stocks present in the litter (mg dry wt/m²) in HMF and LSF are shown in Table 1. The central tendency of each set of samples is reported in the linear (untransformed) scale as the geometric mean. Because of the skewed distribution, the geometric mean better represents central tendency than the mean, which is more sensitive to extreme values.

Student *t*-tests (one-tailed, since my a priori expectation was that food levels in the mesic habitat would exceed those in the xeric habitat) indicated that biomass densities were significantly higher in HMF than in LSF from May to July. Significant differences in the same direction, although smaller, were obtained when all HMF samples collected at a particular time were compared with only the paired LSF samples taken from the deep, shaded litter under clumps of high shrubs where towhees often foraged. Data from the field-inspected samples confirmed these patterns.

Litter inspection samples in 1968 suggested that invertebrates were more abundant in HMF than in LSF as early as the last week of April and the first week of May (HMF: $\bar{x} = 43.4$ mg/m², $n = 10$; LSF: $\bar{x} = 17.8$ mg/m², $n = 9$;

TABLE 2. Total number/m² and percentage of litter invertebrates in different size categories in HMF and LSF, 1968.

Time	N	Size categories (mm)				Total
		2-4	5-9	10-15	> 15	
Hutcheson Memorial Forest (HMF)						
Early May	15	14.2(89.3) ^a	0.9(5.7)	0.5(3.1)	0.3(1.9)	15.9(100.0)**
Early June	20	14.3(66.5)	3.2(14.9)	3.5(16.3)	0.5(2.3)	21.5(100.0)*
Late June	20	15.0(55.6)	8.3(28.5)	2.2(13.8)	0.9(3.1)	26.4(100.0)**
Early July	15	14.6(41.8)	16.9(48.2)	2.9(8.3)	0.6(1.7)	35.0(100.0)**
Lebanon State Forest (LSF)						
Early May	15	3.5(85.4)	0.5(12.2)	0.1(2.4)	0(0)	4.1(100.0)
Early June	20	9.8(93.5)	0.5(5.2)	0.1(1.3)	0(0)	10.4(100.0)
Late June	20	9.5(72.6)	3.2(24.4)	0.4(3.0)	0(0)	13.1(100.0)
Early July	15	9.4(77.1)	2.6(21.3)	0.2(1.6)	0(0)	12.2(100.0)

^a Number/m² (percentage); data from litter inspection samples.

* Distribution of invertebrates in different size categories significantly different between the two study areas, Chi-square test (two-tailed), $P < 0.05$.

** As above, but $P < 0.01$.

Mann-Whitney U test, $P < 0.01$). At this time towhees were returning, establishing territories, and forming pairs, and they obtained most of their food from the litter.

The differences between HMF and LSF in biomass densities of litter invertebrates are due to larger numbers of invertebrates/m² and to more large invertebrates in HMF (Table 2).

My data generally show an increase in litter invertebrate densities in HMF and LSF between early May and early to mid-June. Because of sample characteristics, the increases were not always significant but the trends (most marked in HMF) were consistent.

The information on invertebrate biomass/sample in the low shrub-herb vegetation in HMF and LSF is summarized in Table 3. The estimates are based on relatively slow-moving prey ≥ 2 mm (e.g. spiders, Homoptera, Hemiptera, lepidopteran larvae, etc.) which are most likely to be captured by foraging towhees (Greenlaw 1969). Invertebrates on the foliage near the ground were significantly more abundant in HMF than in LSF in June and July 1968.

TABLE 3. Food supply (mg dry wt/sample) in low herb-shrub foliage in HMF and LSF, 1968.

Time	Location	N	Biomass ($\bar{x} \pm S.E.$)	P^a
June	HMF	15	44.2 \pm 5.36	
June	LSF	15	21.3 \pm 6.21	< 0.05
July	HMF	15	34.7 \pm 7.00	
July	LSF	15	16.1 \pm 5.04	< 0.05

^a Mann-Whitney, one tailed (H_1 : mesic habitat food supply > xeric habitat level).

Because of the presence of a prominent herb layer in HMF, in contrast to LSF, and its early development (late April to early May), sizeable stocks of invertebrates on low foliage were probably present at an earlier date in HMF than in LSF. The feeding behavior of towhees in the two areas seemed to confirm this, as foraging birds in LSF seldom captured food above the ground from late April to mid-May while such maneuvers were frequent at this time in HMF.

The intensity of frass-fall in HMF (heavy) and in LSF (none to light) and the amount of lepidopteran larvae on foliage and litter in these areas suggested that caterpillars were much more numerous in HMF than in LSF.

BREEDING CHRONOLOGY

Table 4 and Figures 1-2 summarize information on the breeding schedule of towhees in the areas I studied. The median date of egg-laying (all nests) was earlier in HMF than in LSF and BNL (early June vs. mid-June, Table 4). The nesting chronology was similar in the two pine barrens areas.

The habitat difference in the timing of the towhee's breeding season can best be appreciated by examining the start of spring nesting in the three study areas. This aspect of avian breeding seasons is interesting because temperate birds tend to lay their eggs several weeks before peak feeding conditions.

In HMF, the first 10% of all nests were started by early to mid-May, depending on spring weather (or related factors). The early nesting season in 1968 (one nest started on 26 April with others initiated in the first week of May, Table 4) correlated with an especially early and warm spring. In contrast, the first

TABLE 4. Median and 10-90 percentile dates of laying of first eggs by Rufous-sided Towhees in HMF, LSF, and BNL.

Location	Year	N	Median date	10-90 percentile
HMF	1966-1967	13	10 June	19 May-27 June
	1968	9	8 June	5 May-2 July
LSF	1966-1968	12	14 June	28 May-10 July
BNL ^a	1961-1962	16	18 June	31 May-16 July

^a Sample somewhat biased towards later nests.

10% of the nests in LSF and BNL were not started until the last half of May, most not until the last week of the month. Records of precopulatory display, copulation, and collecting of nest material on all pairs under regular observation in HMF and LSF (including many pairs for which nest data are not available) confirm that towhees in HMF began building nests and mating at least seven to nine days before those in LSF.

Observations on color-banded birds in HMF and LSF indicated that second broods (a brood following an earlier successful nesting) were not uncommon in the former area but were rare or absent in the latter (Figs. 1, 2). They probably also were rare or absent at BNL, but only a few pairs were color-banded there.

In HMF, second nests usually were begun by the female about one to two weeks after

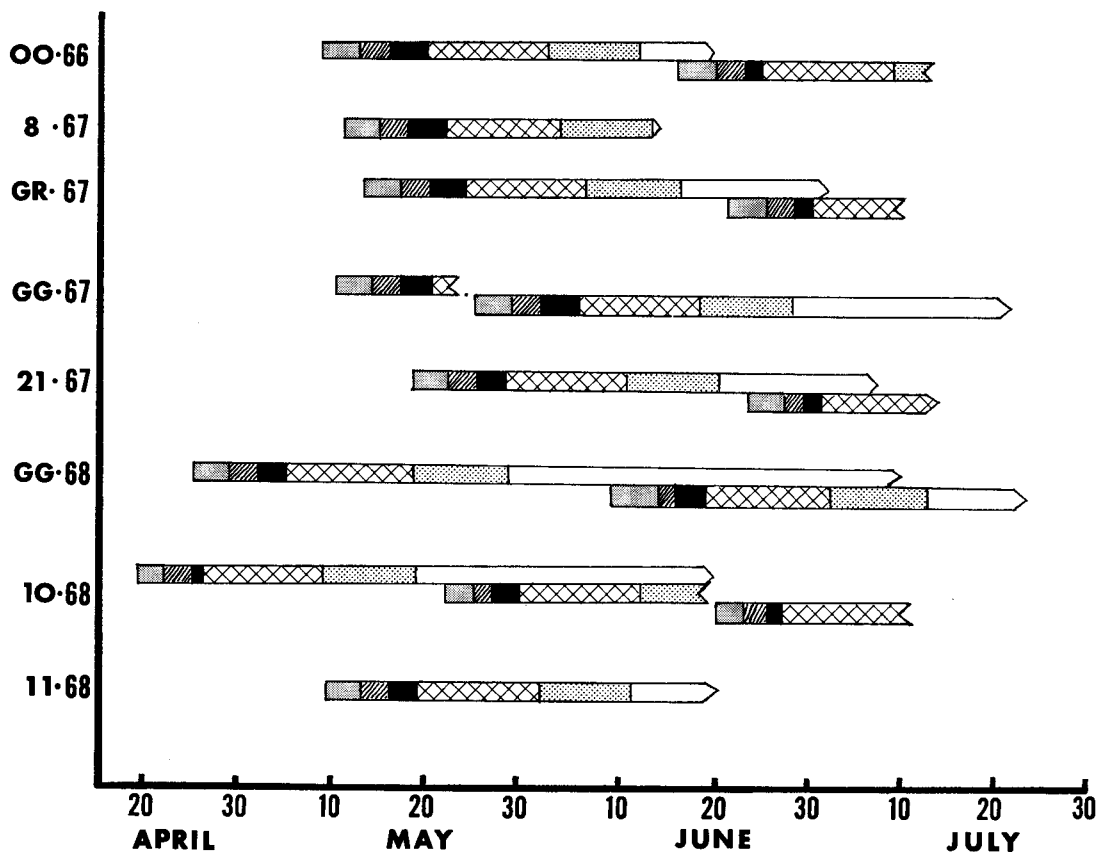


FIGURE 1. Representative breeding cycles of Rufous-sided Towhees in HMF in 1966, 1967, and 1968. The territory's (male's) letter or number designation (left) and the year (right) are given along the ordinate. From left to right, a bar shows the timing and duration of nest-building (fine stippling), pre-laying (hatching), egg-laying (solid), incubation (boxes), nestling (coarse stippling), and fledgling-juvenile (open) stages of a nest cycle. Successive nestings of a pair are illustrated with staggered bars. An arrow indicates indefinite continuance of the stage and an emarginated bar indicates disruption of the stage (e.g. predation). The timing of each nest cycle was determined by estimating the date of first egg-laying if not known (see text). When unknown, the durations of stages in a nest cycle are presented as mean durations reported for northeastern towhees (literature and this study).

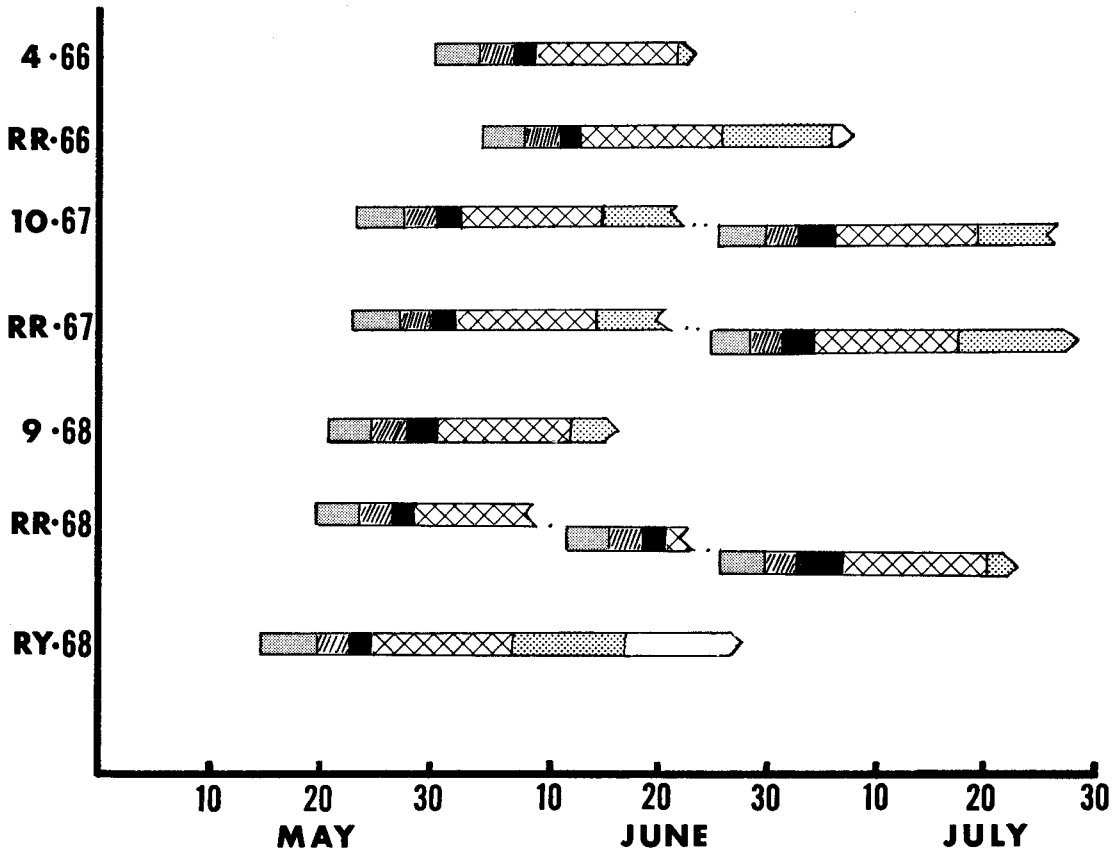


FIGURE 2. Representative breeding cycles of Rufous-sided Towhees in LSF in 1966, 1967, and 1968. Although the season was relatively late in 1966, RR-66 probably had an earlier (late May) nest that was disrupted. See Fig. 1 for explanations.

young from the first nest had fledged. This left the male largely responsible for feeding the dependent young of the first brood and caused an overlap in the two nest cycles (Fig. 1). In all areas, re-nesting was initiated within a few days after an early nest was destroyed (Figs. 1, 2).

CLUTCH SIZE

Mean clutch sizes of towhees in the three study areas are shown in Tables 5 and 6.

Variations are homogeneous in all cases. Both the *t*-test and the non-parametric rank-sums test were used to evaluate the null hypothesis of equality of means. The alternate hypothesis was that clutch sizes were larger in the food-rich habitat than in the food-poor one. The conclusions drawn from the two tests agree.

The mean clutch size of all nests in LSF ($n = 12$) was 2.88 and that in BNL ($n = 16$) was 2.94. The difference is not significant (*t*-test, two-tailed, $P > 0.05$). Because of this,

TABLE 5. Mean clutch sizes in early nests of the Rufous-sided Towhee started during the same time interval in the three study areas^a.

Location	N	Clutch size ($\bar{x} \pm s_x$)	Comparisons with HMF ^b
HMF	10	3.88 \pm 0.29	
LSF	6	2.67 \pm 0.33	$P < 0.01$
BNL	8	3.25 \pm 0.16	$P < 0.05$
LSF + BNL ^c	14	3.00 \pm 0.18	$P < 0.025$

^a First egg laid 25 May–19 June; see text for explanation.

^b *t*-test, one tailed (i.e., H_1 : clutch size in the mesic oak woodland $>$ clutch size in the xeric pine-oak woodlands).

^c Difference between LSF and BNL (within-habitat), two-tailed, not significant ($P > 0.05$).

TABLE 6. Mean clutch sizes of early and late nests of Rufous-sided Towhees in HMF, LSF, and BNL.

Location	Season ^a	N	Clutch size ($\bar{x} \pm s_{\bar{x}}$)	Significance ^b
HMF	early	13	4.00 \pm 0.27	$P < 0.001$
	late	11	3.00 \pm 0.23	
LSF	early	5	2.62 \pm 0.40	n.s.
	late	7	3.30 \pm 0.28	
BNL	early	6	3.33 \pm 0.21	n.s. (0.10 $> P > 0.05$)
	late	10	2.70 \pm 0.21	

^a Median date of egg-laying used as seasonal criterion for separating early and late nests.

^b *t*-tests, two tailed (H_1 : early and late clutches were not equal in size).

the overall ecological similarity between the two areas, and the similar breeding chronology of towhees there, the data on clutch size from LSF and BNL are pooled in subsequent analyses to represent pine barrens habitat.

Clutch sizes of towhees in HMF ranged from two to five with a mode of four. In LSF and BNL, clutch sizes ranged from two to four with modes of three. Records on two nests discovered during the nest-building stage, which were checked daily until the clutches were fully laid, showed that 2-egg sets represent complete clutches. Single eggs were rarely lost during egg-laying and incubation. Of 50 towhee nests with eggs, I found only one instance where an egg disappeared from a completed clutch (BNL). During the egg-laying period, single-egg losses often result from parasitism by the Brown-headed Cowbird (*Molothrus ater*). Parasitism was low in my study areas and the few nests involved are not included here.

The mean clutch size of towhees in the mesic forest ($\bar{x} = 3.45$, S.E. = 0.21, $n = 24$) was significantly larger than that of towhees in the pine barrens ($\bar{x} = 2.92$, S.E. = 0.18, $n = 28$). I considered, however, that the difference between the two habitats might have resulted from the earlier start of breeding in HMF. In the Great Tit (*Parus major*) and in some other species (Perrins 1965, 1970), clutch size decreases throughout the breeding season. Although towhee clutch size in HMF did not appear to decrease until mid-June, I deemed it best to correct for this possibility. Nevertheless, when only early nests started during the same time period in the three study areas are compared (25 May, when nesting was underway in all areas, to 19 June, the median egg-laying date of all nests started on or after 25 May), a similar habitat difference in mean clutch size is still evident (Table 5).

Seasonal changes in clutch size are well known (Lack 1954, 1966). Such changes were evident in the three towhee populations

studied here, particularly in HMF (Table 6), causing no difference in mean clutch sizes between habitats late in the season.

Clutches of four and five eggs were most frequent in HMF nests in May and early June while two and three eggs were prevalent later. Thus in HMF, early first and second nests and early renests usually contained large clutches and late second nests and renests contained small ones. At BNL, clutches of three and four (less common) were frequent through mid-June. As in HMF, 2-egg clutches were found late in the season. The seasonal pattern in LSF is unclear because of my relatively small sample of nests there. In that area, late May (about 20 May to 28 May) nests tended to contain two or three eggs while early and mid-June nests tended to have three or four eggs. Two-egg early clutches were unusual, yet LSF was the only place where I found several such clutches at the very beginning of the nesting season; no late two-egg clutches were found. The single known instance of an early two-egg clutch in HMF (found during nest-building) was that in a nest started unusually early for the area in late April, when the wood was still in its early spring aspect.

DISCUSSION

TIMING OF BREEDING

Towhees, like most other birds, are seasonal breeders. The timing of the favorable period for breeding can influence a bird's reproductive rate because the number of broods that can be raised depends partly on the duration of that period (von Haartman 1971:428).

Towhees in the oak-hickory forest (HMF) commenced breeding up to two weeks before most of those in the pine barrens (Table 4). This difference in timing was associated with a marked difference in the development of foliage between the two habitats. A distinct herb layer appeared in late April and early May in HMF, but did not appear on the

sterile, sandy soils of the pine barrens. I noted that foraging towhees found significant amounts of food from this layer when present. The foliage on the woody plants started developing earlier in HMF than in LSF and completed development about a week or more sooner in mid- to late May, depending on weather conditions.

The start of breeding in towhees thus varies in relation to habitat phenology and weather (early vs. late spring, HMF, Table 4), as is known in other species (e.g. Lack 1954, Snow 1958). The emergence of foliage insects available to breeding birds apparently varies in parallel with these factors.

Of particular interest is the timing of first breeding in pine barrens in relation to spring development of prey populations and the hatching of young towhees. From the end of May through the third week of June in LSF, foliage caterpillars were available (although to a lesser degree than in HMF), other arthropods were abundant on fresh foliage, and litter stocks were at or near their peak. Returning migrants established territories and formed pairs at or about the same time in LSF as in HMF. Foliage development in the former area had barely begun and litter prey stocks were low (Table 3). Most pairs under regular observation did not commence egg-laying until late May when hatching might be expected to begin if young in the nest were to be properly timed with the vernal flush of invertebrates (Lack 1954). In fact, most early hatching did not occur until the second week of June or later, when food supplies were about to become less abundant.

In contrast, in HMF, food supplies in litter and on low foliage began increasing by late April and early May. Here, the early start of nesting (Table 4) ensured that hatching occurred in late May and very early June when prey populations were approaching peak levels (high populations in litter and on herbaceous foliage, caterpillars abundant until mid-June).

I hypothesize that the delayed and relatively brief period of vernal development (early May to late May) in LSF provided insufficient time between the point when food became sufficiently abundant to form eggs and that when food for feeding young became most plentiful. In HMF, the longer period of habitat development (late April to late May) and the larger early stocks of food (Tables 1, 2) gave the towhees ample time to lay and incubate eggs before the time when food for the young reached its peak or began to subside (see Perrins 1970:244).

Thus, at least for towhees in the pine barrens, food for laying females appears to be an important factor in determining the start of nesting. In species which occupy habitats that vary in the timing of suitable conditions for starting nests, selection may favor a general response to some factor such as photoperiod (Farner 1967). The response may be "fine-tuned" to local conditions by the amount of the female's body reserves available for egg-formation and the size and quality of the prevailing food supply during the egg-laying period. Thus, avian species whose date of first laying in a season is affected by food supply may be more numerous than was implied by Perrins (1970: 245-248).

CLUTCH SIZE AND FOOD

In some passerines and nonpasserines dependent on highly variable food resources, food supply seems to have a direct effect on clutch size. For many other species (including the Rufous-sided Towhee) with less variable food supplies, food is denied a role as a proximate factor affecting clutch size because during the season, food levels and clutch size often vary inversely, not directly, as expected (Klomp 1970:13-15). But food must be considered broadly in relation to its availability and quality. Moreover, a female's own food reserves during egg-laying, and her ability to replenish them, must be considered in discussing the relationship between food and clutch size.

Habitat differences in clutch size often have been attributed to differences in the productivity of the habitats (e.g. Kluijver 1951, Lack 1955, Snow 1958, Kluyver 1963). The present study provides another such example. However, when habitats being compared are far apart, the differences in clutch size may reflect adaptive genetic differences between populations rather than a facultative response of females to different food levels. Variation in clutch size between habitats differing in productivity must reflect the relative success of all of a species' adaptations, not just those related to acquiring and handling food.

Other factors known to influence the number of eggs laid cannot fully account for the habitat difference in the early clutch size of towhees reported here. Seasonal variation in clutch size within habitats and the difference in timing of first breeding between them were taken into account in my analysis (Table 5).

An inverse relationship between clutch size and population density has been reported for

a few species of non-emberizines, but the effect may become significant only when variance in population size is large (Klomp 1970). Although population density may account for some of the difference in clutch size between HMF and LSF, it is unlikely to be the sole explanation. The difference in breeding density of towhees between LSF, where they were more numerous, and HMF was relatively small (8 males/10 ha, LSF; 5 males/10 ha, HMF). Moreover, BNL with a little larger average clutch size than LSF (see Results) had a higher, not lower, breeding density (9.5 to 10.0 males/10 ha).

The difference in clutch size between mesic forest and pine barrens is in agreement with Lack's hypothesis (1954, 1966, 1968) that clutch size should vary directly with the food supply available to dependent young. The relative favorability of HMF to towhees feeding nestlings and fledglings (late May, June, July) was evident in all the following respects: (1) size of the food stocks in the litter and on low vegetation, (2) prevalence of invertebrates in larger size categories (≥ 5 mm long), and (3) level of infestation of caterpillars on oak trees in the last week of May and early June. These caterpillars provided the major source of large, soft-bodied food items during a restricted period for towhees in HMF.

Although the difference in clutch size between habitats is in the expected direction, this difference (HMF $1.4 \times$ LSF) is much less than the difference in food supply (HMF about $4 \times$ LSF, food in litter and on low vegetation combined). This discrepancy may be because my measurements of food levels in the feeding zones generally used by towhees overestimated the food actually available to these birds. Chance, competition, food preferences, and the difficulty of finding prey may cause birds to harvest much less food than is actually available. The rates at which feeding towhees pecked at the litter and low vegetation should integrate the impact of these factors, and provide a more direct index of the food actually being harvested. I measured feeding activity in this way, of as many birds as possible at different times of the day. During the egg-laying and incubation period, towhees averaged 5.1 pecks/min in HMF and 1.7 pecks/min in LSF ($P < 0.05$, Mann-Whitney U). The respective rates during the nestling period were 4.0 and 1.9 ($P < 0.05$). The average rate of pecking in HMF was about 2.6 times that in the pine barrens. Considering probable sampling errors, this is

roughly comparable to the difference in clutch size between the areas.

As explained earlier, the late May nests in LSF were better timed in relation to the vernal flush of invertebrates than early and mid-June nests. Hence, I would expect larger May clutches than later ones under Lack's hypothesis. Yet most May nests contained only two or three eggs. It is possible that especially poor feeding conditions on certain towhee territories in LSF in mid-May, when females were forming eggs, directly influenced clutch size.

In contrast to the difference between habitats in the clutch size of early nests, the mean number of eggs in nests started in late June and July did not differ significantly between habitats, even though feeding conditions were still measurably better in the mesic forest at this time (Tables 1 to 3). This shows that it would be an oversimplification to relate variation in clutch size just to food supply, but it does not necessarily negate the importance of that factor.

PLASTICITY OF CLUTCH SIZE

Variation in clutch size is common in many species. Because of an early emphasis on the adaptive significance of the model clutch size in birds (Lack 1954), the persistence of variation in clutch size in a population has been largely ignored until recently (Haukioja 1970).

Lack implied that the sizes of clutches laid by different females in a population are under relatively rigid genetic control (see Kluyver 1963). However, heritability of clutch size in particular females may be rather low (Haukioja 1970, Perrins and Jones 1974). Haukioja (1970:121) documented early clutches in a female Reed Bunting (*Emberiza schoeniclus*) in Finland that varied between three and six eggs under different environmental conditions at different times. I found a marked female towhee in HMF that laid early clutches of two and four eggs during the early spring of 1968. Since environmental factors that influence reproduction in towhees and other birds must vary geographically and temporally, the optimum clutch size should vary accordingly (Williams 1966:173-174). I regard the ability of individual females to vary their clutches relative to local conditions as a significant adaptation in such birds. To the extent that environmental conditions early in the breeding season augur conditions later, as food supply does in this study (Tables 1, 2), selection should favor responsiveness to

factors operating on females while they are forming eggs.

The differences in early clutch size between habitats reported here may simply reflect physiological modifications by laying females, within similar genetically determined limits in each of the populations, to the different energetic situations prevailing in the two habitats. To better understand the operation of food-related factors in this context, future studies must consider food availability (quantity and quality), time and energy budgeting of activities, and the ability of females to mobilize and replenish their body reserves.

SUMMARY

This study examines the relationship between food supply and breeding schedule and clutch size in Rufous-sided Towhees in two habitats. One population of towhees inhabited a mesic oak-hickory forest (HMF) in New Jersey, and two other populations were in xeric pine barrens in New Jersey (LSF) and on Long Island, New York (BNL).

Samples of invertebrates in the litter and on low vegetation in the New Jersey study areas showed that numbers and biomass of potential prey were several-fold higher in the mesic habitat than in the xeric one. Differences in biomass density were noticed as early as late April-early May when returning towhees were establishing territories and pairing.

Towhees in HMF commenced egg-laying about one to two weeks earlier on the average than those in the pine barrens. This difference was correlated with the earlier development of foliage and the concomitantly earlier appearance of additional invertebrates on and near the ground in HMF. The timing of first nests in LSF suggests that towhees there started breeding as early as possible and that poor feeding conditions at the time of egg-formation may have prevented them from initiating nests earlier than they did.

Mean clutch size of early nests in HMF was significantly larger than the mean of those in pine barrens started at the same time. Thus, early clutch size varied directly with food supply between the two habitats.

The importance of food as a possible proximate factor affecting breeding schedule and clutch size and the problem of plasticity in clutch size are discussed.

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