HOW WELL DO ARTIFICIAL NESTS ESTIMATE SUCCESS OF REAL NESTS?¹

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Abstract. Artificial nests frequently are used to assess levels and patterns of nest predation, but how well these nests measure rates of predation or trends in predation rates at real nests is unclear. We compared predation rates between 58 active Wood Thrush (Hylocichla mustelina) nests paired with 58 artificial nests designed to resemble Wood Thrush nests. Paired nests were available to the same predator community both spatially and temporally. Rates of nest predation were significantly lower for active Wood Thrush nests (33%) than for artificial nests (64%). Rates of parasitism by Brown-headed Cowbirds (Molothrus ater) also differed between the two groups. Twenty-six percent of active nests and none of the artificial nests were parasitized by cowbirds. During 1993 and 1994, we conducted three artificial nest trials on six study sites per year. Rates of predation were highest in small woodlots and declined with increasing forest patch size consistent with the trend reported for active nests on the same sites. Within sites, rates of predation varied among trials with the amount of variation highest on sites with high predation rates. Our results suggest that although artificial nests should not be used to measure actual rates of nest predation or parasitism, they may be valuable for detecting trends in rates of predation. However, because there are many potential biases associated with the use of artificial nests that may make interpretation of trend data difficult, we recommend using artificial nests primarily in pilot studies or in conjunction with active nests.

Key words: artificial nest, cowbird parasitism, Hylocichla mustelina, nest predation, Wood Thrush.

INTRODUCTION

Artificial nests are commonly used to assess factors influencing reproductive success of forest birds. An advantage of artificial nests is that the researcher can control the number and distribution of nests in the study. It also is less time consuming to place artificial nests than locate natural nests. The implied assumption when using artificial nests is that they can serve as a suitable substitute for actual bird nests, and some researchers have found that rates of disturbance on artificial nests are similar to rates of disturbance on actual nests (Yahner and DeLong 1992). However, there have been many concerns over the use of artificial nests and the interpretation of results from these studies (Haskell 1995a, 1995b, DeGraaf and Maier 1996). For artificial nests to be a useful tool, researchers need to have a better understanding of how rates of predation on artificial nests compare to rates

Artificial nests differ from natural nests in a number of important ways that may influence predation rates. For example, lack of an incubating adult associated with artificial nests may affect a predator's ability to find nests. If adults either camouflage the natural nest or are able to actively defend the nest from predators, rates of predation may be higher on artificial nests. On the other hand, the absence of adults may result in lower rates of predation on artificial nests, if predators are attracted to natural nests by the behavior of the adults (Martin 1987).

Another important difference between artificial and natural nests is that artificial nests contain eggs but not nestlings. If predators are attracted by the begging calls of nestlings (Redondo and Castro 1992, Haskell 1994), estimated rates of predation will be low for artificial nests. On the other hand, some predators may be able to consume eggs but not nestlings. Consequently, predation rates would be higher for artificial nests than for natural nests. Artificial and natural

of predation on natural nests (Major 1991, Whelan et al. 1994).

¹ Received 23 June 1997. Accepted 16 December 1997.

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nests also may differ in the size and color of the eggs and the odor associated with the nest; all factors that have been shown to influence rates of nest predation.

Our objectives were to: (1) compare rates of predation between artificial and natural nests exposed to the same predator community both spatially and temporally, (2) compare trends in predation rates for artificial nests across woodlots of varying sizes with trends for natural nests determined on the same study sites in an earlier study (Hoover et al. 1995), and (3) determine how predation rates on artificial nests vary temporally within the nesting season.

METHODS

STUDY AREA

This study was conducted in 1993 and 1994 in Berks County, Pennsylvania, at and in the vicinity of Hawk Mountain Sanctuary. Study sites included three areas within contiguous forest (> 100 km²) and seven privately-owned woodlots ranging in size from 16.4 to 126.4 ha (Hoover et al. 1995, Morgan 1995). The seven woodlots were located within the Kutztown quadrangle and were within 20 km of contiguous forest. Study sites were separated from each other by at least 3 km, except for two of the contiguous forest sites which were within 1.2 km of one another and two of the woodlots which were within 1 km of each other. The latter pair of sites was separated by a busy road. Two sites were used during both field seasons. The remainder were used in only one year.

The primary overstory of the study sites was mixed oak (Quercus spp.), with tulip poplar (Lirodendron tulipifera), American beech (Fagus grandifolia), red maple (Acer rubrum), and black tupelo (Nyssa sylvatica). The woodlots were isolated from other areas of forest primarily by areas used for agriculture. Potential nest predators recorded on these sites during this study and previous studies included: black rat snake (Elaphe obsoleta), Blue Jay (Cyanocitta cristata), American Crow (Corvus brachyrhynchos), Common Grackle (Quiscalus quiscula), white-footed mouse (Peromyscus leucopus), eastern chipmunk (Tamias striatus), eastern gray squirrel (Sciurus carolinensis), flying squirrel (Glaucomys spp.), raccoon (Procyon lotor), Virginia opossum (Didelphis virginiana), house cat (Felis silvestris), striped skunk (Mephitis mephitis), weasel (Mustela spp.), and dog (Canis familaris) (Hoover et al. 1995, Morgan 1995).

ARTIFICIAL NESTS

Size, shape, and placement of our artificial nests were designed to resemble Wood Thrush (Hylocichla mustelina) nests. We selected the Wood Thrush as the study species because it is an areasensitive, forest-dwelling Neotropical migrant that has exhibited population declines (Robbins et al. 1989, Askins et al. 1990). In addition, baseline data from a previous study on nesting success of Wood Thrush over a range of woodlot sizes and within contiguous forest were available from the same sites currently being used in this study (Hoover et al. 1995).

Artificial nests were constructed from chicken wire molded into a 10 x 4 cm cup, which is the approximate size of a Wood Thrush nest (Harrison 1975). Artificial nests were painted flat black to reduce glare and lined with leaf litter. Two Northern Bobwhite (*Colinus virginianus*) eggs were placed in each nest. The average size of a Wood Thrush egg is 25.4 x 18.6 mm and the average size of a Northern bobwhite egg is 30 x 24 mm (Harrison 1975). Quail eggs are dull or creamy white, and Wood Thrush eggs are pale blue to blue green (Harrison 1975).

PAIRED ARTIFICIAL AND NATURAL NESTS

We searched all study sites to locate active Wood Thrush nests. Each nest found was paired with an artificial nest. To ensure that active and artificial nests were potentially available to the same predators, the artificial nest was placed within 3 to 4 m of the active nest. When possible, the artificial nest was placed in the same species of vegetation and at the same height as the active nest with which it was paired. The artificial nest also was placed in the same manner as the natural nest. For example, if the natural nest was supported by the crook of a branch, the artificial nest was placed in the crook of a branch. To reduce human scent, rubber gloves and boots were worn when placing nests. Flagging was placed within approximately 5 m of the paired nests for nest identification. During 1993, all artificial nests paired with active nests were equipped with hair catchers to detect mammalian predators (Baker 1980). During 1994, no hair catchers were placed on these nests.

Each artificial nest was assigned an "expected date of fledging" based upon the expected fledg-

ing date of the paired Wood Thrush nest. The Wood Thrush has a 14-day incubation period and a 14-day nestling period (Harrison 1975). When an active nest was found, nest contents were observed, and the approximate number of days remaining in the nesting cycle and expected fledging date were estimated. Active nests were monitored every 4-5 days during incubation and every 2-3 days during the nestling period to determine nest outcome. Artificial nests and paired active nests were checked at the same time to ensure that both nest types received the same number of visits from humans. Nest contents were checked using a convex mirror placed on a pole. Active nests were considered depredated when all eggs or young were found missing before fledging was thought to occur. We never had partial loses for active nests. Artificial nests were considered depredated when one or both of the eggs were missing or damaged. When either natural or artificial nests were depredated, we recorded the final condition of the nest as a potential clue to predator identity (Best and Stauffer 1980). If neither of the paired nests were preyed upon, the artificial nest was considered successful and removed when the young were due to fledge from the active nest. If the active nest was preyed upon first, the artificial nest was left out until it was lost to predators or until the expected date of fledging occurred. An artificial nest was considered successful if it remained undisturbed until the expected date of fledging.

We used a Wilcoxon matched-pairs sign rank test to test for differences between active and artificial nests in the number of nests that failed due to predation and the number parasitized by cowbirds. To conduct the analyses, we coded nest outcome as depredated = 0, successful = 1; and nonparasitized = 0, parasitized = 1. We used a paired t-test to test for differences in number of exposure days between active and artificial nests. In addition, we repeated the analyses after truncating the nest outcome data at the time of hatching, thereby restricting our analysis to the egg stage.

ARTIFICIAL NEST TRIALS

To determine how rates of predation varied over time and with forest patch size, we conducted a series of trials using artificial nests. Six study sites were used in 1993 and in 1994. On each site, artificial nests were placed along transect lines. Transects which extended through the center of the site, from one end to the other, were marked at 50-m intervals and ranged in length from 500 to 1,000 m depending upon the size of the study site. Ten nests were placed at 50to 100-m intervals along the transect line to ensure that nests covered the entire line. Each nest was placed 0-60 m perpendicular to the transect line. Distances (0-60 m) and directions were assigned randomly. Nests were placed approximately 2.2 m (mean nest height for Wood Thrush; Hoover 1992) above ground in a species of vegetation known to have supported Wood Thrush nests in previous years (Hoover 1992). Artificial nests that were lost to predators were removed. Nests showing no signs of disturbance were left for a maximum of 7 days, after which all nests were removed.

To determine how predation rates on artificial nests varied temporally, the study was conducted for 9 weeks (in both 1993 and 1994), which corresponds to the breeding season of the Wood Thrush. We divided the 9-week period into three 3-week time periods. Two sites per week were chosen for artificial nest trials, and each site was used for a nest trial during each of the three time periods. An individual trial lasted for 7 days. When nests were checked, caution was taken to approach the nests from different directions to avoid trampling vegetation, which could create paths to the nests. During two of the trials, we checked nests on the fourth and seventh day of the week. For the third trial, as part of another study (Morgan 1995), nests were checked twice a day at approximately sunrise and sunset. Three hundred fifty artificial nests were used during nest trials. One trial on one site was omitted from analysis because the trial was only 5 days due to a late delivery of quail eggs.

We used a chi-square test to determine whether predation rates on any one site varied significantly among the three trials. We used repeated measures analysis-of-variance to test whether predation rates for all sites combined differed among the three time periods. We used a paired *t*-test to determine whether predation rates differed between trials where nests were checked twice a week and trials where nests were checked twice a day.

To determine whether predation rates varied with forest patch size and to compare our results with those of Hoover et al. (1995), study sites were categorized as small woodlots (forest area

TABLE 1.	Rates of nest predation	and parasitism and	l mean exposure	days for 5	8 active Wo	ood Thrush nests
paired with 58 artificial nests, Berks County, Pennsylvania, 1993–1994.						

	Nest			
Parameter	Active	Artificial	Test statistic	P
No. lost to predators	19 (33%)	37 (64%)	$T^{\rm a} = 297$	< 0.01
\bar{x} exposure days \pm SE	16.1 ± 1.1	11.4 ± 1.0	$t_{57} = 3.6$	< 0.001
No. lost to predators				
(egg stage ^b)	11 (23%)	26 (54%)	$T^{\rm a}=170$	< 0.01
\bar{x} exposure days \pm SE				
(egg stage ^b)	7.9 ± 0.57	7.0 ± 0.58	$t_{47} = 1.3$	0.2
No. parasitized	15 (26%)	0 (0%)	$T^{c} = 120$	0.001

a Wilcoxon matched-pairs sign rank test, where depredated = 0, successful = 1.

< 80 ha), large woodlots (forest area > 100 ha), and contiguous forests; the proportion of nests that were successful in each group was calculated and compared using a chi-square test. We used regression analysis to test the significance of the relationship between predation rates and forest patch size (Hoover et al. 1995). For this analysis, each site was considered a separate sample. For the two sites that were used during both years, results from both years were combined and considered one sample. We used the area value of 500 ha for sites that were located within contiguous forest (Hoover et al. 1995).

RESULTS

PAIRED ARTIFICIAL AND NATURAL NESTS

Fifty-eight active Wood Thrush nests were found and paired with artificial nests. For 17 pairs, both real and artificial nests were successful, and for 15 pairs, both nests were depredated. In 22 cases, the active nest was successful but the artificial nest was depredated, and in 4 cases, the active nest was depredated and the artificial nest was successful. Rates of nest predation were significantly lower for active Wood Thrush nests than for artificial nests (Table 1). Rates of predation did not differ significantly between years for Wood Thrush nests (χ^2 ₁ = 0.6, P > 0.5) or for artificial nests (χ^2 ₁ = 0.0, P > 0.9). The mean number of exposure days, a measure of nest success, was higher for natural nests than for artificial nests (Table 1). Forty-eight Wood Thrush nests were found with eggs. When analyses were restricted to the egg stage, rates of predation were significantly lower for active Wood Thrush nests than for artificial nests, but mean exposure days did not differ between the two groups (Table 1).

The condition of the nest following predation differed between active and artificial nests significantly ($\chi^2_2 = 9.9$, P < 0.01). Of the 19 active Wood Thrush nests lost to predators, 63% showed no sign of disturbance (eggs or nestlings removed but nest intact), 5% were slightly disturbed (nest tilted), and 32% were torn apart. Of the 37 artificial nests lost to predators, 84% showed no sign of disturbance, 13% were slightly disturbed, and 3% were torn apart. No hair was detected on any of the hair-catchers placed on the artificial nests.

Rates of parasitism by Brown-headed Cowbirds (*Molothrus ater*) were higher for natural nests than for artificial nests (Table 1). Rates of parasitism did not differ between years for natural nests ($\chi^2_1 = 0.0$, P > 0.9) or artificial nests ($\chi^2_1 = 0.0$, P = 1.0).

TRENDS IN RATES OF PREDATION

Nest predation differed significantly ($\chi^2_2 = 32.2$, P < 0.001) among small woodlots (n = 180 nests, 53% disturbed), large woodlots (n = 80 nests, 36% disturbed), and contiguous forest (n = 90 nests, 18% disturbed). When the study site was considered as the sampling unit, rates of predation were negatively correlated with forest patch size ($R^2 = -0.65$, $F_{1.8} = 15.0$, P < 0.01).

TEMPORAL VARIATION IN PREDATION RATES

There was no consistent pattern in the temporal variation of nest predation. Predation rates did not vary significantly ($F_{2,20} = 0.6$, P = 0.55) with time of the trial (early, mid, late) (Table 2). In addition, predation rates did not differ between trials where the nests were checked twice a day and those where the nests were checked every 4 days ($t_{10} = 1.3$, P = 0.2). However,

b Analysis restricted to the egg stage.
c Wilcoxon matched-pairs sign rank test, where nonparasitized = 0, parasitized = 1.

		Time period ^b					
Site	Year	Early	Mid	Late	Mean	χ^2_2	P-Value
Owl's Head	1993	30	50	0°	27	6.5	< 0.05
Gun Club	1993	50	d	0	25		_
Snook	1993	60	20	20°	33	4.8	< 0.05
Kunkle	1993	30	80^{c}	20	43	8.4	< 0.05
Kehl	1993	20^{c}	100	100	73	21.8	< 0.001
Lilienthal	1993	50°	100	100	83	11.7	< 0.01
River of Rocks	1994	0	10^{c}	10	7	1.1	ns
Eckville	1994	30	0^{c}	20	17	2.3	ns
Spitsenberg	1994	40°	30	50	40	0.1	ns
Gun Club	1994	50°	50	20	40	2.5	ns
Kunkle	1994	90	30°	20	47	13.3	< 0.01
Dixon	1994	70	40°	10	40	7.5	< 0.05

TABLE 2. Temporal differences in percentage of artificial nests^a that were lost to predators during three 7-day trials on 10 study sites, Berks County, Pennsylvania, 1993–1994.

within-site rates of predation differed significantly among trials on five of the six study sites during 1993 and on two sites in 1994 (Table 2). On one site, rates of predation ranged from 20% to 100%. Sites where predation rates were low showed less variability than sites where mean rates of predation were high.

DISCUSSION

By comparing rates of predation between active Wood Thrush nests paired with artificial nests, we were able to quantitatively assess how closely artificial nests reflected actual rates of predation when both nest types were exposed to the same predator community both spatially and temporally. Consistent with findings of other studies, we observed significantly higher rates of nest predation on artificial nests than on active nests (Storaas 1988, Reitsma et al. 1990).

Rates of predation on artificial nests differ with nest appearance and conspicuousness (Yahner and Wright 1985, Martin 1987). In our study, we designed nests to look as similar as possible to Wood Thrush nests, and we placed them at the same height and in the same species of vegetation as real nests. Consequently, the differences we detected in rates of predation were probably not due to nest appearance or placement. Instead, the artificial nests were either more attractive to predators or the eggs were easier for predators to obtain as a result of one or more of the many differences between artificial and natural nests.

The presence of an adult Wood Thrush at ac-

tive nests may result in lower rates of predation by camouflaging the nest (Brackbill 1958) or because the adults actively defend the nest. Numerous studies have shown that parental birds are able to deter predators and reduce rates of nest predation (see references in Martin 1992). Alternatively, higher rates of nest predation associated with artificial nests may have occurred because some predators were able to consume eggs but not nestlings. Thus, artificial nests may have been more vulnerable because they only contained eggs. However, in a previous study on the same sites (Hoover et al. 1995), no differences were found in rates of nest predation on Wood Thrush nests between the egg and nestling stage when size of the site was taken into account, and in the current study, predation rates were higher on artificial nests than natural nests during both the egg stage and the entire nesting cycle.

A major function of egg color is presumed to be protection from visually oriented predators (Oniki 1985), and egg color influences rates of predation (Yahner and Mahan 1996). The creamy white eggs used in our artificial nests may have been more conspicuous than blue Wood Thrush eggs. Yahner and Mahan (1996) found that white eggs were more vulnerable to predators than brown eggs, but blue eggs also were more vulnerable to predators than brown eggs, at least in the initial days after the nests were set out (Yahner and DeLong 1992).

The difference in odor between artificial and natural nests also may have influenced rates of

a 10 nests per trial.
 b Early = May 22-June 12, Mid = June 13-July 3, Late = July 4-July 24.
 c Trials where nests were checked twice per day.
 d Trial omitted due to a late delivery of eggs.

nest predation. Although we attempted to minimize human scent by wearing rubber boots and gloves when placing nests, the nests were made by human hands and presumably retained some scent of humans. Olfactory-searching mammals are common predators on artificial nests and can cue in on human odors to locate nests (Whelan et al. 1994). Our artificial nests also lacked the odor of an adult bird or nestlings. What effect this had on odor-searching predators is unknown.

In contrast to our study, some researchers report higher rates of predation on natural nests than on artificial nests and attribute this result to the size of the eggs used in the artificial nest (e.g., Roper 1992). A potential bias occurs when the size of eggs used in artificial nests are larger than those in natural nests. In this case, rates of predation on artificial nests may be lower than on real nests because small-mouthed nest-predators like white-footed mice and chipmunks probably cannot consume the larger quail eggs which are typically used in artificial nest experiments (Roper 1992, Haskell 1995b, DeGraaf and Maier 1996). In addition, snakes, important nest predators in many habitats, have never been recorded depredating artificial nests, nor will they eat quail eggs when kept in captivity (Marini and Melo 1998).

In addition to different rates of predation between artificial and active nests, the condition of the nest following predation differed between the two groups, suggesting different types of nest predators. For example, 32% of active Wood Thrush nests were torn apart, a condition generally attributed to large mammals like raccoons (Best and Stauffer 1980), whereas only 3% of artificial nests were torn apart. We did not find any hair on the hair-catchers associated with artificial nests providing further evidence that large mammals were uncommon predators on our artificial nests. Some researchers have speculated that avian predators are more likely to prey upon artificial nests, whereas mammalian predators are more likely to be attracted to natural nests (Willebrand and Marcström 1988). However, there is contradicting evidence including photographs of a variety of mammals depredating artificial nests (DeGraaf 1995, Morgan 1995, Fenske-Crawford and Niemi 1997).

A more important issue than whether rates of predation on artificial nests are accurate estimates of predation rates on natural nests is whether artificial nests can be used to estimate trends or patterns in rates of predation within a local area, across sites, or in relation to habitat edges. In our study, predation rates on artificial nests decreased as forest patch size increased in a pattern similar to the one reported from a study of Wood Thrush reproductive success on the same sites (Hoover et al. 1995), suggesting that artificial nests can be used to detect trends in predation rates (Ammon and Stacey 1997). However, caution must be taken when using artificial nests to detect trends in rates of predation, particularly when the artificial nests are used to represent a community of birds. For example, using artificial ground nests, Fenske-Crawford and Niemi (1997) found higher rates of predation along edges in a forest-dominated landscape, but a concurrent study on an adjacent site found no associated edge effect for natural nests (Hanski et al. 1996). The authors of the artificial nest study suggested that the difference in results was primarily a function of nest placement; the artificial nests were on the ground whereas most of the natural nests were above ground.

Other researchers have cautioned against the use of artificial nests, baited with eggs that differ in size from the eggs in the natural nests, to detect trends in rates of predation across habitat types or woodlots of varying sizes particularly when the abundance and composition of the predator community also is changing across sites (Haskell 1995a, DeGraaf and Maier 1996). When egg size differs between artificial and natural nests, the types of predators that can consume the eggs also differs (Roper 1992, Haskell 1995b, DeGraaf and Maier 1996). Consequently, if the composition of the predator community varies across sites or habitat types, trends in rates of predation on artificial nests across these sites may not be a good index of actual rates of predation on natural nests (Haskell 1995a, DeGraaf and Maier 1996).

Similar to results from other studies, rates of nest predation for all sites as a group showed no consistent temporal pattern. However, during the two years of this study, predation rates varied among trials on 7 of the 12 sites, with the amount of variability greatest on sites where predation rates also were highest. Reitsma et al. (1990) noted that rates of predation were highly variable within a site and attributed the high level of variability to the patchy distribution of

predators. Because eggs constitute only a small portion of the diet of many of these nest predators and they do not search specifically for nests (Angelstam 1986), the high variability in rates of predation may result primarily from the chance event that a predator comes across a nest during a trial. Once they come across a nest, they may spend more time searching for additional nests.

The high variability in predation rates observed in this study and in others (Reitsma et al. 1990, Fenske-Crawford and Niemi 1997) presents problems for researchers because predation rates during any one trial may not be a true reflection of overall rates of predation on that site. Researchers can attempt to minimize this problem and obtain better estimates by conducting multiple trials per site, particularly in areas where predation rates are high. However, as the number of repeated trials on a site increases, the potential for predator learning also increases. On our sites, we did not find an increase in predation rates between trials; however, other researchers have found an increase in predation rates between multiple trials and have suspected predator learning (Vander Haegen and DeGraaf 1996). Consequently, when possible, a better way of improving estimates across different site types would be to conduct one trial per site but maximize the number of sites included in the study.

In some regions of the country and some habitat types, parasitism by Brown-headed Cowbirds has a major influence on nest success (Hoover and Brittingham 1993, Robinson et al. 1995). A shortcoming with the use of artificial nests is that they can not be used to evaluate levels of nest parasitism. Brown-headed Cowbirds generally find nests to parasitize by watching host nest-building activity (Hann 1941). Consequently, artificial nests are rarely if ever parasitized by cowbirds (Thompson and Gottfried 1976, Thompson and Gottfried 1981); a finding confirmed in this study.

There are obvious advantages to using artificial nests, and many of the seminal studies on the effects of habitat fragmentation on reproductive success were discovered through the use of artificial nests. However, researchers need to be aware of potential biases associated with the use of artificial nests. Some of these biases may be reduced by designing nests to simulate the appearance and placement of real nests, using eggs

that are similar in size and color to the species of interest, minimizing human scent associated with the nest, and restricting comparisons to local sites where the predator community does not vary among treatments (Martin 1987, Whelan et al. 1994, DeGraaf and Maier 1996). Other biases, such as the lack of adults or nestlings associated with artificial nests, are more problematic, particularly if the direction or magnitude of the bias differs among habitat types or with attributes of the nests. For example, in one study, the begging intensity of nestlings was positively correlated with increased rates of nest predation for ground nests but not for nests in trees (Haskell 1994).

We suggest that artificial nests be used primarily for pilot studies to test particular hypotheses prior to locating active nests or in conjunction with studies on real nests to provide an independent source of data (Ammon and Stacey 1997). Results from artificial nests should not be used to measure actual rates of predation or to suggest how reproductive success varies with landscape and habitat features in regions where cowbird parasitism has a large impact on reproductive success. Nor should they be used to detect trends in rates of predation across sites if the composition of the predator community differs among sites. Finally, when using artificial nests, researchers should attempt to minimize differences between artificial and natural nests and should maximize the number of independent sites included in the study whenever possible.

ACKNOWLEDGMENTS

Field assistance was provided by G. Noojibal, L. Otterson, J. Giocomo, and volunteers and staff at Hawk Mountain Sanctuary. D. W. Brauning provided assistance in study design, and K. L. Bildstein provided helpful comments on an earlier draft of this manuscript. Many landowners allowed us access to their property. We thank all individuals mentioned above. Funding for this research was provided by Pennsylvania's Wild Resource Conservation Fund, the Pennsylvania Agricultural Experiment Station, and Hawk Mountain Sanctuary Association. This paper is Hawk Mountain Sanctuary contribution number 64.

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