NESTING ECOLOGY OF THE EASTERN PHOEBE IN SOUTHERN INDIANA

HARMON P. WEEKS, JR.

The Eastern Phoebe (*Sayornis phoebe*), a common summer resident in southern Indiana, makes extensive use of bridges and culverts for nesting throughout most of the eastern United States. This adoption of man-made structures has allowed expansion of breeding populations far from their primeval nesting habitats and may offer increased security from terrestrial predators. Nest success, however, may be adversely influenced by human and livestock disturbance. Nests on artificial structures frequently must adhere to vertical elements, with the resulting increased likelihood of falling.

Although Eastern Phoebe nests are easily detected and readily accessible, many aspects of phoebe nesting biology are poorly described. Kendeigh (1952) commented on this paradox, yet little has been accomplished since then. In an attempt to fill some information voids on the breeding biology of this species in the Midwest, I studied a nesting population of Eastern Phoebes in an unglaciated portion of southern Indiana in 1970 and 1971. Special emphasis was placed on evaluating use of and quantifying various success parameters in nests on bridges and culverts in a region of abundant natural nest-sites. An additional objective was to identify the importance of old nests remaining from previous seasons and nest placement on nesting success. Only a few nests in natural locations were examined. No birds were marked.

METHODS

This study was conducted on Crane Naval Weapons Support Center (Crane NWSC), a 251 km² area occupying the northern third of Martin County in south-central Indiana. About 25% of the area is composed of old fields, maintained roadsides and other openings, and industrial complexes; the remaining area is wooded. The combination of 3 dendritic stream systems and 650 km of roads provides many bridges and culverts for potential nest-sites.

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 such as buildings and rock outcrops near roads also were examined. I visited sites at 5–7 day intervals after the first phoebes arrived and recorded nest contents, evidences of new building, and behavioral data. Sites of examined nests included: concrete bridges, creosoted wood bridges, wood and I-beam bridges, concrete culverts, pipe culverts, rock culverts, buildings, natural (rock outcrop), and miscellaneous. I considered any span longer (i.e., linear road distance) than 4 m a bridge and less than that a culvert. After the 1970 nesting season, I removed all old nests to assess the effect of a lack of existing nests on productivity and nest placement parameters in 1971. This

removal eliminated the possibility of separating the effect of presence of old nests from the effect of time in the 1971 nesting season. Data collection in 1971 was similar to 1970.

Because phoebes occasionally began several nests at different locations under a bridge or completed a nest without depositing eggs, all nest success calculations were based on nests known to have received at least 1 egg. A successful nest is defined as one that produced at least 1 fledgling. Nest data were sorted by parameters to be compared, and because of nests with missing data, totals in some comparisons are not the same as in others. All nests with clutches initiated on or before 15 May were classified as early season nests; the remainder were late season nests.

Significance in nest reuse and clutch-size was tested with the Student's *t*-test; all other comparisons were with the χ^2.

RESULTS AND DISCUSSION

Arrival and nest building.—I first observed Eastern Phoebes on the study area on 17 March 1970 and 12 March 1971, when males were singing on territory at bridges that were occupied continuously thereafter. I found the earliest dates for the beginning of nests in 1970 and 1971 to be 2 April and 27 March, respectively. Early season construction of a new nest or renovation of an old one usually took at least 7–8 days and at times as long as 10–12 days. Temperature seemed to be a strong controlling factor during this period; regardless of construction stage, building would often cease completely during days when temperatures were below ca. 10°C. Since nest building seems to be under partial control of temperature, seasonal variation in nest initiation could be considerable. Nests that were evidently complete regularly stood empty for 1–9 days prior to egg-laying (Weeks 1978). Nest construction after mid-May took as little as 5 days for complete construction and 3 days for renovation of existing nests ($\bar{x} = 10.5$ days between fledging and new clutch initiation).

Nest placement and type.—Phoebes built both statant and adherent nests. They often depended on some surface irregularity (e.g. nails, wire, rough concrete, wood splinters, mud dauber [*Trypoxylon politum* or *Sceliphron caementarium*] nests) for initial attachment of nest material for adherent nests, yet the early stages of building in these nests were more difficult than for statant nests. The female, for only females build (Smith 1942), had to hover at the nest-site and "throw" mud against the surface with a flick of her head. This continued until enough of a base was built up to allow perching. Adherent nests were thus characterized by a circle of small mud splashes radiating from the nest.

Adherent nests were more common than statant nests under both bridges (56.1% vs 43.9%) and culverts (66.7% vs 33.3%). Nevertheless, it cannot be concluded that Eastern Phoebes preferred adherent to statant nests, since availability of suitable sites had an overriding effect. A high percentage of

culvert nests were adherent, but there were very few sites for statant nests. Almost all bridges had many potential statant sites, but frequently not in preferred locations. In many concrete and creosoted wood bridges structural elements at bridge supports provided most of the "shelf" situations but these were rarely used. Nests placed in these locations faced across stream flow and parallel with the roadway. Where possible, phoebes strongly preferred to face nests toward the bridge edges. Drainpipes from the road surface, protruding at 90° to 135° from vertical, were the most common support (14 of 17) for statant nests under concrete bridges. In 1971, only 51.7% of nests built under bridges were adherent. The approximately equal distribution of the 2 types of nests may have resulted from the need to construct entirely new nests and the vacancy of a number of preferred statant sites (because of old nest removal), as well as the apparent relative ease of statant construction.

Nests were built on a variety of structures, although the majority were on bridges and culverts (Table 1). All bridges and culverts were associated with maintained roadside vegetation; however, no bridge containing a nest was more than 25 m from a sizable area of woodland. Such an obligatory nest–woodland relationship was suggested by Graber et al. (1974) in Illinois, and Klaas (1970) found in Kansas that some woody vegetation was necessary near nest-bridges.

Culverts vary less in design than bridges, but the smooth vertical sides of concrete culverts required adherent nests. Culverts of corrugated metal pipe of 1–2 m diameter were generally unusable by phoebes unless a construction flaw (e.g., metal strip hanging from top) allowed nest attachment.

For most bridges and culverts, with the exception of pipe culverts, the number of nests and nesting attempts was largely a function of the number of available structures. Only 5 of 21 examined corrugated metal pipe culverts ever had a nest. There was never simultaneously more than 1 active nest on any structure; Ohlendorf (1976) found the same situation in both Say's (*Sayornis saya*) and Black phoebes (*S. nigricans*) in Texas.

In most situations there was somewhat more than 1 nesting attempt per nest (Table 1), which indicates the reuse of old nests for a second clutch; but since a few nests, especially in 1970, received 3 clutches, these data do not accurately reflect the percentage of nests that were reused. Several trends were evident, however. There was significantly more reuse of nests in culverts than on bridges in both 1970 ($t = 6.27$, df $= 60$, P < 0.001) and 1971 ($t = 2.49$, df $= 49$, P < 0.01). This perhaps reflects differences in availability of old nests from which to choose for a second nesting (higher under bridges than under culverts in 1970) and the number of available sites for the construction of a second nest (judged considerably higher under bridges).

TABLE 1

EASTERN PHOEBE NESTS AND NESTING ATTEMPTS ACCORDING TO LOCATION[1]

Nest location	Active 1970			Active 1971		
	Nests	Nesting attempts	Attempts/ nest	Nests	Nesting attempts	Attempts/ nest
Bridges	38 (50.7)	47 (47.5)	1.23[3]	30 (50.0)	44 (48.4)	1.46[2,4]
Culverts	24 (32.0)	36 (36.4)	1.50[3]	21 (35.0)	33 (36.3)	1.57[4]
Buildings	6 (8.0)	7 (7.1)	1.16	5 (8.3)	8 (8.8)	1.60
Misc. structures	7 (9.3)	9 (9.1)	1.28	4 (6.7)	6 (6.6)	1.50
TOTAL ARTIFICIAL	75	99	1.32	60	91	1.51[2]
Natural	8	10	1.25	5	7	1.40
TOTAL	83	109	1.31	65	98	1.50

[1] Data for all nests, including those found at stages after initiation; numbers in parentheses are percent.
[2] Significantly ($t = 6.72$, df $= 133$, P < 0.001 for all structures; $t = 9.68$, df $= 66$, P < 0.001 for bridges) larger than 1970 value.
[3] Means significantly different ($t = 6.27$, df $= 60$, P < 0.001).
[4] Means significantly different ($t = 2.49$, df $= 49$, P < 0.01).

Further indication of the possible effect available old nests may have on nest reuse is revealed by comparison of data from 1970, when old nests were available, and 1971, when all old nests had been removed prior to the nesting season (Table 1). Significantly more attempts per nest were made in 1971 than in 1970, both in total nests on man-made sites ($t = 6.72$, df $= 133$, P < 0.001) and in bridge nests ($t = 9.68$, df $= 66$, P < 0.001). This difference is not reflected in culverts, as would be expected from the aforementioned high reuse in 1970.

Eastern Phoebes on Crane NWSC used old nests not only for second broods but also for earlier attempts. Of 55 old nests in varying conditions marked before the 1970 season, 43 (78.2%) were subsequently renovated and used at some time during the season. Reuse of the same nest after an unsuccessful first clutch was not uncommon. Most researchers agree that Eastern Phoebes occasionally or even frequently reuse a nest for second broods (Klaas 1970, Mengel 1965), but no exact frequencies have been provided. I found 34 sites in 1970 and 33 in 1971 on which 2 or more nesting attempts were made; 16 (47.1%) in 1970 and 17 (51.5%) in 1971 were in the same nest. If only instances in which the first nest was successful are considered, 59.3% (16 of 27) and 81.0% (17 of 21) of the second nesting attempts were in the same nest in 1970 and 1971, respectively. The higher reuse in 1971 was at least partially attributable to the pre-season removal of 1970 nests, which eliminated most old alternate sites, although the removal of all nests in 1971 precludes statistical comparison.

I found little evidence to support the postulate that phoebes often build new nests in succeeding attempts to avoid mite infestations (Bent 1942). There was some mortality of nestlings from the northern fowl mite (*Ornithonyssus sylviarum*), but birds at times reused nests in which the earlier fledged young were heavily infested. In 1970 I found that in instances where birds used a different nest for a subsequent clutch, 62% renovated an old nest rather than build a new one. Since mites survive well from season to season in old nests (Klaas 1975), little reduction in risk of mite infestation would be gained from this nest shift.

A tacit assumption here is that a pair of birds that occupied a structure continuously throughout the nesting season was the same pair. Behavior and event sequences indicated this was usually the case; although there was likely some replacement, the frequency of such replacement could not be determined because the birds were unmarked. Klaas (1970) found that 88% of banded Eastern Phoebes remained at the same site (bridge) throughout the breeding season. Ohlendorf (1976) found similar behavior with Say's and Black phoebes but also found some rapid sequential replacement of breeders. However, in my succeeding considerations the assumption of non-replacement of breeders is not critical to the validity of the presentation.

Egg-laying and clutch-size.—Egg-laying and clutch-size variation have been detailed elsewhere (Weeks 1978). The earliest egg was 10 April in 1970 and 9 April in 1971. In both years 2 definite peaks in egg-laying illustrated the characteristic double-broodedness of the species; the early peak for both years was in mid-April, and the late-season peak in 1970 in late May. The second peak in 1971 was inexplicably delayed by about 10 days. The latest that a clutch was begun was 28 June in 1970 and 21 June in 1971.

The average size for 171 complete clutches was 4.73 ± 0.042 (SE) (range = 3–6 eggs; 67.3% = 5 eggs, 94.7% = 4–5 eggs) with no significant differences in clutch-size between years. I found, however, a significant decline ($t = 3.62$, df = 165, P < 0.001) in clutch-size in late nests (clutches begun after 15 May). Clutch-sizes were substantially lower in some instances where birds built new rather than using old nests and where birds built adherent rather than statant nests (Weeks 1978).

Hatching, fledging and nesting success.—Since I examined most potential sites prior to nest initiation, nearly all nests were known from inception. I therefore include all nests in my measure of nesting success and base the fledging success calculations on total eggs.

Slightly more nesting attempts were made and eggs laid in 1970 than in 1971 (Table 2). Nesting success was higher in 1970, and it is evident that no 1 factor alone caused the decreased 1971 success. Every facet of the reproductive cycle appeared depressed in 1971 compared to 1970. Perhaps

TABLE 2

SUMMARY OF NESTING DATA FOR THE EASTERN PHOEBE ON CRANE NWSC, INDIANA

	1970		1971		Total	
	Number	Percent	Number	Percent	Number	Percent
No. of active nests[1]	99		95		194	
No. of complete clutches	89		82		171	
Total eggs laid	450		417		867	
Eggs per active nest	4.55		4.39		4.47	
Eggs per complete clutch	4.75		4.70		4.73	
Eggs hatched	340	75.6	281	67.4	621	71.6
Eggs hatched per active nest	3.43		2.96		3.20	
Eggs infertile or addled	12	2.7	20	4.8	32	3.7
Eggs lost or abandoned	98	21.8	116	27.8	214	24.7
Young fledged	307		224		531	
Young fledged per active nest	3.10		2.36		2.63	
Young fledged of eggs laid		68.2		53.7		61.2
Young fledged of eggs hatched		90.3		79.7		85.5
Young lost before fledging	33		57		90	
Successful nests	71	70.3	55	57.3	126	64.0

[1] Excludes nests found after hatching.

the high productivity in 1970 resulted in a 1971 population abnormally high in first year birds, which are generally conceded to be less successful breeders than experienced adults (von Haartman 1971, Lack 1966). In addition, the lack of old nests in 1971 could have had an influence.

My limited number (N = 10) of exact determinations of incubation period (i.e., last egg laid to last egg hatched) and nestling period (N = 18) agreed with most published reports (Graber et al. 1974, Stoner 1939) that 16 days was the modal length for each; Klaas (1975) found an average in-nest period of 18 days for phoebes. In most instances all eggs hatched within a 24-h period. Hatchability of eggs that survived the incubation period was 95.1% for combined years; as with other factors, it was higher in 1970 (96.6%) than 1971 (93.4%).

I found a significantly higher (χ^2 = 134.6, df = 1, P < 0.001) survival rate for nestlings than for eggs, with 71.6% of all eggs laid hatching and 85.5% of all young that hatched fledging. Using 21 days (including laying) as the average time that eggs remained in nests and 16 days as the average nestling period, I found a loss rate of 1.35%/day for eggs and 0.91%/day for nestlings. Both rates are substantially lower than most reports for open-nesting altricial birds (Knupp et al. 1977, Roseberry and Klimstra 1970). The higher rate of egg than nestling loss is evidently normal in altricial species (Nice 1957)

and would be expected, since almost all nestling losses are to predators, but many agents cause egg losses.

Similarly, slightly more nests failed in the egg (52.4%) than the nestling (47.6%) stage. The pattern of nest failure suggested that once the egg-laying and early incubation period was completed, the nest was relatively secure until hatching. Nearly 35% of unsuccessful nests failed during egg-laying or very early incubation, while only 14% of the failures occurred from that point through hatching. This loss pattern might be predicted since abandonment was most common in this early stage, and the most readily seen and accessible nests would be taken quickly by opportunistic predators. After hatching, the feeding activity of the adults could attract predators to the more concealed nests. The daily nest mortality rate was 0.97% based on a 37-day period (including 5-day laying period), considerably less than the 2.4% average calculated by Ricklefs (1969) for open-nesting passerines.

Nice (1957) found that nesting success in open-nesting altricial birds in the North Temperate Zone averages 49% (46% fledging success). Though she gave no mean, she stated that nesting success in hole-nesting birds was substantially higher with a fledging success of 66%. Nesting success for the Eastern Phoebe might be intermediate between these extremes, since it builds an open nest under protective cover. Nesting success for both years combined was 64.0%, slightly lower than the 66.7% figure for dated nests. This success is similar to the mean success for hole-nesters given by Nice (1957), which is itself probably an inflated value (Mayfield 1961). Success based on dated nestings was significantly ($\chi^2 = 13.1$, df = 1, P < 0.001) higher in 1970 than 1971 (Table 3). Graber et al. (1974) found substantially lower nest success for central and southern Illinois phoebes (36–57%), as did Klaas (1970) in Kansas (52%) for nests not parasitized by Brown-headed Cowbirds (*Molothrus ater*). Possible reasons for the difference in success on Crane NWSC and other areas include variations in nest-sites and predator populations. The lack of human and livestock interference on Crane NWSC undoubtedly also played a role. As observed by Nice (1957), fledging success, based on total eggs laid, was lower than nesting success, based on total nests (Table 2). However, differences were small because infertility was low, overall success was high, and predators tended to take complete clutches or broods.

Success parameters (hatching, nestling and fledging) were all significantly higher ($\chi^2 = 13.6$, $\chi^2 = 23.6$, $\chi^2 = 38.1$; df = 1, P < 0.001, respectively) in 1970 than 1971 (Table 2). Additionally, nestling success was higher ($\chi^2 = 112.0$, $\chi^2 = 39.0$; df = 1, P < 0.001; 1970, 1971, respectively) than hatching success in both years. When only successful nests are considered, the infrequency of partial nesting failure is evident; for combined years, hatching success was 92.8% and nestling success 98.0%. Even in the relatively lower

TABLE 3

NESTING SUCCESS FOR EASTERN PHOEBES ON CRANE NWSC, INDIANA,
CATEGORIZED BY SEASON AND NEST SITE[1]

	1970			1971		
	Early (%)	Late (%)	Total (%)	Early (%)	Late (%)	Total (%)
Bridges	16/21(76.2)	15/21(71.4)	31/42(73.8)	14/22(63.6)	13/21(61.9)	27/43(62.8)[2]
Culverts	13/18(72.2)	12/16(75.0)	25/34(73.5)	10/17(58.8)	4/13(30.8)	14/30(46.7)
Misc. structures	5/5(100.0)	5/7 (71.4)	10/12(83.3)	5/6 (83.3)	2/4 (50.0)	7/10(70.0)
Natural	1/3 (33.3)	4/5 (80.0)	5/8 (62.5)	2/3 (66.7)	3/4 (75.0)	5/7 (71.4)
TOTALS	35/47(74.5)	36/49(73.5)	71/96(74.0)	31/48(64.6)	22/42(52.4)	53/90(58.9)

[1] Sample population includes all nests found before hatching in which date of first egg was known, early season = 1 April–15 May, late season = 16 May–30 June.
[2] Success significantly higher (χ^2 = 6.7, df = 1, P < 0.01) than for 1971 culvert nests.

hatching success figures, most of the failure to hatch was attributable to egg infertility rather than egg disappearance.

Nesting success for both years combined differed very little between early (69.5%) and late (63.7%) seasons. The difference is almost totally attributable to a moderate late season decline in success in 1971; success was almost identical in both seasons of 1970 (Table 3). Graber et al. (1974) also found a decline in nesting success in the late season in southern Illinois (their division of seasons was identical to mine). This apparent decline of nesting success with time is contrary to the situation found in most altricial species (Nolan 1963, Longcore and Jones 1969, Roseberry and Klimstra 1970). In addition, fledging success also tended to be higher in the early than late season; no general monthly decrease in fledging success was evident, with May having the highest success for any month in 1970 and lowest in 1971 (Table 4). Fledging success was, however, always highest in the months and seasons when the greatest number of eggs were laid.

Longcore and Jones (1969), citing entomological data (Holling 1961), suggested that a partial explanation for low success in Wood Thrushes (*Hylocichla mustelina*) in the early season when many nests were active might be a functional response by predators, i.e., to take a higher proportion of prey when more are available. This concept cannot be accepted as an axiom in vertebrate communities (Smith 1974). Phoebes do not depend on vegetative concealment for nests, and it appears that predator responses to prey (egg and young) density differ between nesters in this niche and species nesting in vegetation. Most passerines use vegetation for nesting cover, which should afford greater concealment as the season advances (Lanyon 1957, Longcore and Jones 1969); cover for phoebe nests does not change appreciably. Gulls

TABLE 4

ANALYSIS OF NESTING SUCCESS COMPONENTS BY TIME PERIOD FOR EASTERN PHOEBES
ON CRANE NWSC, INDIANA

Year	Division	Hatching success		Nestling success		Fledging success	
		ratio[1]	%	ratio[1]	%	ratio[1]	%
1970	April	121/177	68.4	116/121	95.9	116/177	65.5
	May	151/189	79.9	133/151	88.1	133/189	70.4
	June	68/84	81.0	58/68	85.3	58/84	69.0
	Early (1 April–15 May)	170/226	75.2	160/170	94.1	160/226	70.8
	Late (16 May–30 June)	170/224	75.9	147/170	86.5	147/224	65.6
1971	April	156/210	74.3	134/156	85.9	134/210	63.8
	May	33/66	50.0	23/33	69.7	23/66	34.8
	June	92/141	65.2	67/92	72.8	67/141	47.5
	Early (1 April–15 May)	165/231	71.4	139/165	84.2	139/231	60.2
	Late (16 May–30 June)	116/186	62.4	85/116	73.3	85/186	45.7

[1] For hatching = no. of eggs hatched/no. of eggs laid, for nestling = no. of young fledged/no. of eggs hatched, for fledging = no. of young fledged/no. of eggs laid.

(*Larus* spp.) laying at the peak of the nesting season are more successful than those laying earlier or later (Patterson 1965, Brown 1967). Though it is difficult to segregate colony effects, the similarity of these gull and phoebe data may be more than coincidental. Given species that depend on structural or geomorphological concealment and/or relative inaccessibility of nests as predator defenses, and given a relatively stable predator population with limited mobility, a constant number of nests would be taken regardless of the number available, i.e., a smaller proportion as numbers increase. This evidently occurs in this Eastern Phoebe population.

For both years combined, nesting success appeared higher in statant (69.0%) than adherent (61.3%) nests though the difference was not statistically significant; this apparent elevated success was general in seasonal and yearly breakdowns. In 1971, success for statant nests (65.2%) was significantly ($\chi^2 = 4.1$, df = 1, P < 0.05) higher than for adherent (51.1%). Statant nests had slightly higher overall fledging success than adherent nests, 64.0% and 60.4%, respectively. This difference was not consistent between years, with adherent success higher in 1970 (70.6% vs 66.7%) and statant in 1971 (61.6% vs 47.3%). For all successful nests, however, fledging success was highest ($\chi^2 = 8.0$, df = 1, P < 0.01) in adherent nests (93.4% vs 88.1%). This elevated success was consistent between years and was contributed to by both hatching and nestling success. This may indicate that nest predators that usually take single eggs (e.g., *Peromyscus* spp.) can more easily reach

statant nests, as would be expected. Other losses in adherent nests must be proportionately higher.

Although adherent outnumbered statant nestings (106 vs 87), my overall impression was that if a suitable statant site was available it was preferred. These success figures, as well as clutch-size data (Weeks 1978), indicate that a preference for statant sites has definite adaptive advantages, although these remain unknown.

Because of numerous factors, most related to susceptibility to nest predation, certain nest-sites seem to be more secure than others (Nice 1957, Cody 1971, Knupp et al. 1977). With phoebes, one might expect nest success to be higher on bridges than in culverts, because culvert nests average much lower and closer to the stream, thus increasing their availability to opportunistic ground predators. This does not seem to have been the case in 1970, for success appears almost equal (Table 3). In 1971, however, success was significantly lower ($\chi^2 = 6.7$, df $= 1$, P < 0.01) in culverts; the difference was especially evident late in the season.

Fledging success was slightly higher on bridges (60.9%) than in culverts (57.5%). However, the success was not consistent between years, with culvert success higher in 1970 (71.6% vs 63.3%) and bridge success higher in 1971 (58.2% vs 41.0%). For successful nests, fledging success was higher ($\chi^2 = 17.7$, df $= 1$, P < 0.001) in culverts (94.5% vs 88.7%); this difference was consistent between years and was reflected in both hatching and nestling success. It appears, therefore, that while losses of complete clutches (broods), rather than partial losses, is the rule, this tendency is most pronounced in culvert nests. Partial losses appear more common in bridge nests, and thus, other losses must be correspondingly higher in culvert nests.

I found nesting success significantly lower ($\chi^2 = 7.5$, df $= 1$, P < 0.01) on creosoted wood than concrete bridges, 55.0% vs 78.8%. Jackson and Burchfield (1975) found that Barn Swallows (*Hirundo rustica*) rarely used creosoted wood bridges in Mississippi and speculated about noxious effects of creosote or increased susceptibility to predation. Because the increased losses I found on creosoted wood bridges were not from lowered hatchability or nestling survival, I do not think lowered success was attributable to any chemical characteristics of creosote. Wooden bridges have many structural support elements, e.g., braces, bolts, etc., to supply passage for predators and wood presents an easier climbing surface than concrete.

No information is available on post-fledging and adult survival in phoebes. If a population remains stable, however, and adult mortality is about average for temperate passerines, i.e., 50% (Ricklefs 1973), post-fledging juvenile mortality is high. A rough estimate of young fledged/pair may be obtained using the method of Nice (1937) and the conservative estimate of 2.18

attempts/pair: 1970—6.76 young/pair; 1971—5.14 young/pair; both years
—5.97 young/pair. Therefore, the post-fledging survival required to balance
adult losses would be 14.8% in 1970, 19.5% in 1971, and 16.7% overall.
Since phoebes move north very early, they are periodically victims of spring
storms. In such years, increased first-year survival could prevent a prolonged
population depression.

Causes and stage of nest failures.—Causes of nest losses on Crane NWSC
were varied, but no losses in the 2 years were attributed to human or livestock
interferences. Almost half (49.3%) of the losses, constituting 18.2% of all
attempts, was attributed to nest predators; 3 times as many losses were from
predation as from the next leading factor. However, both the percentage of
total nesting attempts lost to predators and the proportion of total losses
attributed to predation were lower in these data than in many studies of
nidicolous species. Nolan (1963) attributed 88% of all failures in deciduous
shrub habitat to predation, while Lack (1954) thought that 75% of failures
in open-nesting species were attributable to predation.

Since phoebe nesting success was generally higher than that for open-
nesting altricial birds and the percentage of total losses attributed to predators
was less, I conclude that nest-site selection by the Eastern Phoebe affords
them a certain degree of security from predation. I believe the principal nest
predators were the black rat snake (*Elaphe o. obsoleta*), raccoon (*Procyon
lotor*), and white-footed mouse (*Peromyscus leucopus*). Because no House
Wrens (*Troglodytes aedon*), House Sparrows (*Passer domesticus*), or Com-
mon Grackles (*Quiscalus quiscula*) nested on structures with phoebes, and
since Blue Jays (*Cyanocitta cristata*) were never observed at bridges, I believe
that avian nest predation was minor if it occurred at all.

Abandonment, always in the egg stage, accounted for over 15% of losses,
but its cause was generally unknown. Losses from nests falling (12.7%) or
from flooding (7.0%) were lower than expected. Various mites are common
in phoebes and frequently infest young but in only 4 infestations was the
parasite load sufficient to cause nestling death. In 3 of 11 instances of clutch
abandonment, nests were heavily infested with mites, and the eggs were
covered with dark stains from mite droppings. These large populations may
have caused the abandonment.

Although cowbirds are common on Crane NWSC, only 7 phoebe nests
(3.6% of all nesting attempts) failed from cowbird interference; 3 additional
nests received at least 1 cowbird egg, but 2 of these were successful and the
other was destroyed by a predator. This yields a parasitism frequency of
5.1%. Although it appears that cowbird interference in this phoebe popu-
lation is light (Mayfield 1965), Friedmann (1963) identified the Eastern
Phoebe as a very important cowbird host. In addition, Klaas (1975) found

parasitism frequency of 24% in his study; and Graber et al. (1974), in central and southern Illinois with the exception of the extreme southern counties, found 30% of all nests affected. A more critical examination of my data revealed that 5 of 15 (33%) nests in natural locations received cowbird eggs while only 6 of 186 (3%) on artificial structures were parasitized. This difference is significant ($\chi^2 = 33.6$, df = 1, P < 0.001). Although Graber et al. (1974) gave no nest-site breakdown, their discussion suggested that a considerable number were in natural locations. Klaas (1975), on the other hand, examined only nests on bridges and culverts; on his study area there were no natural sites for nests. He stated that because it is an early breeder, the phoebe "receives most of the cowbird's attentions" early in the season. Although only a small number of nests in natural sites were examined on Crane NWSC, it appears that the same may be true for these nests in southern Indiana. Reduced cowbird parasitism alone could have been a significant selective factor in the substantial adoption of man-made structures as nest-sites, even in areas of plentiful natural sites.

Failure rate appeared higher for adherent than statant nests, but the apportionment of losses among the various causes was very similar. Five of the 7 losses to cowbird interference were of statant nests, reflecting the fact that most nests in natural sites were statant. The only rather substantial difference was higher abandonment of adherent nests (19.5% to 11.1%), possibly an indication that higher energy demands of adherent nest construction (Weeks 1978, Klaas 1970) lowers the energy reserves of females.

SUMMARY

Nesting ecology of Eastern Phoebes was examined in south-central Indiana in 1970 and 1971. The majority of the nests examined were on bridges and culverts.

Nest building began about 1 April, took 7–12 days, and completed nests stood empty for 1–9 days before egg-laying began. Both adherent and statant nests were built, the former being larger and apparently more energy demanding. Phoebes frequently used nests from previous years and reused the same nest (47.1% in 1970 and 51.5% in 1971) for a scond brood.

Nesting success in 1970 (70.3%) was significantly higher than in 1971 (57.3%), as was fledging success. Success changed little or declined slightly as the season advanced and varied according to nest-site.

Fledging success was highest in months when nesting intensity was highest. Fledging success was slightly higher in statant than adherent nests, but partial clutch (brood) losses were highest in statant nests. Similarly, success was somewhat higher on bridges than culverts, but probability of partial losses was greater on bridges. An average of 5.97 young/pair/year was fledged.

Predation was the major cause of nest failure with 49.3% of all losses, constituting 18.2% of all nest attempts, attributed to predation. Abandonment was the next leading cause, with Brown-headed Cowbird interference causing failure of only 3.6% of attempts. Cowbirds parasitized a significantly higher percent of nests in natural than artificial sites.

Nest losses were greatest in early egg or mid- to late nestling stages. Nest mortality rate was 0.97%/day. Mortality rate was higher for eggs (1.35%/day) than nestlings (0.91%/day).

LITERATURE CITED

BENT, A. C. 1942. Life histories of North American flycatchers, larks, swallows, and their allies. U.S. Natl. Mus. Bull. 179.

BROWN, R. G. B. 1967. Breeding success and population growth in a colony of Herring and Lesser Black-backed Gulls, *Larus argentatus* and *L. fuscus.* Ibis 109:502–515.

CODY, M. L. 1971. Ecological aspects of reproduction. Pp. 461–512 *in* Avian biology, vol. 1 (D. S. Farner and J. R. King, eds.). Academic Press, New York.

FRIEDMANN, H. 1963. Host relations of the parasitic cowbirds. U.S. Natl.. Mus. Bull. 233.

GRABER, R. R., J. W. GRABER AND E. L. KIRK. 1974. Illinois birds: Tyrannidae. Ill. Nat. Hist. Surv., Biol. Notes No. 86.

HOLLING, C. S. 1961. Principles of insect predation. Ann. Rev. Entomol. 6:163–182.

JACKSON, J. A. AND P. G. BURCHFIELD. 1975. Nest-site selection of Barn Swallows in east-central Mississippi. Am. Midl. Nat. 94:503–509.

KENDEIGH, S. C. 1952. Parental care and its evolution in birds. Ill. Biol. Monogr. 22: 1–356.

KLAAS, E. E. 1970. A population study of the Eastern Phoebe and its social relationship with the Brown-headed Cowbird. Ph.D. thesis, Univ. Kansas, Lawrence.

———. 1975. Cowbird parasitism and nesting success in the Eastern Phoebe. Occ. Pap. Univ. of Kansas Mus. Nat. Hist. 41:1–18.

KNUPP, D. M., R. B. OWEN, JR. AND J. B. DIMOND. 1977. Reproductive biology of American Robins in northern Maine. Auk 94:80–85.

LACK, D. 1954. The natural regulation of animal numbers. Oxford Univ. Press, London.

———. 1966. Population studies of birds. Oxford Univ. Press, London.

LANYON, W. E. 1957. The comparative biology of the meadowlark (*Sturnella*) in Wisconsin. Publ. Nuttall Ornithol. Club 1.

LONGCORE, J. R. AND R. E. JONES. 1969. Reproductive success of the Wood Thrush in a Delaware woodlot. Wilson Bull. 81:396–406.

MAYFIELD, H. F. 1961. Nesting success calculated from exposure. Wilson Bull. 73: 255–261.

———. 1965. The Brown-headed Cowbird, with old and new host. Living Bird 4:13–28.

MENGEL, R. M. 1965. The birds of Kentucky. AOU Ornithol. Monogr. No. 3.

NICE, M. M. 1937. Studies in the life history of the Song Sparrow, vol. 1. Trans. Linnean Soc. 4:1–247.

———. 1957. Nesting success in altricial birds. Auk 74:305–321.

NOLAN, V., JR. 1963. Reproductive success of birds in a deciduous scrub habitat. Ecology 44:305–313.

OHLENDORF, H. M. 1976. Comparative breeding ecology of phoebes in Trans-Pecos Texas. Wilson Bull. 88:255–271.

PATTERSON, I. J. 1965. Timing and spacing of broods in the Black-headed Gull, *Larus ridibundus*. Ibis 107:433–459.

RICKLEFS, R. E. 1969. An analysis of nesting mortality in birds. Smithsonian Contrib. Zool. 9:1–48.

———. 1973. Fecundity, mortality, and avian demography. Pp. 366–435 *in* Breeding biology of birds (D. S. Farner, ed.). Natl. Acad. Sci., Washington, D.C.

ROSEBERRY, J. L. AND W. D. KLIMSTRA. 1970. The nesting ecology and reproductive performance of the Eastern Meadowlark. Wilson Bull. 82:243–267.

SMITH, R. L. 1974. Ecology and field biology. Harper and Row, New York.

SMITH, W. P. 1942. Nesting habits of the Eastern Phoebe. Auk 59:410–417.

STONER, D. 1939. Temperature, growth and other studies on the Eastern Phoebe. N.Y. State Mus. Circ. 22:1–42.

VON HAARTMAN, L. 1971. Population dynamics. Pp. 391–459 *in* Avian biology, vol. 1 (D. S. Farner and J. R. King, eds.). Academic Press, New York.

WEEKS, H. P., JR. 1978. Clutch size variation in the Eastern Phoebe in southern Indiana. Auk 95:656–666.

DEPT. OF FORESTRY AND NATURAL RESOURCES, PURDUE UNIV., WEST LAFAYETTE, INDIANA 47907. ACCEPTED 14 AUG. 1978.

RESOLUTIONS COMMITTEE

The Chairwoman of the Resolutions Committee for 1979-80 is Helen S. Lapham, Laboratory of Ornithology, Cornell University, Ithaca, New York 14850. Any member who knows of an issue upon which it would be appropriate for the Wilson Society to take an official position should communicate this information to Ms. Lapham before the annual meeting in March 1980. The resolutions adopted at each annual meeting are the only way in which the membership can unite to express, through the Society, a formal position on conservation matters.