

CLUTCH SIZE VARIATION IN THE EASTERN PHOEBE IN SOUTHERN INDIANA

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ABSTRACT.—Clutch sizes were examined in Eastern Phoebe nests in southern Indiana in 1970 and 1971. The majority of the nests was on bridges and culverts. Nest building began in late March with birds regularly using old nests and building both statant and adherent new nests. Phoebes raised two broods with peaks in clutch initiation in mid-April and in late May–early June. Average clutch size was 4.73 with little variation between years; the most common clutch size was five. Within a year, clutch size declined significantly late in the season. Mean clutch size was lower in adherent than in statant and new as opposed to pre-existing nests; the energy cost of nest building is discussed as a possible cause of these reductions. *Received 29 August 1977, accepted 5 April 1978.*

THE Eastern Phoebe (*Sayornis phoebe*) is a common summer resident throughout much of the eastern United States, including Indiana and surrounding states (Butler 1898, Mengel 1965, Graber et al. 1974). In its phylogenetic development the Tyrannidae experienced an incredible degree of divergence in nest site selection. In this process the Eastern Phoebe developed a nest site requirement (i.e. rocky bluffs and outcrops, mouths of caves, or streambanks with overhangs) that undoubtedly made it an uncommon and local breeder in pristine times. Although the Eastern Phoebe has widely accepted man's dwellings, bridges, and culverts as nesting substrates and thereby extended its distribution considerably, these birds are at the mercy of continually changing engineering design (Whitaker 1974). For example, this species, in nesting on vertical elements of concrete bridges as opposed to older wooden or I-beam structures, may have to divert energy from egg production into construction of adherent nests. This adaptive behavior might affect clutch size and, ultimately, population numbers.

The evolution of clutch size in various species and the influence of extrinsic and intrinsic factors on intraspecific variation was treated in detail by Lack (1954) and von Haartman (1967). In their research, predominantly with European cavity nesters, they had the opportunity to examine large numbers of easily available nests. The nest site selection of the Eastern Phoebe should make it an equally attractive research subject. Because of its widespread use of bridges and culverts for nesting substrate, nests are easy to find, often easily accessible, and, in many areas, numerous. Kendeigh (1952) commented on the surprising paucity of information on the breeding biology of this common species, a dearth that continues to the present.

I studied Eastern Phoebe nesting biology in southern Indiana in 1970 and 1971. Emphasis was on birds nesting under bridges and in culverts, although some nests on other structures and in natural sites were included. On many of the larger bridges, Eastern Phoebes nested synchronously with Barn Swallows (*Hirundo rustica*) throughout much of the season.

METHODS

The study area was Crane Naval Weapons Support Center, a 251-km² area occupying the northern part of Martin County in unglaciated south-central Indiana. Approximately 75% of the area is wooded and the remainder is old fields, maintained roadsides and other openings, and industrial complexes. The

Center is drained by three major streams each with a dendritic drainage pattern that grades from deep precipitous valleys in the north and east into broad, alluvial floodplains flanked by wall-like bluffs in the south and west. This pattern coupled with 650 km of roadways results in a large number and good distribution of bridges and culverts.

In February 1970 I inspected all bridges and culverts on the study area for old Eastern Phoebe nests, numbered each nest found, and recorded its condition and location. Other potential nest sites including buildings and other structures and natural sites proximate to roads were also examined. After the arrival of the first phoebes, I visited each site at 5–7 day intervals and recorded nest contents, new construction, and behavioral information. After the 1970 nesting season all phoebe nests were removed in order to assess the effect of a lack of existing nests on various productivity and nest placement parameters in the succeeding year. All data collection in 1971 was identical to 1970. Only clutches known to be complete were included in analyses. Weather data were obtained from a small weather station on Crane NWSC. Changes in the population of clutch sizes were examined with the χ^2 test. Other comparisons, including some of clutch size changes, were with the Student's *t*-test.

RESULTS AND DISCUSSION

Nest types and placements.—In both years the phoebes arrived on the study area in mid-March and nest building began in late March–early April. Construction of early nests was slow, with time of construction varying between 7 and 12 days. There was an interval of 1–9 days between nest completion and laying of the first egg, a characteristic pattern in Eastern Phoebes (Graber et al. 1974, Klaas 1970). Klaas (1970) found this interval to be longer in adherent than statant nests and questioned whether adherent nest building was an extra physiological drain leading to a delay in ovulation. My observations are not sufficiently intense to allow this comparison but my clutch size data indicate a possible energy cost of nest building.

Phoebes constructed both adherent and statant nests (Fig. 1). Statant nests averaged smaller (less than 200 g) than adherent (usually greater than 400 g) nests. The support for a statant nest also provided perching for the female during construction. In addition to being larger, adherent nests appeared more difficult to construct as birds had to hover to apply nesting material throughout the early stages.

Phoebes frequently used old nests rather than constructing completely new ones. More than 78% of pre-existing nests were used by phoebes during the 1970 season. Old nests were always renovated before use by the addition of new moss to the rim and a new lining. Old Barn Swallow nests were occasionally modified in the same manner and used by phoebes (Weeks 1977). About 50% of the second clutches were laid in the same nest as the first clutch. In instances where the first brood fledged successfully, 60% in 1970 and 80% in 1971 of the second nesting attempts were in the same nest as the first (Weeks unpublished MS).

Nests were found in many situations including concrete bridges, creosoted-wood bridges, wood and I-beam bridges, square-formed concrete culverts, round corrugated metal pipe culverts, rock culverts, buildings, other miscellaneous structures, and natural rock outcrops (Fig. 1). Most of the nests examined were under bridges or in culverts. Most bridges had numerous potential sites for statant nests but culverts often had none. Many of the pipe culverts were unusable unless a construction flaw allowed the attachment of a statant nest.

In the following clutch size considerations, I assume that birds continuously occupying a given structure were the same pair. Behavior and event sequence indicated that this was usually the case, and Klaas (1970) found that 88% of his banded Eastern Phoebes remained at the same bridge throughout the breeding season. However, the validity of the presentation does not hinge on the correctness of the assumption.

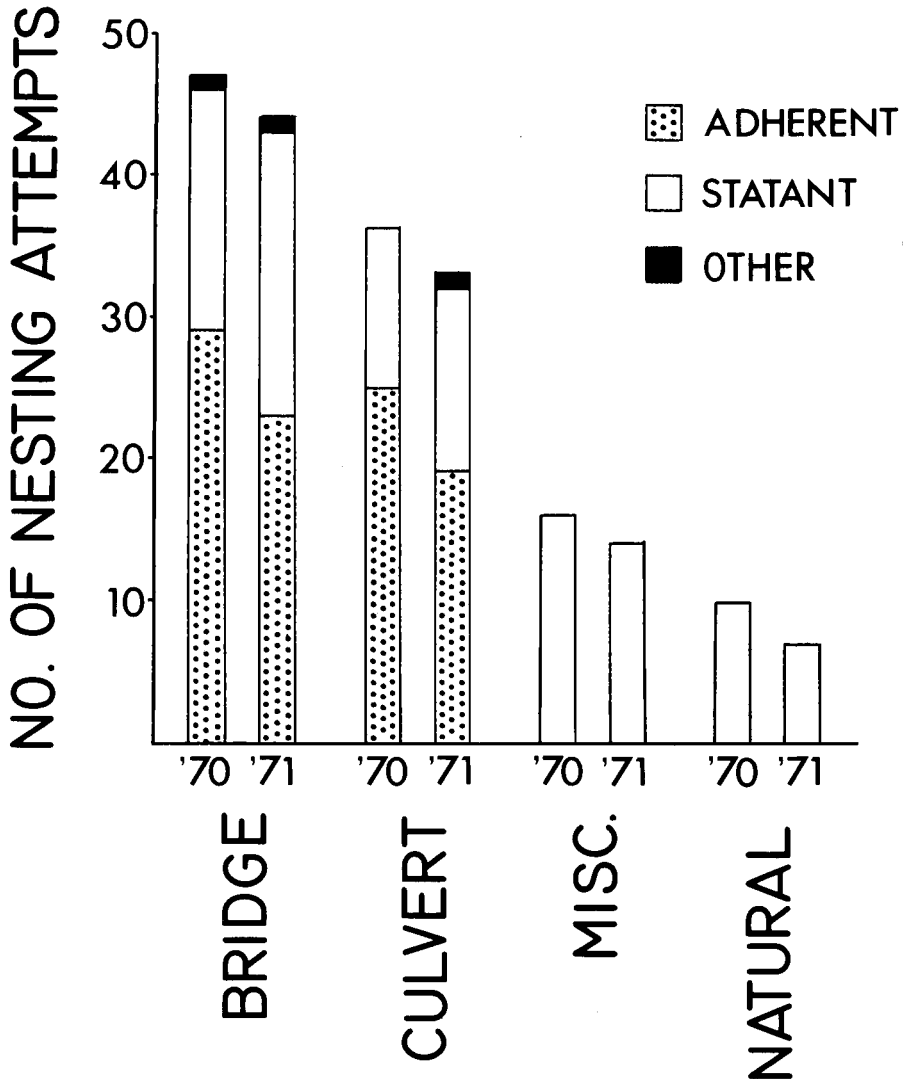


Fig. 1. Distribution of nesting attempts of the Eastern Phoebe in south-central Indiana by year, nest site, and attachment type.

Chronology of egg laying.—The chronology of egg laying was similar in both years (Fig. 2). The first eggs laid in 1970 and 1971 were on 10 April and 9 April, respectively, while the last clutches were begun on 28 June and 21 June in the 2 years. These late clutches were third nesting attempts, as were most late June clutches; in all instances at least one of the previous attempts had failed. No attempt to rear a third successful brood was encountered. Two distinct peaks occurred in clutch initiation in both years.

The early laying peaks for the 2 years were almost identical although more protracted in 1970. This extension may have been chiefly because of an extremely rainy period on 19–24 April, marked by stream flooding from a 7.4-cm rainfall on 24 April that destroyed several culvert nests. Reconstruction of destroyed nests began almost

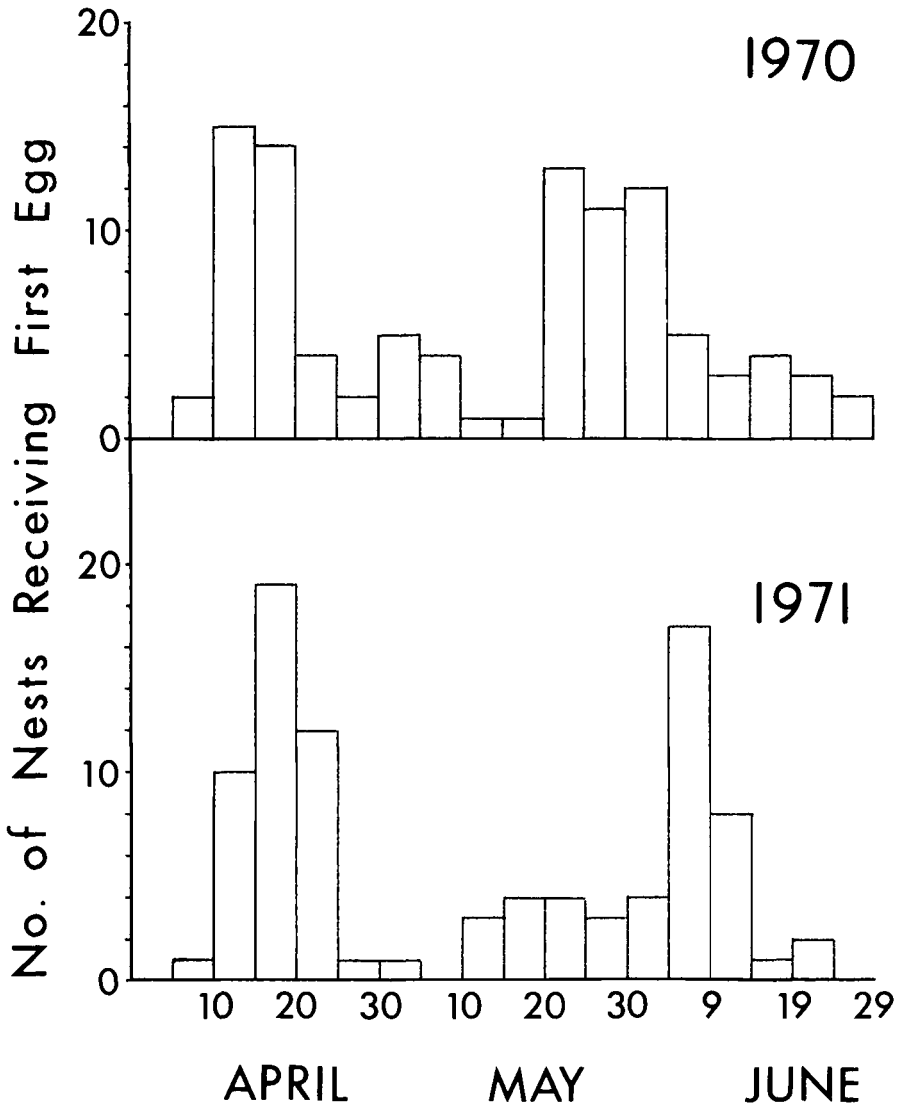


Fig. 2. Timing of initiation of clutches of the Eastern Phoebe in south-central Indiana in 1970 and 1971.

immediately and laying shortly thereafter, contributing to the several early May clutches (Fig. 2). There was a definite lull in clutch initiation in early and mid-May of both years and 15 May was chosen as the dividing point between first and second clutches in subsequent clutch size considerations.

The second peak in clutch initiation was not as distinct as the first, owing in large part to the damping effect of nest failures and resulting renestings. This was most evident in 1971 when overall nesting success was lower (58.2%) than in 1970 (72.5%). In 1970, the second peak in clutch initiation was separated from the first by about 40 days (Fig. 2), about the minimum recycling time from the first egg of one successful clutch to the first egg of the second (i.e. 5 days laying + 16 days incubation

TABLE 1. Variation in size of Eastern Phoebe clutches within and between the breeding seasons of 1970 and 1971 in south-central Indiana

Seasonal division	Number of eggs				N	$\bar{x} \pm SE$
	3	4	5	6		
1970 Total	3	18	66	2	89	4.75 \pm 0.058
April	1	4	27	0	32	4.77 \pm 0.048
May	0	4	32	1	37	4.92 \pm 0.060
June	2	10	7	0	19	4.26 \pm 0.150
1 April–15 May	1	5	36	0	42	4.83 \pm 0.067
16 May–30 June	2	13	30	1	46	4.65 \pm 0.089
1971 Total	0	29	49	4	82	4.70 \pm 0.062
April	0	6	28	4	38	4.95 \pm 0.084
May	0	4	7	0	11	4.64 \pm 0.152
June	0	18	12	0	30	4.40 \pm 0.091
1 April–15 May	0	7	29	4	40	4.93 \pm 0.083 ^a
16 May–30 June	0	21	18	0	39	4.46 \pm 0.081 ^a
Both years total	3	47	115	6	171	4.73 \pm 0.042
April	1	10	55	4	70	4.89 \pm 0.059
May	0	8	39	1	48	4.85 \pm 0.059
June	2	28	19	0	49	4.35 \pm 0.080
1 April–15 May	1	12	65	4	82	4.88 \pm 0.053 ^a
16 May–30 June	2	34	48	1	85	4.56 \pm 0.061 ^a

^a Differences highly significant ($P < 0.001$)

+ 16 days nestling + 5 day nest repair = 42 days). In 1971, however, the second peak was about 50 days later than the first. This approximately 1-week delay in renesting in 1971 was confirmed through examination of the mean interval between successful fledging of the first brood and the beginning of the second clutch in the same nest in the 2 years. In 1970 this interval averaged 7.8 days ($n = 21$), a significantly ($P < 0.001$, t -test) shorter period than the 13.3 day mean ($n = 23$) in 1971. An explanation for this delay is not readily discernable. Although late May, when the second peak would have begun if the 1971 interval was the same as 1970, was relatively cool with highs in the 18°C range and lows near 7°C, this should not have been sufficient to delay ovulation.

Although the mean interval between nestings was relatively long, several instances of an interval as short as 1–3 days were observed, both in the same nests and renovated, pre-existing ones. In one instance, renovation of a second nest was begun while large young were still present in the first nest. Klaas (1970) found a mean interval between termination of successful first nests and the beginning of another to be 7.5 days. He commented that since this interval was shorter than his observed physiological recycling times (i.e. time necessary to produce eggs after loss of clutch or brood during nesting) of 9–10 days, the inhibition to ova development must end while young of previous successful broods are still in nests. My findings generally concur with his observations.

Clutch size variation.—As with most studies (Davis 1955), clutch sizes here refer to the number of eggs found in nests presumed to contain complete clutches. However, as these nestings were highly localized and most nests were observed from inception, my counts should be very accurate. Nevertheless, the possibility exists that single eggs were removed by predators during laying and thus not recorded. No clutch size was assumed for the few nests containing young at discovery. The mean clutch size for 171 nestings was 4.73 ± 0.042 (Table 1). Little variation between years was evident in clutch size with 1970 and 1971 averaging 4.75 ± 0.058

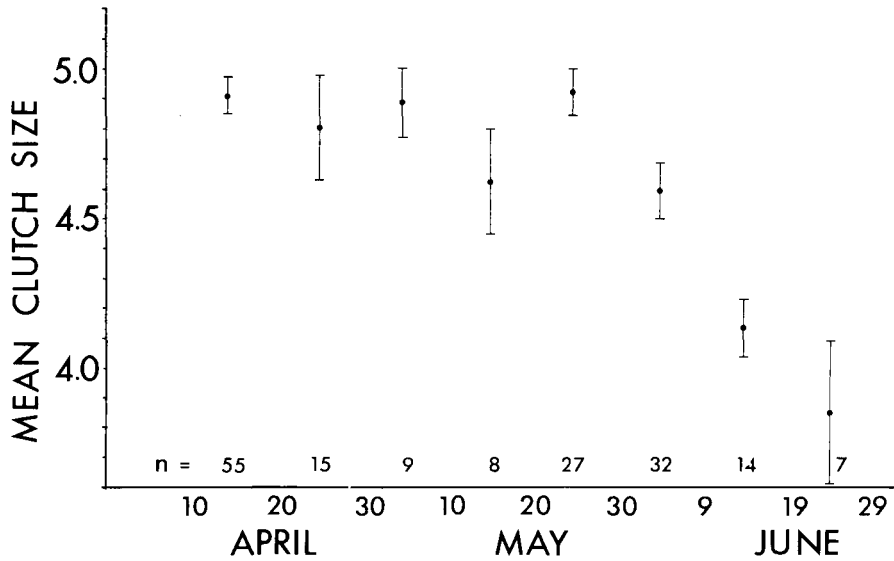


Fig. 3. Mean clutch size in the Eastern Phoebe by 10-day periods in 1970-1971 in south-central Indiana. Vertical lines represent one standard error.

(SE) and 4.70 ± 0.062 , respectively. Few comparative data are available, but Klaas (1975) found a mean clutch size of 4.34 in nests non-parasitized by cowbirds in Kansas. In Michigan studies, where observation intensity may not have been equally distributed through the year, Cuthbert (1962) found a mean of 4.69 and Middleton and Johnston (1956), whose data were primarily on first nestings, observed 4.49 eggs per clutch.

By far the most common clutch size was 5 with 74.2% of 1970 and 59.8% of 1971 clutches of this size (Table 1). Graber et al. (1974) found similar percentages for five-egg clutches in Illinois but other studies (Cuthbert 1962, Middleton and Johnston 1956, Klaas 1975) showed five-egg clutches to compose approximately 50% of total clutches. Clutch size appears to be closely controlled in the Eastern Phoebe; I found approximately 95% of all clutches to be of four or five eggs. Clutches of three or six eggs were relatively rare. I found three successful nests that contained two-egg clutches in 1971, but in two of these locations previous events indicated partial clutch predation, probably by *Peromyscus leucopus*, was likely and the third was probably affected by pre-existing abandoned eggs. None of these was considered normal and all were excluded from clutch size compilations. Graber et al. (1974) similarly observed that all of their one- and two-egg clutches may have been the result of predation. Klaas (1975) recorded eight (2.7%) nests with two eggs; although these nests were presumably non-parasitized by cowbirds, the high incidence of parasitism found in his study area (24%) leaves open the possibility that cowbirds removed eggs from these nests without depositing any of their own.

Clutch size was found to vary between phases within the breeding seasons (Table 1). Lower mean clutch size in the late season was found in both years, with these differences significant ($P < 0.001$, *t*-test) in 1971 and when years were combined. This decline in clutch size with season is a generally observed phenomenon (Davis 1955). Such a decline has been hypothesized as being adaptive (Lack 1954, Haukioja

TABLE 2. Clutch sizes in Eastern Phoebes in south-central Indiana, categorized by type of nest construction

Seasonal category	Con- struction type	N	Clutch size				$\bar{x} \pm SE$
			3	4	5	6	
1970 Total	Adherent	51	2	11	38	0	4.71 \pm 0.076
	Statant	37	1	7	27	2	4.81 \pm 0.094
1 April-15 May	Adherent	26	1	4	21	0	4.77 \pm 0.101
	Statant	17	0	1	15	1	5.00 \pm 0.086
16 May-30 June	Adherent	25	1	7	17	0	4.64 \pm 0.114
	Statant	20	1	6	12	1	4.65 \pm 0.150
1971 Total	Adherent	41	0	14	27	0	4.66 \pm 0.075
	Statant	38	0	14	20	4	4.74 \pm 0.105
1 April-15 May	Adherent	23	0	4	19	0	4.83 \pm 0.081
	Statant	18	0	4	10	4	5.00 \pm 0.162
16 May-30 June	Adherent	18	0	10	8	0	4.44 \pm 0.121
	Statant	20	0	10	10	0	4.50 \pm 0.115
Both years total ^a	Adherent	92	2	25	65	0	4.68 \pm 0.053
	Statant	75	1	21	47	6	4.77 \pm 0.070
1 April-15 May ^a	Adherent	49	1	8	40	0	4.80 \pm 0.065
	Statant	35	0	5	25	5	5.00 \pm 0.092
16 May-30 June	Adherent	43	1	17	25	0	4.56 \pm 0.084
	Statant	40	1	16	22	1	4.58 \pm 0.094

^a Significant trend toward larger clutches in statant nests [$P < 0.05$, $\chi^2 = 8.85$ (total) and 8.90 (early season)]

1970) with the ultimate controlling factor being a decline in late season availability of food for young.

Although the seasonal differences that I found in mean clutch size were significant, the decline was not a gradual one throughout the season as illustrated for the Eastern Meadowlark (*Sturnella magna*) by Roseberry and Klimstra (1970). Rather, it was marked by a constancy through most of the period with a substantial late season decline (Fig. 3) similar to that demonstrated for Reed Buntings (*Emberiza schoeniclus*) by Haukioja (1970). Most of these late clutches were third clutches, after failure of an earlier attempt. Although the overall mean clutch sizes for April and May were almost identical (Table 1), there was no consistency between years since the May mean was substantially higher in 1970 and lower in 1971 than the April mean. Similarly when the mean clutch sizes for the peak laying periods of each year (Fig. 2) are compared (i.e. periods when the majority of the second clutches represent normal second attempts following successful completion of a first), 1970 values were not appreciably different (4.86 vs. 4.96) while late clutches were considerably smaller in 1971 (4.96 vs. 4.55).

Spurred by the observed difficulty in construction of adherent as opposed to statant nests and the strong tendency of birds to use old nests when available, I examined clutch size as it varied with these sets of factors (Tables 2 and 3). Interaction of factors is of course possible, but there was no evident trend in adherent or statant placement of new nests under bridges and culverts, with eight early season 1970 new nests divided equally and eight of 10 late season nests adherent. In 1971, 52% of 79 early-season new nests were adherent while 67% of 12 late-season new nests were statant.

The mean clutch size for statant nests was consistently larger than that for adherent nests (Table 2), although this difference was substantial only in the early season of both 1970 and 1971. In neither instance was this difference statistically

TABLE 3. Clutch sizes in Eastern Phoebes in south-central Indiana, characterized by history of nest. Nests were removed at the end of the 1970 season; the unavailability of pre-existing nests in the early 1971 season confounds analyses of cases marked with an asterisk (*)

Seasonal category	Nest history	N	Clutch size				$\bar{x} \pm SE$
			3	4	5	6	
1970 Total ^a	Pre-existing	69	2	11	54	2	4.81 \pm 0.063
	New	20	1	7	12	0	4.55 \pm 0.135
1 April-15 May	Pre-existing	35	0	4	30	1	4.91 \pm 0.063
	New	8	1	1	6	0	4.63 \pm 0.263
16 May-30 June	Pre-existing	34	2	7	24	1	4.71 \pm 0.108
	New	12	0	6	6	0	4.50 \pm 0.151
1971 Total	Pre-existing	*					*
	New	*					*
1 April-15 May	Pre-existing	*					*
	New	40	0	8	28	4	4.90 \pm 0.085
16 May-30 June	Pre-existing	26	0	12	14	0	4.54 \pm 0.098
	New	13	0	8	5	0	4.38 \pm 0.135

^a Significant trend toward larger clutches in pre-existing nests ($P < 0.01$, $\chi^2 = 11.59$)

significant, but the differences were consistent. When the 2 years are combined the t -value rises to 1.869 ($0.05 < P < 0.10$) and I believe the differences to be real. In addition, the trend toward larger clutches in statant nests was significant in the early season ($P < 0.05$, $\chi^2 = 8.85$) and in the total season ($P < 0.05$, $\chi^2 = 8.90$) for both years combined. The 1971 values are especially indicative since all early nests were new nests. However, only eight of the 43 early season 1970 nests were constructed that year, an indication that factors in addition to difficulty of nest construction may be operating.

New nests, i.e. those completely built just prior to oviposition, had lower mean clutch sizes in all seasons where comparisons were valid (Table 3). Again, however, the differences within individual seasons of 1970 were not statistically significant, largely because of low numbers of new nests, and when means for the whole year are compared ($t = 1.903$, $n = 89$) the normal seasonal difference in clutch size complicates the establishment of statistical differences. Again, however, I believe the differences are real, since the trend toward larger clutches in pre-existing nests in 1970 was significant ($P < 0.01$, $\chi^2 = 11.59$). Since all nests were removed prior to the 1971 season, no pre-existing nests were available to afford a comparison.

Much debate still exists as to the ultimate factor(s) in the evolution of clutch size and its variation with season, age, latitude, and other factors (Welty 1975). Primary theories include Lack's (1954) ideas that the controlling factor is the maximum number that the parent(s) can adequately nourish; that of Skutch (1967) where clutch size is adjusted to compensate for mortality; and that birds tend to lay the largest clutches that they can produce (von Haartman 1971). The latter suggestion is refuted to a degree by several observations, especially work with indeterminate layers (von Haartman 1967). Regardless of the ultimate factor(s) that contributed to determination of clutch size, some proximate factor(s) operates to control variation seen within a species population. It seems most likely that this proximate factor revolves around the bioenergetics of breeding, including the effects of nutrition and energy budgets.

Although an increasing amount of work is being done on the energetics of avian reproduction, little has yet been concluded regarding energy partitioning and relationships in wild populations. King (1973) concluded that there is significant energy

cost (prior to hatching) only in the production of the ova, and Zwickel (1973) believed reproduction not to be significantly curtailed by caloric shortage under natural conditions. Kendeigh (1973) considered incubation an important reproduction energy cost, and Drent (1975) presented evidence to support Kendeigh's position. Additionally, King (1973) concluded that the period of feeding and parental care of young is the part of the breeding season in which caloric shortage exerts its major effects on reproductive potential. Zwickel (1973) however, pointed out that the timing of the breeding season had evolved to correspond with peak food abundance for young and cited Cody's (1971) observation that the incidence of young dying of starvation in the nest was surprisingly low. In these considerations of energy limitations, emphasis is on the energy cost to the female up to the time of hatching; after hatching the number of calories received by developing young is the major concern. Nourishment of young is of course important to the population dynamics of the species, but also important is the drain of the feeding task on the energy reserves of the female, which must often subsequently produce replacement or second clutches.

The activity of nest building is very similar to feeding of young and, if the number of trips is similar, is probably equally costly energetically. There is of course a difference in material collected, a factor which may make nest building more expensive than feeding young. The collection of food for young may be merely an extension of the bird's normal feeding activities and the bird is free to eat occasional catches, and probably does. Gathering nest material requires different search images and probably is not done in concert with normal feeding so that energy reserves may be utilized during periods of active nest construction.

The female Pied Flycatcher (*Ficedula hypoleuca*) in Finland has been shown to lose 17% of her body weight by the end of the nestling feeding period (Welty 1975), but no such measurements have been made for any species with respect to nest building. Kendeigh (1973) indicated, from the work of El-Wailly (1966) with Zebra Finches (*Taeniopygia castanotis*), that the energy cost of egg production cannot easily be separated from the cost of nest building and early incubation. However, all species commonly used in captive studies build very simple nests. As Hinde (1973) pointed out, construction of even simple nests requires behavior of great complexity but not, I think, an energy output approaching that a wild bird must expend in building a large nest. This energy expenditure immediately precedes and in most species overlaps with a second, established energy output, the production of eggs. In species that regularly raise a second brood, as does the phoebe, construction of the second nest is nearly a continuum in time with the energetically costly activity of feeding young and may affect succeeding reproductive performance.

There are several other aspects of the Eastern Phoebe's nesting ecology that indicate that the energy cost of nest construction may be important. The phoebe builds a relatively large nest, requiring several days. The reduced clutch size in newly built nests and in the larger adherent nests suggests energy partitioning. This energy cost may be a dominant factor in the evolution of several nesting traits noted above: 1) the use of old conspecific nests if available, even occasionally those of other species, in preference to building new ones (Table 3); 2) the reuse of the same nest for second broods, even though the risk of parasite problems may be greater; and 3) the construction of a statant nest when support in a suitable location is available (Table 2).

Additionally, the delay between nest completion and clutch initiation in the Eastern Phoebe may be energy related. Klaas (1970) found this delay to be longer in phoebes that constructed adherent, as opposed to statant, nests. This compliments

my finding of reduced clutch size in adherent nests and suggests a larger drain on energy reserves in more extensive and difficult nest construction. King (1973) indicated that follicular growth, and associated energy drain, begins in small songbirds about 4 days prior to oviposition. This means that in almost all instances with the Eastern Phoebe, nest building ceased prior to the beginning of follicular development, thus preventing the concurrent imposition of two energy drains.

CONCLUSIONS

Although Eastern Phoebes on Crane NWSC commonly use culverts and bridges for nesting and enjoy a high degree of nesting success, this appears to be at some cost in terms of egg production. The durability of existing nests from season to season on these structures is of real benefit, as it relieves the birds of the energy costly task of constructing completely new nests. However, nests frequently must be rebuilt in culverts when destroyed by high water or predators, and new nests are occasionally built beneath bridges for unknown behavioral reasons. These nests are often adherent. The act of building, especially of adherent nests, evidently has an energy cost to the female, paid in reduced clutch size.

Whitaker (1974) recommended an artificial nesting shelf in new pipe culverts so that Eastern Phoebes and Barn Swallows could use these structures. Such shelves would undoubtedly increase population productivity on Crane, for few pipe culverts had suitable nest sites and almost every culvert or bridge that did have a suitable nest site was occupied. My findings of the importance of pre-existing nests and the probable energy cost of adherent construction indicate that nesting shelves may have benefits on other structures as well. Placed in preferred locations on any structure, they would allow construction of statant nests and simultaneously assure greater durability. Preferred sites may be intuitively recognized by an individual familiar with phoebe nesting biology, or may be determined by erecting several shelves.

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A **Symposium on Birds of the Sea and Shore** will be held at the University of Cape Town, South Africa, on 19-23 November 1979. Both formal sessions and excursions are planned, and the formal proceedings will be published as a supplement to *The Cormorant* (bulletin of the Southern African Seabird Group). Persons interested in attending the symposium should write to the **Organizing Secretary, Mr. G. D. Underhill, 12 Roseberry Road, Mowbray 7700, South Africa**; those wishing to deliver a paper should also write **Mr. J. Cooper, Southern African Seabird Group, % FitzPatrick Institute, University of Cape Town, Rondebosch 7700, South Africa**, giving details of their proposed paper.