Is nest predation on two endangered bird species higher in habitats preferred by snakes?[1]

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Abstract: Higher predation on birds' nests is often associated with habitat fragmentation and edges, but little research has addressed whether these predation patterns result from non-random habitat use by predators. Using 2 endangered bird species, black-capped vireo (*Vireo atricapilla*) and golden-cheeked warbler (*Dendroica chrysoparia*), and their primary nest predator, the Texas ratsnake (*Elaphe obsoleta*), we test the hypothesis that birds nesting in habitats preferred by ratsnakes suffer higher nest predation than those nesting in non-preferred habitats. Ratsnakes did not use their habitat randomly, instead preferring locations with more structure and closer to cover objects and edges. Despite large sample sizes (186 nests and 31 snakes with radio transmitters), however, we did not find clear relationships between snake habitat preference and avian nest survival. Our results, in conjunction with those of another study, suggest that warbler nests were at greater risk if edge was abundant near the nest. Thus, reducing edge could promote nest survival. Additionally, because ratsnakes preferred warbler habitat over vireo habitat, vireos might suffer less predation in larger habitat patches that would increase average distances of nests from the snakes' preferred habitat. In making one bird species' habitat less attractive to ratsnakes, however, we may increase snake predation on other species.

Keywords: habitat, nest site, nest survival, predator–prey, snake.

Résumé : Une prédation plus importante des nids d'oiseaux est souvent associée à la fragmentation de l'habitat et à la présence de bordures, mais peu de recherches ont été effectuées dans le but de savoir si ces patrons de prédation résultent de l'utilisation non aléatoire de l'habitat par les prédateurs. En utilisant 2 espèces d'oiseaux menacés, le viréo à tête noire (*Vireo atricapilla*) et la paruline à dos noir (*Dendroica chrysoparia*) et leur principal prédateur de nids, le serpent ratier du Texas (*Elaphe obsoleta*), nous testons l'hypothèse que les oiseaux nichant dans des habitats préférés par les serpents ratiers sont soumis à une pression de prédation plus élevée que ceux nichant dans des habitats non préférés. Les serpents ratiers n'utilisaient pas leur habitat aléatoirement, ils préfèrent les sites ayant plus de structure et localisés plus près du couvert et des bordures. Malgré de grandes tailles d'échantillons (186 nids et 31 serpents avec des émetteurs radio), nous n'avons pas trouvé de relations claires entre la préférence d'habitat du serpent et la survie aviaire au nid. Nos résultats, ainsi que ceux d'une autre étude, suggèrent que les nids de parulines sont plus à risque lorsque les bordures sont abondantes près du nid. Ainsi, réduire les bordures pourrait favoriser la survie au nid. De plus, puisque les serpents ratiers préfèrent l'habitat de la paruline par rapport à celui du viréo, les viréos pourraient être soumis à une pression de prédation plus faible dans des parcelles d'habitat plus grandes qui augmenteraient les distances moyennes entre les nids et l'habitat préféré des serpents. Cependant, en rendant l'habitat d'une espèce d'oiseau moins attirant pour les serpents ratiers, nous pourrions faire augmenter la prédation sur d'autres espèces.

Mots-clés : habitat, prédateur-proie, serpent, site de nidification, survie au nid.

Nomenclature: Grzybowski, 1995; Ladd & Gass, 1999; Crother *et al.*, 2003.

Introduction

Predation is a major cause of nest failure in birds (Ricklefs, 1969; Martin, 1993a) and an important factor influencing avian nesting ecology (Martin, 1988; 1993a; 1995). Birds reduce their risk of nest predation through a variety of mechanisms, including changes in clutch size (Slagsvold, 1982; 1984), parental behaviour (Skutch, 1949; Martin, Scott & Menge, 2000), and nest site selection (Martin, 1995; 1998). Extensive research has documented bird responses to predation, but few studies have investi-gated the ecology of nest predators (Chalfoun, Thompson & Ratnaswany, 2002; Lima, 2002; Weatherhead & Blouin-Demers, 2004). Our goal in this study was to examine the association between avian nest predation and predator habitat use for 2 endangered bird species and the snake that is their principal nest predator.

Many studies have found that nest predation varies with habitat (reviewed by Martin, 1993b). In particular, habitat fragmentation is generally acknowledged as an important conservation issue (Robinson *et al.*, 1995; Heske, Robinson & Brawn, 2001), with higher rates of nest predation on edges (Gates & Gysel, 1978; Paton, 1994; Donovan *et al.*, 1995). This increase in predation is thought to result from differences in predator diversity, abundance, or behaviour

on edges (Söderström, Pärt & Rydén, 1998; Rangen, Clark & Hobson, 1999; Larivière, 2003; Thompson & Burhans, 2003; Tewksbury *et al.,* 2006). Previous work has found that effects of edges on predator abundance vary by habitat type and predator taxon, although predator behaviour on edges has received little attention (Chalfoun, Thompson & Ratnaswamy, 2002). In addition, of the 3 principal predator groups known to prey on birds' nests (birds, mammals, and snakes), the majority of studies have focused on edge use by avian and mammalian predators, with much less attention focused on snakes (review in Chalfoun, Thompson & Ratnaswamy, 2002).

Smaller-scale nest site characteristics also has an impact on nest survival, with variables such as height of nest (Martin, 1993b; Burhans *et al.,* 2002), nest cover (Martin, 1992), and vegetative structure (Martin, 1993b; Powell & Steidl, 2000) influencing nest success. Many studies of nest sites have suggested that characteristics of the site can decrease predation by concealing nests or directly deterring predation (*e.g.*, thorns; Schmidt & Whelan, 1999) and that birds choose nest sites that are safer (Martin, 1993a). Again, better understanding of how nest site selection affects predation risk seems likely to be achieved by identifying habitat selection patterns of nest predators.

Many recent studies have identified snakes as the primary predator of bird nests (Thompson, Dijak & Burhans, 1999; Morrison & Bolger, 2002; Renfrew & Ribic, 2003; Stake & Cimprich, 2003; Thompson & Burhans, 2003; Stake, Faaborg & Thompson, 2004). This result suggests that by studying snakes that are nest predators, we could advance our general understanding of avian nesting ecology and potentially identify management techniques for avian conservation (Weatherhead & Blouin-Demers, 2004). To date, however, no research has directly addressed the question of how habitat use by snakes affects predation risk for birds' nests.

To understand the relationship between predator habitat use and nest predation risk, we would ideally want to identify the predators of all bird nests in all habitats in which the habitat selection patterns of the principal predator populations are documented. With current technology and at the scale necessary to generalize patterns, such a study is not logistically feasible. What is feasible, however, and also represents an important step forward in our understanding of nest predation, is to monitor simultaneously habitat-specific nest survival and habitat use by the principal nest predator to determine if nest survival is lower in predator-preferred habitats. This is the approach we employ here.

The 2 endangered bird species we studied were the black-capped vireo (*Vireo atricapilla*) and golden-cheeked warbler (*Dendroica chrysoparia*). Previous studies that took place at our study site in Fort Hood, Texas and that incorporated extensive video camera monitoring of nests found Texas ratsnakes (*Elaphe obsoleta*) to be the most important nest predator for both species, accounting for 27% of black-capped vireo nest predation (Stake & Cimprich, 2003) and 44% of golden-cheeked warbler nest predation (Stake, Faaborg & Thompson, 2004). More recent video camera work at Fort Hood and in adjacent areas has confirmed the importance of ratsnakes as predators of golden-cheeked

warbler nests, with Texas ratsnakes accounting for 40% of predation events (Reidy, Stake & Thompson, 2008). Here we test the general hypothesis that if nest sites selected by vireos and warblers influence predation risk and ratsnakes choose habitats non-randomly, then birds nesting in habitats preferred by ratsnakes should suffer higher nest predation than those nesting in non-preferred habitats. The fact that ratsnakes account for less than half of all nest predation for both bird species might weaken the association between the birds and snakes. However, elsewhere we showed that predation risk for vireos and warblers was correlated with seasonal activity patterns of ratsnakes (Sperry *et al.,* 2008), which strengthens our expectation that overlap in habitat use between the birds and snakes should also affect nest survival.

Ratsnakes in the northern and central parts of their range preferentially use edges, as well as habitats with more structure such as logs, rocks, and large trees (Blouin-Demers & Weatherhead, 2001a; Carfagno & Weatherhead, 2006). If the same is true for Texas ratsnakes, we predict that birds nesting near edges or in more structured habitats would have lower nest survival than those further from edges and in more open habitats. Fort Hood has the largest remaining breeding populations of both endangered bird species primarily because of extensive land cover of preferred habitat types. In relating patterns of nest survival to predator habitat use our goal was to determine the potential for enhancing nest survival through habitat management.

Methods

We conducted this study in 2006–2007 at Fort Hood, an 87 890 ha military installation in central Texas (30° 10' N, 97° 45' W). The habitat of Fort Hood is predominantly oak–juniper (*Juniperus ashei* and *Quercus* spp.) woodlands and oak savannahs. Black-capped vireos typically nest in early successional, scrubby habitat, with nests often placed about 1 m off the ground, usually in oak species (Graber, 1961). In contrast, golden-cheeked warblers typically nest in dense woodland habitats, often 5–7 m off the ground in mature juniper (Ladd & Gass, 1999). At Fort Hood these 2 habitat types occur in a relatively small-scale mosaic (woodland patches typically < 200 m in diameter). The mature oak–juniper used by the warblers is the late-successional habitat in this area, whereas the early-successional habitat used by the vireos is often produced as a result of disturbance (*e.g.*, fire, human activity) of the oak–juniper habitat.

Nest searching and monitoring were conducted in 4 relatively small study areas for black-capped vireos (sized 23.2, 46.3, 95.0, and 88.4 ha) and 1 large study area for golden-cheeked warblers (250 ha). Fieldwork spanned the complete breeding season for both species in each year of the study (April to July for vireos, March to June for warblers). Nests were monitored every 2 to 4 d until fledging or failure.

One of our 2 snake study areas encompassed 3 of the vireo study areas and the warbler study area and the second encompassed the remaining vireo study area. Data from a third snake study area located away from bird study areas were not included here, although snake habitat preferences were similar in all 3 areas (J. H. Sperry, unpubl. data).

Radio-transmitters were surgically implanted in snakes, and the snakes were released, typically less than a week after capture, at their capture location. Only snakes for which the transmitter would weigh < 3% of body weight had transmitters implanted. Snakes with transmitters ranged in weight from 315 g to 825 g and averaged 528 g. Transmitters were implanted using Blouin-Demers and Weatherhead's (2001a) modification of the surgical technique described by Reinert and Cundall (1982). Transmitters weighed 9 g and 13 g with batteries lasting 12 and 24 months, respectively (Model SI-2T, Holohil Systems Incorporated, Carp, Ontario). Snakes were located approximately every 48 h, most often in the morning or early afternoon. Texas ratsnakes are primarily diurnal during the cooler months and nocturnal or crepuscular in the summer months (Werler & Dixon, 2000; J. H. Sperry, unpubl. data). Time, location, and behaviour (basking/resting, traveling, or concealed) were recorded.

Snakes that were traveling when located, representing 12% of total locations, were not included in the analysis because these locations may not represent preferred habitats and could be influenced by researcher activities. Snakes traveling in open habitats have been observed retreating from researchers as they approach (J. H. Sperry, unpubl. data). This potentially causes snakes to move into microhabitats they otherwise would not have chosen. Furthermore, available evidence suggests that snakes locate birds' nests by observing activity of nesting birds (Eichholz & Koenig, 1992; Mullin & Cooper, 1998) rather than by active searching. Thus, we assume that excluding traveling snakes from our analyses does not eliminate habitat associated with foraging.

HABITAT MEASUREMENTS

Using the same variables (see below) we quantified habitat at snake locations, random locations, and at vireo and warbler nests. We quantified snake habitat data at every second snake location. At every second snake location at which habitat was quantified (*i.e.*, every fourth location overall) we also measured habitat at a random location. Random sites were chosen by selecting a UTM coordinate at a random distance (10–200 m) and bearing from the snake location. Although we used snake locations as the starting point to select random sites, these sites provide an estimate of the habitat available in the study area used by both birds and snakes. Habitat measurements were also taken at black-capped vireo nests and golden-cheeked warbler nests in 2007. We quantified habitat 1 to 3 weeks after fledging or failure. To increase sample size for warblers, we also relocated nests we had monitored in 2006. Using GPS coordinates, old flagging tape, and remnants of the nests themselves, we successfully relocated most of 2006 warbler nests. We measured habitat at these nests during the 2007 breeding season. The habitat variables we measured were unlikely to change much between years because warblers typically nest in late-successional habitats.

The macro- and microhabitat variables we recorded at snake, nest, and random sites (Table I) were chosen because they are important for ratsnakes in other parts of their range (Blouin-Demers & Weatherhead, 2001a; Carfagno & Weatherhead, 2006). The only additional variables we included for the birds were nest height and nest tree diam-

TABLE I. Variables used in the snake habitat use analysis at Fort Hood, Texas, 2006–2007. Of these variables, only those that differed significantly between snake-use and random sites were included in the daily nest survival analysis (see text).

Variable	Description
DBHSUBST	Dbh (cm) of nest tree, birds only
DBHNEAR	Dbh (cm) of nearest tree (≥ 7.5 cm dbh)
NESTHT	Height (m) of nest, birds only
HCAN	Height (m) of canopy
CANCLO	Canopy closure (%)
DCOVER	Distance (m) to nearest rock (≥ 20 cm length) or log (≥ 7.5 cm diameter) in 30-m radius
DOVER	Distance (m) to nearest overstory tree (≤ 7.5 cm dbh) in 30-m radius
DUNDER	Distance (m) to nearest understory tree (≥ 7.5 cm dbh, ≥ 2 m height) in 30-m radius
TREES	Number of trees (≥ 7.5 dbh) in 10-m radius
SNAGS	Number of snags (≥ 7.5 dbh) in 10-m radius
NUNDER	Number of understory trees (≤ 7.5 cm dbh) in 5-m radius
LITTER	Litter depth (cm) at 4 cardinal directions in 1-m radius
%GRASS	Coverage (%) of grass in 2-m radius
%BARE	Coverage (%) of bare ground in 2-m radius
%WOOD	Coverage (%) of woody debris in 2-m radius
%ROCK	Coverage (%) of rock in 2-m radius
%HERB	Coverage (%) of herbs in 2-m radius
DEDGE	Distance (m) to nearest canopy opening (> 3 m in diameter)

eter. Ground cover and canopy height were estimated using a sighting tube with a crosswire at one end, similar to Winkworth and Goodall's (1962) apparatus. For ground cover, we aimed the sighting tube at 50 random locations within a 2-m radius and recorded the type of substrate in the crosshairs. These values were multiplied by 2 (to create a total of 100 locations) to estimate percent cover of each substrate type. Canopy cover was similarly estimated as the number of canopy "hits" recorded out of 20 random sightings at an angle > 45° from horizontal. Canopy and nest height were estimated using a clinometer. Canopy included any tree vegetation layer > 2 m in height. We assumed that from a snake's perspective, an edge is any opening in the canopy that would allow a snake easy access to direct sunlight. For that reason, distance to edge was determined by measuring distance from the snake location or nest to the nearest canopy break > 3 m in diameter.

STATISTICAL ANALYSIS

Our general analytical approach was first to determine which variables were important in differentiating between snake-selected sites and random sites. We then examined how individual habitat variables preferred by snakes affected nest survival. Finally, we used discriminant function analysis (DFA) to illustrate how the 3 species used the available habitat.

We compared habitat variables for snake-selected and random sites during the bird breeding seasons (2006–2007) using MANOVA in the program NCSS (Hintze, 2006). Snake-selected and random locations were included in analyses only if they were in wooded areas (both early and late successional) and not in grassland habitats because both bird species nest in trees and snakes generally avoided grassland habitats (7% of snake locations compared to 58% of random locations, $\chi^2 = 267.64$, df = 1, $P < 0.001$). Thus, the question we address is whether the snakes' use

of microhabitat within wooded habitat affects nest predation. For the primary analysis, we pooled locations from all snakes, with no individual accounting for more than 7% of the total data. Mean habitat variables were also analyzed separately for each snake to ensure that no individual was unduly biasing the group means. Because these individual results were consistent with results from the pooled analysis, we present only the latter. Correlations between variables were examined using a Pearson correlation matrix. All pairwise correlations were ≤ 0.50, so all variables were kept in analyses. Wilk's lambda was used to determine if snake-selected sites differed from random sites. To address our hypothesis that avian nests in snake-preferred habitats suffer greater predation than those in non-preferred habitats, we included only the individual variables that differed significantly between snake-selected and random sites in the nest survival analysis.

To determine nest survival, we monitored nests every 2–4 d and recorded whether the nest was active, fledged, or failed at each observation. We then used an information-theoretic approach to examine the relative support for 17 candidate models potentially affecting daily nest survival (Burnham & Anderson, 2002). We used the logistic exposure method (Shaffer, 2004) and PROC GENMOD (SAS Institute, 2004) to model nest survival in terms of these explanatory variables and to determine model-averaged estimates of nest survival. Candidate models incorporated both temporal and habitat variables. Temporal variables (year and season) were included to determine the relative support for temporal or habitat variables and to control for seasonal changes in habitat such as leaf phenology. We included both year and day of year for the warbler analysis and only day of year for vireos because we had nest site data only from 2007. Habitat models included all variables for which snake-selected sites and random sites differed significantly. We also included all two-way combinations of models, a null model with intercept only, and a global model with all variables. All variables were tested for correlations using a Pearson correlation matrix. The global model was evaluated for overdispersion using the Pearson χ^2 test statistic and for goodness-of-fit with a Hosmer and Lemeshow (2000) goodness-of-fit test. Models were ranked according to Akaike's information criterion for small sample sizes (AIC$_c$; Burnham & Anderson, 2002).

To determine which variables discriminate species habitat use and to generate a graphical representation of habitat use, we conducted a discriminant function analysis (Systat, 2004) incorporating all measured habitat variables at snake-selected sites and black-capped vireo and golden-cheeked warbler nest sites. We used canonical discriminant functions standardized by within variances to determine which variables separated the 3 groups.

Results

We tracked 30 snakes in the 2 study plots during the bird breeding seasons of 2006 and 2007. Tracking produced 1248 locations, which were reduced to 605 unique locations because of snakes re-using sites. We quantified habitat at 272 of the snake-selected locations and at 141 random locations. Of these, 256 snake-selected and 67 random locations were in wooded areas and therefore included in our analyses. Of these snake-selected sites, 35% were found in tree cavities, 27% were in trees, 19% were on or below ground, and 18% were under cover objects such as rocks, logs, or brush piles. For many of the locations classified simply as "in tree", snakes were most likely in cavities but the snake and/or cavity was not visible.

MANOVA indicated that snake-selected and random sites differed (Wilk's Lambda = 0.78, df = 16, 257, $P \leq 0.001$). Similar to ratsnakes in other parts of their range (Blouin-Demers & Weatherhead, 2001a; Carfagno & Weatherhead, 2006), the Texas ratsnakes we studied preferred areas with increased structure and habitat edges. ANOVA indicated that, compared to random sites, snakes were near larger trees, in areas with more litter, and closer to understory trees, cover objects, and edges. Snakes were also found in areas with less grass, rock, and bare ground, features typical of open areas (Table II).

Nest habitat was analyzed for 119 vireo nests and 67 warbler nests, which were monitored for a total of 866 and 534 d (observation days), respectively. Using the habitat variables that were important for snakes, our nest survival logistic exposure analysis included distance to edge (DEDGE) as a separate model, whereas the remaining variables were combined into 3 models: a nest tree model, which included DBHSUBST and NESTHT; a cover distance model, which included DUNDER and DCOVER; and a ground cover model, which included LITTER, %GRASS, %BARE, and %ROCK (Table I). Our habitat data met the criteria for the nest survival analysis: variation inflation factors were all ≤ 1.64, overdispersion parameters (ĉ) were 1.12 for the vireo analysis and 1.06 for the warbler analysis, and the Hosmer and Lemeshow (2000) goodness-of-fit test indicated that the global models fit the observed values ($\chi^2 = 5.13$, $P = 0.74$ for vireos and $\chi^2 = 9.03$, $P = 0.34$ for

TABLE II. Mean (± SE) of habitat variables at snake-selected, random, black-capped vireo (BCVI) and golden-cheeked warbler (GCWA) nest sites at Fort Hood, Texas. See Table I for description of abbreviated variables.

| | Snake | | Avian nest | |
| | Use | Random | BCVI | GCWA |
Variable	(*n* = 256)	(*n* = 67)	(*n* = 119)	(*n* = 67)
DBHNEAR	23.97 ± 1.09*	16.95 ± 1.09	12.32 ± 0.51	21.05 ± 1.53
LITTER	39.44 ± 1.63*	30.96 ± 3.05	37.23 ± 2.07	40.72 ± 2.34
HCAN	6.42 ± 0.17	6.02 ± 0.33	3.83 ± 0.12	7.31 ± 0.27
CANCLO	11.67 ± 0.36	11.96 ± 0.66	9.93 ± 0.55	13.81 ± 0.44
DCOVER	1.23 ± 0.13*	1.85 ± 0.37	1.92 ± 0.18	1.60 ± 0.19
DOVER	3.14 ± 0.39	4.47 ± 0.91	8.81 ± 0.85	0.77 ± 0.14
DUNDER	1.06 ± 0.10*	2.26 ± 0.62	0.67 ± 0.04	1.42 ± 0.14
TREES	10.21 ± 0.53	9.75 ± 0.83	3.83 ± 0.40	15.58 ± 0.84
SNAGS	0.99 ± 0.10	0.88 ± 0.16	0.57 ± 0.09	1.13 ± 0.13
NUNDER	19.52 ± 0.79	18.64 ± 1.68	37.50 ± 2.14	13.64 ± 1.10
%ROCK	7.95 ± 0.87*	11.94 ± 1.77	5.82 ± 1.04	6.90 ± 1.17
%GRASS	5.01 ± 0.64*	7.82 ± 1.37	11.77 ± 1.46	6.12 ± 0.92
%BARE	3.88 ± 0.61**	7.73 ± 1.64	5.15 ± 0.94	6.51 ± 1.30
%HERBS	6.49 ± 0.44	5.01 ± 0.63	8.98 ± 0.70	6.49 ± 0.44
%WOOD	16.66 ± 1.37	12.24 ± 1.26	9.02 ± 0.72	12.02 ± 1.06
DEDGE	7.47 ± 0.85**	15.39 ± 2.86	2.26 ± 0.25	13.78 ± 2.34

*Indicates significant ($P \leq 0.05$) or ** highly significant ($P \leq 0.01$) differences between snake use and random site using MANOVA.

warblers). Temporal effects (day of year) had the strongest effect on vireo nest survival, with survival declining as the season progressed (Table III). Day of year was included in both top models (< 2 ΔAIC_c; Burnham & Anderson, 2002), and the 95% confidence interval for the estimate did not encompass zero (model-averaged parameter estimate = –0.03, 95% CI = –0.04, –0.01). Edge was included in the second highest supported model and was negatively associated with nest survival (*i.e.*, nests closer to edges survived better). This resulted from vireos having a stronger affinity for edges than did ratsnakes (mean distance to edge for vireo nests and ratsnakes: 2.3 *versus* 7.5 m; Table II). Because the 95% confidence intervals encompassed zero, the association between vireo nest survival and edge was not significant. All other model-averaged estimates were very close to zero, with 95% confidence intervals encompassing zero.

For golden-cheeked warblers, nest tree (nest tree dbh and nest height) had the strongest effect on nest survival; this variable was included in all 4 of the top models, combining for 60% of total weight (Table III). Nest height had a negative effect on nest survival and substrate dbh had a positive effect. However, the 95% confidence interval for both variables encompassed zero.

The first discriminant function (DF1) from the DFA including snake-selected sites and nests of both bird species accounted for 91.5% of the explained variance (eigenvalue = 1.16). Factor loadings indicated that DF1 represented a gradient of tree size and abundance and canopy height. The second discriminant function accounted for only 8.5% of the explained variance (eigenvalue 0.11) and so is not included in interpretation of group differences. DF1 indicated significant group differences (Wilks' Lambda = 0.44, F = 13.39, df = 32, 850, P = < 0.001), although there was considerable overlap between groups (Figure 1). Within-group variation indicated that there was more habitat similarity between warblers and snakes

(F = 3.60, df = 16, 425) than between warblers and vireos, or vireos and snakes (F = 20.08 and 23.20, respectively, df = 16, 425). DF1 separated vireo nest sites from warbler nest sites and snake sites, with vireos in areas with lower canopy, fewer large trees, and more small trees (Table II, Figure 1).

Discussion

Ratsnakes at Fort Hood did not use wooded habitat randomly. Similar to what has been shown in other parts of their range (Blouin-Demers & Weatherhead, 2001a; Carfagno & Weatherhead, 2006), our results showed that ratsnakes in Texas prefer habitat that has more structure and that is closer to edges. Both in Texas and across their range, ratsnakes are most often found in retreat sites such as inside tree cavities or under rocks and logs. Habitats with more structure are more likely to have these retreat sites, although Texas ratsnakes will readily travel through more open habitats if thermal conditions allow (J. H. Sperry, unpubl. data). Because black-capped vireos nest in more open habitats and golden-cheeked warblers nest in areas with more structure, we would expect that the effect of snake habitat use on predation risk would differ between species.

Black-capped vireo nest survival was strongly and negatively affected by temporal, seasonal variables, whereas golden-cheeked warbler nest survival was affected by nest site characteristics. These results are consistent with a concurrent study (Sperry *et al.*, 2008) in which we found that seasonal variation in snake activity (a temporal variable) was a better predictor of nest predation for vireos than for warblers. Based on that result, we had speculated that nest site habitat should influence nest survival more for warblers than for vireos, and our results here support that hypothesis.

For golden-cheeked warblers, nest tree (nest height and substrate dbh) was the most important variable in determining nest survival, with predation increasing with nest height.

TABLE III. Model selection results from logistic exposure analysis examining temporal and habitat factors affecting black-capped vireo (BCVI) and golden-cheeked warbler (GCWA) daily nest survival at Fort Hood, Texas in 2007. K is the number of parameters in each model including the intercept, ΔAIC_c is the difference between each model and the model with the lowest AIC_c score, and w_i describes the relative support for each model; n is the effective sample size for observation days. Competing models (< 2 ΔAIC_c; Burnham & Anderson, 2002) are in boldface.

Model	BCVI (n = 1797)			GCWA (n = 760)		
	K	ΔAIC_c	w_i	K	ΔAIC_c	w_i
Edge distance	2	15.08	0.00	2	4.38	0.03
Ground cover	4	18.60	0.00	5	3.47	0.04
Nest tree	3	16.85	0.00	3	0.00	**0.25**
Temporal effects	2	0.00	**0.42**	3	2.53	0.07
Cover distance	3	16.74	0.00	3	5.23	0.02
Edge distance and ground cover	6	18.70	0.00	6	5.43	0.02
Edge distance and cover distance	4	18.38	0.00	4	7.22	0.01
Ground cover and cover distance	7	20.88	0.00	7	6.73	0.01
Nest tree and edge distance	4	18.32	0.00	4	1.94	**0.09**
Nest tree and ground cover	7	21.23	0.00	7	1.24	**0.13**
Nest tree and cover distance	5	20.34	0.00	5	3.80	0.04
Temporal effects and nest tree	4	3.69	0.07	5	1.27	**0.13**
Temporal effects and distance to edge	3	0.26	**0.37**	4	4.32	0.03
Temporal effects and cover distance	4	2.77	0.11	5	5.59	0.02
Temporal effects and ground cover	6	5.22	0.03	7	3.11	0.05
Global model	11	9.86	0.00	12	7.58	0.01
Null model	1	13.64	0.00	1	2.44	0.07

Snakes were often seen basking on the top of canopies (J. H. Sperry, pers. observ.), and thus from the snakes' perspective the canopy may have the same physical properties that make edges attractive. Previous work found that ratsnakes prefer edges for their thermoregulatory properties (Blouin-Demers & Weatherhead, 2001a,b). Forest edges allow snakes easy access to sun or shade, thereby facilitating behavioural thermoregulation. The junipers in which the warblers nest form a dense canopy that is relatively uniform in height. Such a canopy would also allow snakes easy access to sun or shade. Although higher vulnerability of warbler nests near the top of canopies is consistent with the canopy-as-edge interpretation, we cannot rule out other possibilities, such as higher nests being more easily found by avian predators, which account for almost 30% of predation (Stake, Faaborg & Thompson, 2004).

Given the preference for habitat edges by Texas ratsnakes, we had expected that proximity to habitat edge would affect nest survival for both bird species, and yet we found little evidence in support of that prediction. This was particularly surprising for golden-cheeked warblers because a recent study at Fort Hood had found a negative association between warbler nest survival and habitat edge (Peak, 2007). However, we defined edge as the distance to the nearest canopy break, whereas Peak (2007) quantified the amount of forest edge in a 100-m buffer around each nest. Although we found that snakes chose locations that were close to edges, Peak's (2007) results suggest that, at a larger scale, snakes may be selecting habitat in which edges are more abundant (assuming snake predation was responsible for the edge effect in Peak's study). Thus, proximity to a single canopy opening may not put a warbler nest at risk, but being in an area with many canopy openings may do so.

Our goal was to determine the potential for decreasing predation risk on the endangered bird species' nests by managing habitat to make it less attractive to ratsnakes. In addressing this objective we draw on both our results and those of Peak (2007) since the latter are from a study of the same warbler population. Obviously, the timing of breeding of vireos cannot be manipulated; similarly, modification of nest height for warblers is not possible. However, the snakes' preference for edge and cover should provide some opportunity for management. In the case of golden-cheeked warblers, Peak's (2007) demonstration of the negative effects of edge density on nest survival suggests that preventing further habitat fragmentation and, ideally, reducing current fragmentation in habitat would be beneficial. These actions would by no means eliminate nest predation by ratsnakes, but maintaining or creating large, continuous habitat patches should reduce predation.

The situation for black-capped vireos appears quite different, because vireos nest on edges and breed only in successional habitat in which edge is abundant. Thus, reducing edge is not an option. However, the results of our DFA suggest an approach that might be beneficial. DFA showed that ratsnakes use warbler habitat more than vireo habitat, presumably because of the prevalence of retreat sites such as tree cavities and logs. The fact that snakes are still found in vireo habitat could be a function of the proximity of that habitat to preferred (*i.e.*, warbler) habitat. At Fort Hood, the 2 habitat types occur primarily in a mosaic of relatively small patches, with woodland patches often less than < 200 m in diameter. Because ratsnake home range sizes are typically larger than those patches (Sperry & Weatherhead, 2009), this mosaic may allow snakes to use retreat sites in warbler habitat and make forays into vireo habitat to forage. By increasing the patch size of vireo habitat, mean proximity to warbler habitat would decrease, thereby reducing predation risk. Thus, moving from the current habitat mosaic to larger habitat patches should be beneficial to vireos. Because vireo habitat is often created by clearing juniper, removal of the resulting brush and logs might further reduce the attractiveness of the vireo habitat by reducing cover preferred by ratsnakes. A concern, of course, is that ratsnakes could respond to less-attractive vireo habitat by spending even more time in warbler habitat. Thus, any improvement in success for one bird species could be offset by reduced success for the other. Research on ratsnake habitat use at the landscape scale is needed to assess whether large-scale habitat manipulations can be used to improve reproductive success of both bird species.
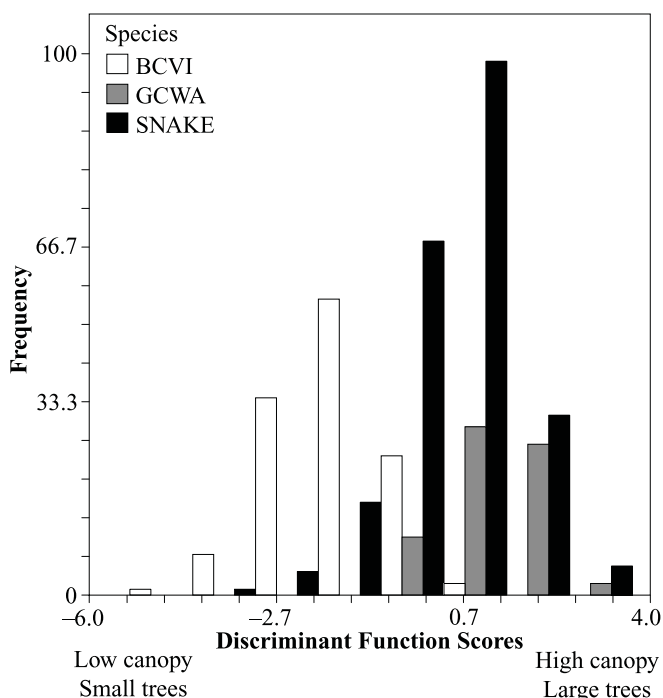
FIGURE 1. Discriminant function scores (DF1) from snake-selected sites, black-capped vireo nests (BCVI), and golden-cheeked warbler (GCWA) nests at Fort Hood, Texas. White bar indicates black-capped vireo nest sites, grey bar indicates golden-cheeked warbler nest sites, and black bar indicates snake-selected sites. See text for explanation of factor loadings.

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