

# AN EXPERIMENTAL STUDY OF NEST PREDATION IN ADJACENT DECIDUOUS, CONIFEROUS AND SUCCESSIONAL HABITATS<sup>1</sup>

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**Abstract.** Predation of quail eggs in artificial nests was measured to assess potential nesting success of songbirds in adjacent deciduous, coniferous, and successional habitats at three locations in York County, Pennsylvania. During the simulated 12-day incubation period, survivorship of nests in the successional habitats was greater than nest survivorship in the coniferous and deciduous habitats. Overall, survivorship of ground nests was greater than that of above ground nests. The Conewago location had lower predation than both Kain and Pinchot. This difference was primarily due to the low above ground nest predation in the deciduous and coniferous habitats at Conewago compared to that at both Kain and Pinchot. At all locations predation of ground nests in successional habitats was less than that of above ground nests. Level of predation did not correlate significantly with any of eight measures of habitat structure. Differences in predation among the three locations may be due to anthropogenic factors as well as other characteristics of the surrounding landscape.

**Key words:** Egg predation; habitat fragmentation; artificial nests; songbird declines.

## INTRODUCTION

Studies involving the fragmentation of habitats have emphasized the relationship between predators and songbird nesting success (Gates and Gysel 1978, Wilcove et al. 1986, Yahner and Scott 1988, Andrén and Angelstam 1988, Gates and Giffin 1991, Andrén 1992). Thus, Wilcove (1985) and Small and Hunter (1988) found predation on eggs in artificial nests greater in smaller woodlots than in more extensively forested tracts. Habitats of suitable quality for nesting by migratory songbirds in suburban and rural areas are often forest fragments surrounded by farmland and residential development. In eastern North America, these fragments are part of a mosaic of vegetation types which include mature deciduous forest, early stages of secondary succession, and coniferous plantations or stands. Predation pressures on songbird nests may vary among these habitat types due to the access and movement of predators. For example, Wegner and Merriam (1979) found that the eastern chipmunk (*Tamias striatus*), a known nest predator, did not move from woodlots into adjacent grasslands; such

habitat boundaries may also restrict other nest predators. Differences in predation of artificial nests were found between adjacent habitats of marsh, upland meadow, and upland thicket (Picman 1988) and in adjacent Costa Rican rainforest, deciduous forest, and swamp (Janzen 1978). From another perspective, when comparing the Ovenbird (*Seiurus aurocapillus*), a temperate forest ground dwelling species, with ground nesting field species, Ricklefs (1969) suggested that position of the nest (at various heights or on ground) rather than habitat may have a greater influence on nesting success.

Predation is a dominant cause of songbird nesting mortality (Lack 1968, Martin 1992, Ricklefs 1969) and may be due to reptiles, birds, and mammals that consume eggs and young or to nest competitors that may harm eggs or young (Nice 1957). The diversity of predators and the variety of cues used in nest detection should favor adaptations that decrease predation potential, such as the use of less accessible habitats and concealed nest positions. Thus, habitat selection is one of the mechanisms underlying the interactions between predators and songbirds. Both predators searching for food and songbirds selecting nesting locations respond to a variety of habitat types. Selection of habitat can occur at a broader scale (e.g., a fragmented woodlot) and then be further refined at a smaller scale (e.g., mosaic of vegetation types within the woodlot) (Kotliar and Wiens 1990).

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We used artificial nests to compare the potential for predation in three common terrestrial habitats of the mid-Atlantic region. (1) Mature deciduous forest that is an important and declining habitat for numerous forest dwelling songbirds. (2) Coniferous forest that is a human-made, simplified forest habitat and may be an alternative habitat for songbirds requiring forested sites. (3) Early successional habitat that generally provides nesting habitat for different species of songbirds not found in forested habitats. We hypothesized that in situations where they are adjacent, these three habitats may experience different levels of nest predation which in turn may differently influence the success of songbird nesting strategies. The effect of nest position (above ground versus on ground) on predation in these three habitats was also tested to examine the relative importance of habitat type as compared to nest position. In addition, as discussed by Ricklefs (1969), we attempted to assess within-nest (partial) loss of eggs as compared to loss of the entire clutch.

## STUDY AREAS

Field work was conducted from 3 June to 17 June 1991 in York County located in southeastern Pennsylvania. This particular time period was chosen to correspond to the average time and duration for songbird breeding in the area. Three separate locations were utilized, each containing adjacent habitats of mature deciduous forest, early secondary succession, and conifers. Each location was part of an isolated island of park or privately owned conservation land surrounded by agricultural land and residential development. The three locations were (1) Gifford Pinchot State Park, a 946 ha park surrounding a 138 ha lake, located in a rural, residential, and agricultural area; (2) William H. Kain County Park, a part of a 730 ha park surrounding a 200 ha lake, located in close proximity to the city of York in a residential and agricultural area; and (3) a privately owned 64 ha property which is part of an ~800 ha forested corridor of private land zoned for conservation along the Conewago Creek in a rural, residential area. All locations were at least 7 km apart.

These locations were chosen based on similarities of the characteristics and size of the three adjacent habitats of mature deciduous forest, early secondary succession, and conifers. The nine habitat patches were surveyed and mapped. To quantify the similarities in vegetative character-

istics among the habitats, a vegetation analysis was performed using the technique of James and Shugart (1970) and James (1978). In each of the nine habitats six 0.04 ha circles were randomly chosen for analysis. The habitat variables measured were shrub density, percent canopy cover, percent ground cover, canopy height, and density, size, and species of trees.

Each of the three habitat types was similar at the three locations. The mature deciduous forest habitats were generally oak-hickory dominated by an overstory of red oak (*Quercus rubra*), white oak (*Quercus alba*), chestnut oak (*Quercus prinus*), and hickory (*Carya* spp.). At the Conewago location American beech (*Fagus grandifolia*) occurred with the oak-hickory species. The coniferous habitats at both the Conewago and Kain locations were planted stands dominated by white pine (*Pinus strobus*). The Conewago conifer habitat included Norway spruce (*Picea abies*), Virginia pine (*Pinus virginiana*), and eastern red cedar (*Juniperus virginiana*). The Pinchot coniferous location was late pine-scrub successional stage dominated by eastern red cedar and Virginia pine. The successional habitats were all covered with dense ground cover of various grasses, forbs, and shrubs. Staghorn sumac (*Rhus typhina*), raspberry (*Rubus* sp.), poison ivy (*Rhus radicans*), honeysuckle (*Lonicera japonica*), and multiflora rose (*Rosa multiflora*) were common. The small conifers and deciduous species interspersed in these successional habitats provided relatively little canopy cover.

To assess the degree of fragmentation the total linear edge and the total wooded area were measured from aerial photographs (1982 U.S.D.A. Soil Conservation Service 1:1,000 scale). We examined a 1.6 km<sup>2</sup> area centered on each location. Linear edge and total wooded area were estimated with a gridwork and map measurer. These data were incorporated into an index of fragmentation (linear edge [m]/total area [ha]).

## METHODS

The technique utilizing artificial nests was similar to that used by Wilcove (1985) and Loiselle and Hoppes (1983). The eggs and nests were chosen to simulate most accurately songbird nests and eggs with readily available commercial items. The nests used were bamboo straw colored open nests with a 10 cm diameter and 5 cm depth. Three fresh Japanese Quail (*Coturnix coturnix*) eggs were placed in each nest.

Although the habitats varied somewhat in size,

only 2.8 ha were used when placing the artificial nests in each habitat. The nests were placed using compass orientation to walk a transect line parallel to the habitat edge. The direction and the number of the transects were chosen so as to distribute the nests uniformly in each habitat. Four nests, two ground and two above ground (1–2 m), were placed in an area of 0.4 ha. Each 2.8 ha habitat contained 14 ground and 14 above ground nests. Therefore, each location received 84 nests, 28 each in mature deciduous, early successional, and coniferous habitats. Every 50 m a station was marked along the transect lines with an orange ribbon. One nest was placed on the ground and one above ground within approximately 10 m right or left of the marker. At each station the two nests were no closer than 5 m and generally were 10–20 m apart. Nests were placed so as to minimize the effects of artificially crowding the habitats with nests, and to keep the distribution of the nests fairly constant in the habitats and among locations.

Each nest was placed in the most concealed location in proximity to its station. Ground nests were hidden next to fallen logs, rocks, in dense grasses or forbs, and at bases of trees. The nests were partially covered by fallen leaves, conifer needles, or small branches. Nests above ground were placed in shrubs, deciduous saplings, or conifers where, if possible, the nest was surrounded with concealing foliage. Light gauge wire secured the above ground nests to prevent spilling of the nests due to predators or inclement weather. Latex gloves which were changed intermittently during nest placement were used to reduce human scent on the nests and eggs. By using these procedures, we sought to simulate as closely as possible nest placement, timing, and construction for species that potentially nest in the habitats.

Nests were placed in three locations on three consecutive days in order to minimize possible phenological influences. Simultaneous comparison of nest predation at the three locations decreased the likelihood of bias due to both random events and temporal factors. The use of three locations prevented overlooking the patchy occurrence of nest predation most likely due to the non-uniform distribution of predators (Reitsma et al. 1990) and, also, the incidental nature of predation (Vickery et al. 1992). Because visits to the nest do not appear to influence nest success (Gottfried and Thompson 1978, Wray et al. 1982), the nests in each location were checked

for predation on days 3, 6, 9, and 12 after placement. The four checks were performed to assess closely the rate and manner at which predation occurred. During checks neither nests nor eggs were touched and, when possible, were observed from a distance to minimize human scent.

The data were compiled by determining the number of nests depredated at each check in each habitat at all locations. A nest was considered depredated if one or more eggs was found missing or harmed. Conversely we considered a nest successful if all three eggs survived until day 12. Cumulative nests depredated through day 12 were used as experimental units in a three-way ANOVA to examine the effects of location (Conewago, Pinchot, and Kain), habitat (deciduous, coniferous, and successional), and nest position (ground and above ground). Habitat and position were treated as fixed factors (Sokal and Rohlf 1981). Location was treated as random and, thus, eliminated as a tested main effect because locations are unique and we desired a test of the applicability of our hypotheses to a variety of locations. The Tukey procedure was used for a posteriori comparison of means when the ANOVA indicated significant effects.

The period of 12 days was chosen to simulate the typical songbird incubation time. Day 12 results were used in the three-way ANOVA because ultimately egg success must include survival through the entire incubation period. Artificial nests may be easier for predators to locate than natural nests; in addition, predators may develop search images for artificial nests. Thus, our artificial nests may have experienced reduced survival by day 12. Thus, focusing only on day 12 without considering survivorship during the incubation period would omit potentially pertinent data. Analysis of survival at days 3, 6, 9 provides further insight into differences in accessibility of nests between habitats and positions, and was accomplished by using Proc Lifereg (SAS Institute 1990).

Pearson product-moment correlation coefficients were used to detect correlations between both vegetation variables and the fragmentation index with nest predation. This correlation was performed on total nest predation numbers on day 12 with above and ground results analyzed separately.

Although we chose eggs, nest, and incubation period to simulate as accurately as possible the natural situation this obviously was not an identical simulation, particularly since parental ac-

TABLE 1. Total number of nests experiencing predation from each of three habitats at three locations. Each habitat contained 14 nests both above and on the ground each containing three fresh Japanese Quail eggs. Numbers are the total nests in which one or more eggs was missing or damaged up to and including day 12 of the experiment.

Locations	Habitats					
	Deciduous		Coniferous		Successional	
	Above	On	Above	On	Above	On
Conewago	3	3	0	5	5	1
Kain	14	5	14	8	12	3
Pinchot	14	10	14	11	11	5

tivity was absent. Previous studies have demonstrated that predation of artificial nests is comparable to predation of natural nests (Gottfried and Thompson 1978, Møller 1988). In contrast, Reitsma et al. (1990) suggested that artificial nest predation may not always reflect predation rates of natural nests and provided an insightful discussion on the use of artificial nests. We suggest that the validity of using artificial nests can be justified not as an authentic simulation of natural nests, but instead as a tool for answering comparative questions regarding the intensity of predation. A number of studies have utilized this comparative approach with artificial nests (Picman 1988, Small and Hunter 1988, Reitsma et al. 1990, Berg et al. 1992).

## RESULTS

Total cumulative predation by day 12 at Conewago was 17 nests (20% of the total initially available) while predation at Kain and Pinchot was 56 and 65 nests respectively (67% and 77% of all nests initially available at each location). Above ground predation was 8, 40, and 39 nests (15%, 77%, and 75% of all nests initially available above ground at each location) respectively for Conewago, Kain, and Pinchot and ground predation was 9, 16, and 26 nests (17%, 31%, and 50% of all eggs initially available on ground at each location) respectively (Table 1).

The pattern of predation of ground nests among the three habitat types generally was similar at all locations (Table 1). At Pinchot and Kain, all above ground nests experienced predation in the deciduous and coniferous habitats (Table 1), and above ground predation in the secondary habitats was 11 and 12 nests (of 14 available) respectively. Conewago did not follow the same

TABLE 2. Three-way Analysis of Variance for the cumulative total of nests depredated by day 12. Comparisons were made for overall predation with location (a random factor), habitat, and nest position.

Source	df	SS	MS	F	P
Location	2	217.00	108.50		
Habitat	2	21.00	10.50	2.62	0.187
Position	1	72.00	72.00	2.75	0.239
Loc•Hab	4	16.00	4.00	2.40	0.209
Loc•Pos	2	52.33	26.17	15.70	0.013
Hab•Pos	2	19.00	9.50	5.70	0.067
Error	4	6.67	1.67		
Total	17	404.00			

pattern in that the successional habitat had five nests depredated and deciduous and coniferous forests lost three and zero nests respectively. The one consistent pattern at all three locations was the greater above ground predation as compared to ground predation in successional habitats.

Forty-four of the 252 nests experienced within-nest loss during one or more of the interval checks at days 3, 6, 9, and 12. Of these 44 nests, 15 had incomplete predation (i.e., one or two intact eggs remaining by day 12), whereas 29 of these nests exhibited complete predation (i.e., all three eggs harmed by day 12). Ninety-four nests experienced catastrophic or complete egg loss during one of the three-day periods.

## ANALYSIS OF VARIANCE

Significant interaction effects between location and position (Table 2) in the multiple ANOVA precluded emphasis on main effects. A posteriori analysis revealed that this interaction was chiefly due to the low number of above-ground nests depredated at Conewago as compared to that at both Pinchot and Kain (Table 1 and Fig. 1). The interaction of position and habitat for depredated nests was marginally significant (Table 2). This interaction was caused by the lower ground egg predation in the successional habitat as compared to the greater ground egg predation in the coniferous habitat (Fig. 1).

## SURVIVORSHIP ANALYSIS

Initially, nest success in the successional habitats was higher than in the forest habitats, but steadily decreased over the 12 day period to approach the lower survivorship reached more rapidly in the other two habitats (Fig. 2). Proc Lifereg analysis (SAS Institute 1990) revealed that survivorship of nests in the successional habitat was

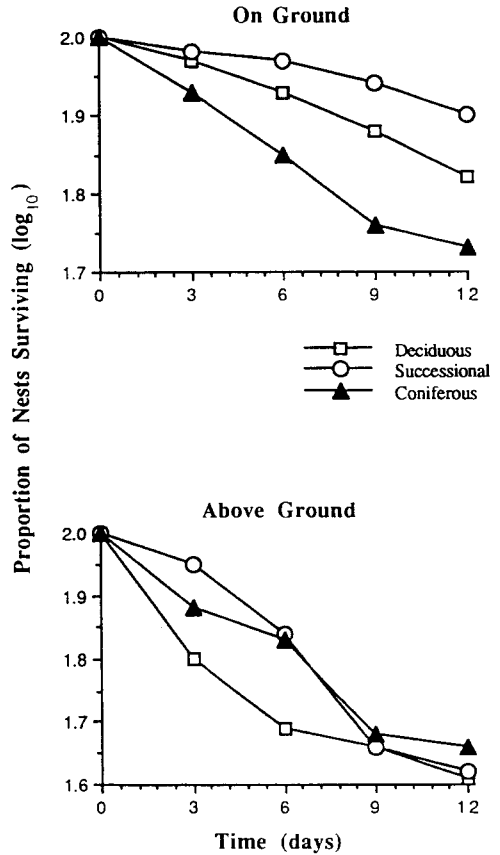
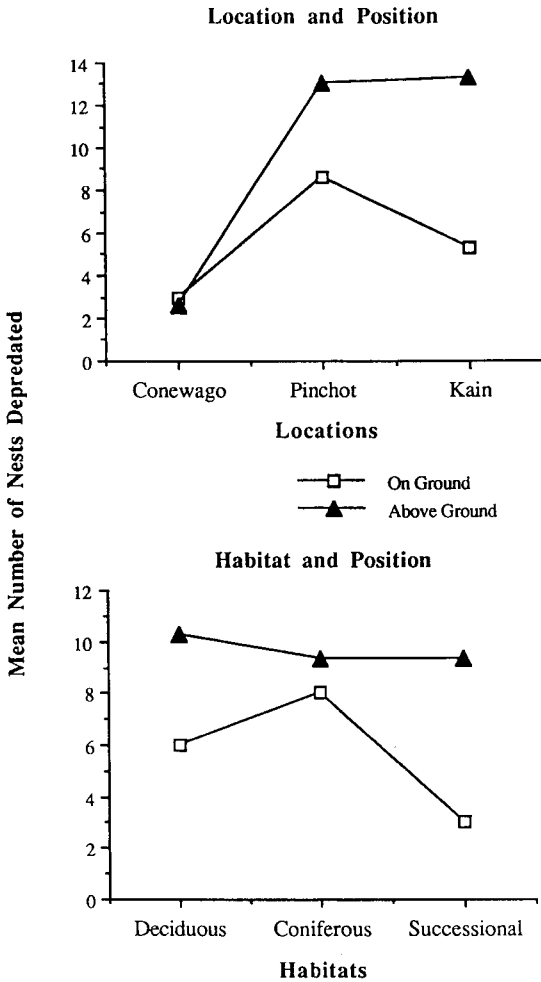


FIGURE 2. Survival of ground and above ground nests at days 3, 6, 9, and 12 according to habitat type. Values are the  $\log_{10}$  of the proportion of the nests with no egg loss.

FIGURE 1. The interaction of position and location and the interaction of position and habitat (in the three-way ANOVA) on the mean number of nests depredated.

greater than that in both coniferous habitat ( $\chi^2 = 7.16, P = 0.008$ ) and deciduous habitat ( $\chi^2 = 6.64, P = 0.010$ ). Survivorship of ground nests was significantly greater than that of above ground nests ( $\chi^2 = 24.22, P < 0.001$ ).

**CORRELATION TO VEGETATION AND FRAGMENTATION**

No significant correlation was found between nest predation on day 12 and the vegetation analysis variables (Table 3) (the correlation coefficients for above and ground nests respectively are [ $n = 9; P > 0.05$ ]: shrubs/hectare,  $r = 0.325, 0.678$ ; % canopy cover,  $r = 0.054, 0.514$ ; % ground cover,  $r = 0.023, 0.584$ ; canopy height,  $r = 0.040,$

$0.209$ ; mean density/sq. hectare,  $r = 0.051, 0.629$ ; mean basal area,  $r = 0.179, 0.016$ ; Shannon index,  $r = 0.311, 0.385$ ; and species richness,  $r = 0.259, 0.004$ ). The index of fragmentation for the Conewago, Pinchot, and Kain locations was 70, 133, and 197 m/ha respectively. No significant correlation was found between the index of fragmentation and above ground predation ( $r = 0.844$ ) or on ground predation ( $r = 0.307$ ) by day 12 ( $n = 3$ ).

**DISCUSSION**

**SIGNIFICANCE OF HABITAT TYPE AND NEST POSITION**

The marginally significant interaction of position and habitat ( $P = 0.067$ ; Table 2) was chiefly the result of the lower ground nest predation in the successional habitat than that in the coniferous

TABLE 3. Vegetation analysis of the nine study areas used in this project. The results are calculated from six 0.04 ha circles sampled in each of the areas. The shrub density designates the number of woody stems under 7 cm, and both Shannon index and species richness refer to tree species.

	Habitats								
	Deciduous			Coniferous			Successional		
	Cone-wago	Pinchot	Kain	Cone-wago	Pinchot	Kain	Cone-wago	Pinchot	Kain
Mean tree density/ha	567	796	834	1,318	1,860	530	101	175	171
Mean basal area (cm <sup>2</sup> )/tree	474	479	349	259	148	249	248	87	154
% Canopy cover	60	70	78	70	61	65	22	8	19
% Ground cover	38	36	33	30	28	62	100	89	100
Canopy height (m)	28	27	22	18	13	21	10.4	6	14
Shrub density/ha	3,466	1,183	850	317	1,067	1,033	3,733	2,283	2,316
Shannon index <sup>1</sup>	0.776	0.887	0.875	0.735	0.353	0.297	0.65	0.578	0.595
Species richness	10	11	10	9	4	4	5	4	5
Area of habitats (ha)	5.2	3.4	3	3.5	3	3.7	3	3.3	2.9

<sup>1</sup> Shannon and Weaver (1949).

habitat. Differences in predation may reflect variables in the habitats that allowed for easier access and detection of eggs by predators. The ease with which predators can move and visually locate nests on the relatively barren coniferous forest floor as compared to the dense successional ground cover may explain the greater predation in the conifers. Likewise, predation was lower in the dense ground vegetation of a marsh than in an adjacent upland thicket (Picman 1988). However, we found no significant correlation of predation to either percent ground cover or shrub density.

The possibility of the ease of movement and vision affecting predation also was evident in the difference in nest survivorship between habitats at days 3, 6, and 9 (Fig. 2). Predation occurred more rapidly in both the coniferous and deciduous habitats than in the successional habitats. For instance, by day 3 the successional stands experienced 9% predation as compared to 26% and 25% in the deciduous and coniferous stands respectively. This difference was more striking regarding above ground predation. Mean tree density/ha was less in the successional stands as compared to the deciduous and coniferous habitats (Table 3). Because the successional habitats lacked a closed canopy, individual trees had dense foliage at 1–2 m above the ground allowing for placement of above ground nests in well camouflaged positions. This greater concealment of nests in the successional habitat and the denser growth of shrubs and ground cover may be responsible for the lower incidence of predation there than in either deciduous or coniferous habitats. A study of Hermit Thrush (*Catharus gut-*

*tatus*) nests found decreased predation with a higher density of small firs surrounding the nest and increased side cover (Martin and Roper 1988). Gottfried and Thompson (1978) instead found that concealment did not influence the amount of predation on natural and artificial nest eggs in an old field successional habitat. Martin (1992) provides a review of pertinent research.

The edge between successional habitat and forest is characterized by a high density of vegetation due to spatial overlap of successional and woodland species. Predators may avoid both the dense vegetation of the actual edge and the restrictive vegetation of the successional habitat and opt for foraging on the forest side of the edge which may exacerbate the intensity of predation in the forest.

As Ricklefs (1969) suggested, nest position was more important than habitat type in our study. Generally ground nest survivorship was greater than survivorship of above ground nests (Fig. 2); Martin (1992) demonstrated similar results for actual passerine nests. Our results differed from those of others (Loiselle and Hoppes 1983, Wilcove 1985, Yahner and Scott 1988) in which ground predation was greater than or similar to that above ground (but see Martin 1988). This difference may be the result of the relative influence of different predator types, e.g., avian as compared to mammalian, or our success at camouflaging the ground nests. Greater above ground as compared to ground predation also could be the result of the lack of well concealed nest sites 1–2 m above ground (or our inability to detect them) in the deciduous and coniferous habitats. This lack of camouflage for above ground nests

may have allowed predators to more readily develop a search image for the experimental nests. Yet at the Conewago site above ground nests experienced almost no predation. Thus, variations in predators may be more of a factor than vegetation variables.

The similar predation results in the deciduous and coniferous habitats generally suggest no selective advantage for songbirds nesting in either habitat. The only exception is the more rapid rate of ground predation in the coniferous habitat suggesting a selective advantage for ground nesting in the deciduous habitat as compared to the coniferous habitat. The lower numbers of breeding bird species in coniferous habitats as compared to deciduous habitats (James and Wamer 1982) may be more strongly associated with factors other than predation (e.g., food supply).

Greater nest survivorship on the ground in the early successional stands suggests that songbird species that prefer such nesting sites and positions may be less adversely affected by predation in fragmented habitats than woodland species (see also Whitcomb et al. 1981).

#### IDENTITY OF POSSIBLE PREDATORS

Identities of the predators remain at best speculative. Mammals and snakes as well as birds could have reached above ground nests. Neither the position of the nest or the way that predation occurred, such as broken eggs versus missing eggs, can be equated to a particular predator. For instance, although above ground predation resulting in eggs broken in the nest could be assumed to be avian based on a preconception of avian mobility and predation methods, many mammals just as likely could have reached the above ground eggs and, also, could have broken the eggs rather than removed them.

Potential predators in the region include American Crow (*Corvus brachyrhynchos*), Blue Jay (*Cyanocitta cristata*), Common Grackle (*Quiscalus quiscula*), rat snake (*Elaphe obsoleta*), common garter snake (*Thamnophis sirtalis*), raccoon (*Procyon lotor*), opossum (*Didelphis virginiana*), eastern chipmunk (*Tamias striatus*), red fox (*Vulpes fulva*), red squirrel (*Tamiasciurus hudsonicus*), gray squirrel (*Sciurus carolinensis*), white-footed mouse (*Peromyscus leucopus*) and striped skunk (*Mephitis mephitis*). This study was not designed to detect the identities of nest predators, nor did we witness any predation events. Further study in 1992 indicated that Blue Jays

and raccoons were the most common predators on artificial nests (Seitz and Zegers, unpubl. data).

#### SIGNIFICANCE OF LOCATION

Although we did not emphasize the main effect of location in our statistical analysis, there were obvious location differences (Table 1; Fig. 1). The Kain and Pinchot locations, both recreational parks, experienced similar nest predation. In contrast, the Conewago site, part of a tract of privately owned conservation land, differed drastically with negligible above ground predation in both the coniferous and deciduous habitats and less than half (36%) the above ground egg predation of both Pinchot and Kain (78% and 86% respectively) in the successional habitat. Unlike that above ground, on ground predation was not drastically different among the locations.

Several factors may contribute to these differences among locations. Perhaps, they are indicative of either uneven variation in predators (Møller 1988) or incidental predation (Vickery et al. 1992). The Conewago site is part of a generally contiguous corridor of mature deciduous forest and had a lower index of fragmentation (70 m/ha) than Pinchot and Kain (133 and 197 m/ha respectively). Perhaps, a more extensive contiguous deciduous forest at Conewago allowed for greater nest survival. Moreover, recreational areas may harbor higher levels of generalist predators than privately owned conservation lands where human traffic and refuse are minimal. Also, private property may contain fewer predators due to less controlled hunting as compared to that in the recreational parks.

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