J. Field Ornithol., 65(1):52–57

PRE-LAYING NEST ROOSTING IN THE EASTERN PHOEBE: AN ENERGY-CONSERVING BEHAVIOR?

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Abstract.—Nests of Eastern Phoebes (*Sayornis phoebe*) were examined nocturnally for on-nest roosting during 8 yr on Crane Naval Weapons Support Center, Martin Co., Indiana. In early-season nests, females invariably roosted in the nest cup from the time the cup was well formed, sometimes several weeks before egg laying. Later in the season, females beginning second attempts exhibited this behavior in only 56% of nests observed. It is hypothesized that the behavior is an adaptation that allows energy conservation during the cool nights experienced by this early-season nester.

PERNOCTACIÓN EN SUS NIDOS, PREVIO A LA PUESTA, POR PARTE DE *SAYORNIS PHOEBE*: ¿UNA CONDUCTA PARA AHORRAR ENERGÍA?

Sinopsis.—En un estudio que se llevó a cabo por ocho años en la compañía Crane Naval Weapons Suport Center, de Indiana, se examinaron nidos de *Sayornis phoebe* durante la noche para determinar si éstos estaban siendo utilizados para pernoctar. Al principio de la temporada reproductiva, las hembras durmieron en los nidos (que son en forma de copa), una vez éstos estaban bien formados. En ocasiones los nidos fueron utilizados para dormir varias semanas antes de la puesta del primer huevo. No obstante para el final de la temporada, las hembras que comenzaban un segundo intento de anidamiento, exhibieron este tipo de conducta en tan sólo el 56% de las ocasiones. Se postula que esta conducta es una adaptación que permite ahorrar energía durante las noches frías, ya que esta ave comienza a anidar muy temprano cuando las temperaturas en ocasiones bajan del punto de congelación.

The Eastern Phoebe (*Sayornis phoebe*) makes considerable use of human structures, especially bridges and culverts, for nest sites. Nests are thus protected from weather and quite durable, often being used with minor modifications for several years in succession (Weeks 1979). Phoebes are double-brooded and begin construction or renovation of first nests in late March in southern Indiana. Work on early nests is at a casual pace, whereas between broods, nests are renovated or built very rapidly. In either case, however, seemingly completed nests stand empty for several days before clutch initiation (Klaas 1970, Weeks 1978). Phoebes are rarely observed diurnally at nests during this hiatus.

Mueller et al. (1982) observed a female Eastern Phoebe begin nocturnal roosting in the nest cup 3 d prior to the laying of the first egg. Roosting in the nest by cavity nesters is not uncommon, but pre-incubation roosting by a passerine in an open, cup-shaped nest had not been found (e.g., Brackbill 1985, Nolan 1978) before the observation of Mueller et al. (1982). They suggested that phoebe roosting habits be examined further before their observation be branded unusual; I undertook this investigation to verify the occurrence and scope of this behavior.

METHODS

The study area was Crane Naval Weapons Support Center (CNWSC), a 252 km^2 area in south-central Indiana (38°50′N, 86°50′W). CNWSC has many bridges, culverts, and natural rock outcrops that are used as nest sites by Eastern Phoebes. I conducted nocturnal inspections of individual nests of known status and occasionally groups of nests known to be in similar stages phenologically. I used a flashlight to illuminate nests from a sufficient distance to avoid flushing birds that might have been present. I knew the complete history of each nest examined.

I surveyed groups of nests in 1983 and 1989 before first clutch initiation; in 1986 and 1988 I examined nests after first broods had fledged and prior to second clutch initiation. In addition, I periodically made nocturnal examinations of over 100 individual nests from 1983 through 1990. Differences in occurrence of roosting in the nest cup prior to early season and late season clutches were examined with a χ^2 2 × 2 contingency table analysis.

RESULTS

In early spring, before renovation began, nests had no cups because of compaction from the previous year's broods, and birds roosted perched on the nest rim. Once renovation began during the early season (20 March–20 April), females always roosted in the nest cup once a cup with some lining was present. In this season, nocturnal low temperatures averaged 3.6 C (range −7.3–16.6 C) and complete nests often remained eggless for extended periods. Roosting in the nest cup regularly commenced 10–14 d before egg laying and sometimes >20 d (Table 1).

The rapidity of nest renovation or construction between successful first and second attempts limits time available for on-nest roosting. In a normal year (1989), the time between the fledging of the first brood and the first egg of a second clutch in the same nest averaged 10.9 d (n = 38; range 6–18 d). The roosting pattern during this period differed significantly (χ^2 = 14.01, df = 1, $P < 0.001$) from that of early nests, with only 56% of nests with equivalent cups being used for on-nest roosting (Table 1). Mean low temperature during this period (1 May–1 June) was 12.3 C (range 0.5–20.5 C).

In all cases and for all broods, once egg laying began the female roosted on the nest every night. Diurnal incubation usually began with the last egg but did not reach full intensity for a few days; the pattern described by Mueller et al. (1982) appears typical (long periods of diurnal inattentiveness during first 2 d, little thereafter).

DISCUSSION

The Eastern Phoebe seems unique among open-nesting passerines in the use of nests for roosting prior to egg laying (Brackbill 1985, Nolan 1978). The phoebe is, however, a structure nester and thus may be thought of as intermediate between ground/vegetation nesters and hole nesters.

TABLE 1. Results from night inspections of multiple nests for Eastern Phoebe nest-roosting behavior on Crane NWSC, Indiana. "Second broods" are inspection dates after fledging of first brood and prior to egg-laying for the second. ON means roosting in nest cup; OR means roosting on rim of nest.

Date of night inspection	Total nests inspected	Nests w/cup			Nests w/o cup			Min. roost days before egg	
		#	Bird ON	Bird OR	#	Bird ON	Bird OR	$\bar{X}$	Range
First Brood									
31 Mar. 1983	16	5	5	0	11	0	11	14.0	9–23
6 Apr. 1983	16	8	8	0	8	0	8		
14 Apr. 1989	11	11	11	0	0	0	0	4.7	1–14
Second Brood									
5 May 1986	2	2	1	0	0	0	0	4.0	2–6
19 May 1986	13	13	7	0	0	0	0	4.1	
22 May 1988	15	10	6	0	5	0	1	3.3	2–6

My results provide some insight as to the origin of this behavior and its adaptive function. At least three possibilities exist: (1) nest-site defense against conspecifics, (2) assessing security of site from predation (Mueller et al. 1982), and (3) energy savings (Mueller et al. 1982).

Competition for nest sites undoubtedly exists in the Eastern Phoebe, as suitable sites are not uniformly distributed. On CNWSC, occupancy of suitable structures is almost 100%, and platforms erected in previously unusable pipe culverts were occupied immediately (29 of 30) with no abandonment of adjacent traditional sites (Weeks 1984). Territorial behavior restricts structure occupancy to a single pair. Even though competition is keen, it is difficult to surmise why on-nest roosting would better establish occupancy than roosting on the nest rim or at some other location on the structure.

I doubt that the primary function of pre-laying roosting is assessing security from nocturnal predators. Birds (principally females) roost at the nest continuously from the time territorial occupancy is established, on-rim early and then shifting to an on-nest position. It is difficult to believe that one position would be more effective in monitoring than the other. Furthermore, in the almost total darkness within a culvert or beneath a bridge, monitoring predator activity would be virtually impossible. Additionally, I have observed that >98% of all nests that are initiated receive eggs unless destroyed by predators, suggesting that abandonments due to proximity of predators rarely occur.

The final possibility, that on-nest roosting imparts an energy savings due to the insulative value of the nest, seems more plausible. Eastern Phoebes are very early nesters and nocturnal temperatures in late March occasionally fall below 0 C. As phoebes begin breeding before insect abundance increases, it is possible that females are food (energy) limited during this period. Breeding is linked to prevailing weather conditions, principally temperature, and begins substantially earlier in warm springs (M. T. Murphy, pers. comm.; Klaas 1970). M. T. Murphy (pers. comm.) also found larger mean egg size in a warm spring than in normal springs and a sequential increase in intraclutch egg size in normal springs, which he concluded resulted from increases in food availability over the laying period. Weeks (1978) found that early season clutch sizes were larger for birds reusing old as opposed to constructing new nests, suggesting partitioning of limited energy supplies. Additionally, there is evidence that the hiatus between nest completion and laying (Klaas 1970, Weeks 1978) is related to the energy drain associated with nest construction and cool environmental temperatures. It might be surmised that other early nesting passerines should have developed this trait as well. The Eastern Phoebe is the earliest breeding, open-nesting passerine in this region, with the possible exception of the American Crow (*Corvus brachyryncos*). Eastern Phoebe nest-building and clutch initiation usually predates that of the early nesting Blue Jay (*Cyanocitta cristata*), American Robin (*Turdus migratorius*) and Northern Cardinal (*Cardinalis cardinalis*) by 2–3 wk. Additionally, its habit of frequently reusing old nests and building in

sheltered locations maximizes the potential of development and fixation of this trait in the Eastern Phoebe. Roosting in the nest cup once the first egg is present is requisite to prevent freezing of eggs during this period of vacillating temperatures.

Nests generally are conceded to function to insulate eggs and young as well as simply serving as a receptacle (Collias and Collias 1984). Nolan (1978) for Prairie Warblers (*Dendroica discolor*) and Ramsey (1987) for Carolina Wrens (*Thryothorus ludovicianus*) have documented an inverse relationship between seasonal temperatures and nest size. Walsberg and King (1978) calculated that the heat expenditure of an incubating female White-crowned Sparrow (*Zonotrichia leucophrys*) was 15% lower than for a bird perched outside the nest; a savings of this magnitude could be critical for small birds.

Mueller et al. (1982) mentioned such an energy savings as being an explanation of on-nest roosting, but dismissed it because temperatures were unseasonably warm during that incident. Viewed in the context of a universal early-season behavior rather than an isolated occurrence, however, it seems that selective forces have fixed this behavior in the population to such a degree that transient deviations from the normal cool night temperatures of early spring do not modify behavior. The reduced degree to which females roost on the nest between first and second clutches may simply be an artifact of extended care of recently fledged young. The relatively warm nights of late May, however, coupled with an abundant arthropod biomass (Robins 1970), should greatly reduce the energy constraints under which female Eastern Phoebes operate. As nests are occasionally destroyed by nocturnal predators, the behavior would become maladaptive once the energetic advantages are assuaged.

ACKNOWLEDGMENTS

I would like to thank the personnel of CNWSC, especially Lynn Andrews, for their cooperation on this project. I am grateful to R. K. Swihart, P. J. DuBowy, E. E. Klaas, I. G. Warkentin and two anonymous referees for their thoughtful comments on earlier drafts of this paper. This is Journal Paper No. 13153 from the Purdue Agricultural Experiment Station.

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Received 13 Nov. 1992; accepted 1 Mar. 1993.