

Snake activity affects seasonal variation in nest predation risk for birds

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Variation in predator behavior has been proposed, but not tested, as a mechanism producing seasonal declines in avian nest success. We test this hypothesis by documenting seasonal activity of Texas ratsnakes *Elaphe obsoleta* and nest failure of endangered black-capped vireos *Vireo atricapilla* and golden-cheeked warblers *Dendroica chrysoparia* on which the snakes prey. Nest survival analysis was based on 880 vireo and 228 warbler nests and 3,060 snake locations from 62 radio-tracked snakes. Although nest success varied with snake activity for both birds, specific patterns differed substantially. Vireo daily nest survival was negatively correlated with snake activity over the three-year study, despite substantial variation among years in weather, and the fact that these birds are almost certainly a minor prey species of the ratsnakes. Warblers exhibited less clear-cut seasonal variation in nest success, and the association between nest success and snake activity was less pronounced than for vireos. Increased activity at warmer temperatures explained some of the seasonal change in snake movements, although mating may have accounted for a mid-season peak in activity. These results indicate that variation in predator behavior can be associated with and potentially cause seasonal changes in nest success, but also that these relationships are species specific even within the same community and may depend on aspects of the nesting ecology of the prey such as nest site selection.

Seasonal variation in reproductive success is common in many animals, including fish (e.g., Schultz 1993), mammals (e.g. Green and Rothstein 1993), arthropods (e.g. Brambilla 1982), and reptiles (e.g., Fowler 1979, Harris 1980). This phenomenon is particularly well documented in birds, with nest success usually declining as the season progresses (Perrins 1970, Price et al. 1988). Mechanisms proposed to explain seasonal trends in avian reproductive success include declining environmental conditions across the season (e.g. food supply or temperature; Wiggins et al. 1994, Wardrop and Ydenberg 2003), later breeding by lower quality adults (Verhulst et al. 1995, Hansson et al. 2000; Arnold et al. 2004), and seasonal changes in predator abundance (Grant et al. 2005), or behavior (Burhans et al. 2002, Wilson et al. 2007). Hypotheses addressing variation in environmental and parental quality have received considerable attention but little research has examined predator-mediated seasonal declines in nesting success. Here we test the predator behavior hypothesis by documenting the association between seasonal activity of Texas ratsnakes *Elaphe obsoleta* and nest failure of two endangered songbirds on which the snakes prey.

Predation is the primary cause of nest failure in birds (Ricklefs 1969, Martin 1993). Therefore, understanding variation in nest success ultimately requires information about predator behavior. However, the vast majority of

work on seasonal effects of predation on avian nest survival has focused only on birds and even the identity of the predators is usually unknown. The few studies that have examined predator activity in relation to nest success have used indirect measures such as track plates or capture rates for small mammals (Cain et al. 2006, Schmidt et al. 2006), avian predator point counts (Zanette and Jenkins 2000), reptile visual encounter surveys (Cain et al. 2003), or evidence of past predator activities (e.g., digging; Vickery et al. 1992). Lack of direct examination of predators leaves researchers attempting to infer predator behavior from patterns of nest success (Weatherhead and Blouin-Demers 2004).

Variation in snake activity has been hypothesized to be responsible for nest success patterns in several studies (e.g. Best 1978, Ricketts and Ritchison 2000, Morrison and Bolger 2002), and improved camera technology that allows identification of nest predators has confirmed the importance of snakes (Weatherhead and Blouin-Demers 2004). The next step, and that which we take here, is to study snakes and birds simultaneously to determine whether nest success varies in response to changes in snake activity. We conducted the study in the oak-juniper *Juniperus ashei* and *Quercus* spp. woodlands of central Texas, where black-capped vireos *Vireo atricapilla* and golden-cheeked warblers *Dendroica chrysoparia* are locally abundant,

although both species are federally endangered. Previous studies in this area using video cameras found that Texas ratsnakes were the most frequent nest predator for both bird species, accounting for 27% of observed black-capped vireo predation events and 44% of golden-cheeked warbler predation events (Stake and Cimprich 2003, Stake et al. 2004). We test the hypothesis that if seasonal variation in nest success is a result of variation in predator activity, then nest success and ratsnake activity should be negatively correlated. Because activity of ectotherms is constrained by temperature (Huey 1982), we also determine whether variation in ratsnake activity during the avian nesting season is a function of seasonal changes in temperature.

Methods

We conducted this study at the Fort Hood military installation located in central Texas (30° 10'N, 97° 45'W) between 2005 and 2007. The Nature Conservancy (TNC), in cooperation with Department of Defense, has been monitoring populations of both endangered bird species at Fort Hood since 1993. There are five intensive study areas for black-capped vireo monitoring and three for golden-cheeked warbler. Snake capture areas were chosen to overlap TNC intensive bird study areas, but to obtain adequate sample sizes we also caught snakes in locations adjacent to those areas. Although snakes we tracked were certainly not responsible for all predation events included in this study, it is reasonable to assume that activity of these snakes is representative of that of the general population of ratsnakes at Fort Hood.

Black-capped vireos typically nest approximately 1 m off the ground in shrubby (often *Quercus* spp.) vegetation (Graber 1961). Vireos typically begin nesting in mid April and the majority of nests are completed by early July (Graber 1961, Grzybowski 1995). Golden-cheeked warblers typically nest 5–7 m off the ground in mature juniper (Ladd and Gass 1999) and nest from early April until mid June (Peak 2007). Early successional habitat of vireos and late successional habitat of warblers occur as a small-scale mosaic at Fort Hood. Approximately 11- and 12-member field crews, respectively, searched for and monitored vireo and warbler nests each year. Nests were monitored every one to four days until the nest fledged or failed.

Snakes were caught opportunistically by hand throughout the field season. Radio-transmitters were surgically implanted and snakes were released at their capture location. Only snakes for which the transmitter would weigh <3% of body weight had transmitters implanted. Transmitters were implanted using Blouin-Demers and Weatherhead's (2001) modification of Reinert and Cundall's (1982) surgical technique. We used transmitters weighing either 9 or 13 g, which had batteries lasting 12 and 24 months, respectively (Model SI-2T, Holohil Systems Limited, Ontario). Snakes were relocated at various times throughout the day at approximately 48 h intervals and locations were recorded using GPS (Global Positioning System). If the snake was not visible (e.g. under cover or in trees) we could determine snake locations to within several meters based on signal strength and direction. We used daily ambient temperature data from a weather station

located on Fort Hood for 2005–2006. Due to malfunction of the Fort Hood weather station, we used temperature data from Robert Grey airfield (approximately 20 km from field sites) for 2007 (National Climatic Data Center).

Following methods described by Shaffer (2004), we used PROC GLM (SAS Institute, Cary, North Carolina) to analyze daily survival rates of nests. Only nests that were active for >2 observations were included in analysis (Dinsmore et al. 2002). Models were developed using snake activity, year and Julian date (season), all two-way combinations of these variables and constant survival (intercept only). Snake activity was a fixed, continuous variable and was calculated as mean daily distance traveled by a snake, averaged across all snakes. Each observation day of the nesting season corresponded to mean snake distance traveled for that day. Distance moved is strongly, positively correlated with frequency of movement (J. H. Sperry unpubl. data) and thus is an appropriate index of snake activity. We tested for multicollinearity using the tolerance values from PROC REG (SAS Institute, Cary, N. Carolina) and the global model (all variables included) was tested for overdispersion using Pearson χ^2 test statistic (Burnham and Anderson 2002). Goodness-of-fit for the global model was tested by visually comparing observed and expected daily survival values at 10-d intervals across the season (Shaffer and Thompson 2007). We calculated distance traveled using Hawth's Analysis Tools (Beyer 2004) in ESRI ArcGIS version 9. We used Akaike's Information Criterion for small sample sizes (AIC_c) to rank models.

To portray seasonal trends of nest success and snake activity graphically we determined daily nest survival by dividing the breeding season into 10-d intervals and calculating mean daily survival rates (Shaffer and Thompson 2007) for each interval. The final intervals at the end of the season were removed from analysis because of small number of nests and observation days. Mean snake distance traveled was calculated as average distance each snake traveled across the 10-d interval, averaged across all snakes tracked during that interval. The relationship between daily mean distance snakes traveled (averaged across all snakes) and daily temperature was analyzed using linear regression in program NCSS (Hintze 2006).

Results

We monitored 270 black-capped vireo nests in 2005, 328 in 2006, and 334 in 2007. Of the 932 nests monitored, 524 were depredated, 297 succeeded, 89 were abandoned, 6 were destroyed (e.g. wind), and 17 failed for unknown reasons. Because analytical results were nearly identical whether or not abandoned and destroyed nests were included, here we report results based only on depredated and successful nests because causes of abandonment almost certainly included factors that were not natural (e.g. researcher or military activity). The remaining 821 nests resulted in 13,666 observation days with a mean of 16.65 (± 0.27) observation days per nest. For golden-cheeked warblers, 60 nests were found in 2005, 93 in 2006 and 75 in 2007, resulting in 1408 observation days (mean 10.06 \pm 0.55 per nest). All 228 nests were included in analyses because inaccessibility of nests meant that cause of failure

could not be determined reliably, although circumstances were generally consistent with predation. We radio tracked 62 Texas ratsnakes, producing 3,060 relocations during the bird breeding seasons.

Variance inflation factors were all ≤ 1.89 indicating multicollinearity was not a problem. The overdispersion factor (c) was 1.07 for vireo analysis and 1.02 for warblers indicating no overdispersion in the global models. Although we detected deviation between observed and expected daily survival values in visual assessment of goodness-of-fit of the global model, the fact that our overdispersion test was negative and analytical and plotted results were consistent within species, suggest that our model analysis was valid.

Daily nest survival of black-capped vireos exhibited pronounced seasonal variation that was matched closely by seasonal variation in ratsnake activity (Fig. 1). Analysis of daily survival indicated that the model combining effects of snake movement and season accounted for virtually all (99.5%) of total Akaike weight (Table 1). The analysis indicated that estimate of the independent effect of snake movement (-0.006) had a strong effect on nest survival because 95% CI ($-0.009, -0.003$) did not encompass zero.

Compared to vireos, there was not as distinct seasonal relationship between ratsnake activity and golden-cheeked warbler nest survival (Fig. 2). The logistic exposure analysis for warblers contained more uncertainty than the vireo analysis, with the top model accounting for less than 50% of total Akaike weight (Table 2). Four models including season, combined effects of season and snake movement, and snake movement alone accounted for the majority of the weight, followed by constant survival model. Snake movement again had a negative effect on daily survival but 95% CI of the model averaged estimate encompassed zero (estimate: -0.001 , 95% CI: $-0.006, 0.004$).

Snake were more active on warmer days, although the relationship between activity and temperature was stronger with minimum daily temperature than with maximum daily temperature ($R^2 = 0.21$ and 0.09 , $F = 33.33$ and 85.38 , respectively, both $P < 0.001$). Throughout the early portion of the avian nesting season, increase in snake activity closely matched increase in minimum daily temperature. However, later in the season, when only vireos were still nesting, snake activity declined despite temperatures remaining high (Fig. 3). Linear regression analysis between snake

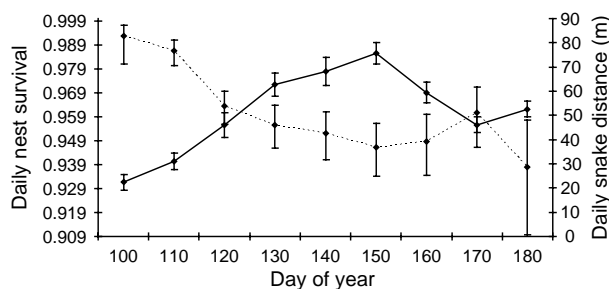


Figure 1. Mean black-capped vireo daily nest survival rates (with 95% CI) over 10-d intervals and daily distance traveled by snakes (averaged across all snakes, \pm SE) through the vireo nesting season at Fort Hood, Texas, 2005–2007. Dashed lines indicate daily nest survival and solid indicates snake distance. Number of observation days for each interval varied from 256 to 1299.

Table 1. Model selection results from logistic exposure analysis examining temporal factors effecting black-capped vireo daily nest survival at Fort Hood, Texas, 2005–2007. $\text{Log}_e(L)$ is maximized log-likelihood, K is number of parameters in each model including the intercept, ΔAIC_c is difference between each model and the model with the lowest AIC_c score, and w_i describes relative support for each model. Effective sample size is 12,952.

Model	$\text{Log}_e(L)$	K	AIC_c	ΔAIC_c	w_i
Snake+season	-1772.07	3	3550.14	0.00	0.99
Season+year	-1775.58	4	3559.15	9.01	0.01
Season	-1778.86	2	3561.73	11.59	0.00
Snake+year	-1786.11	4	3580.21	30.07	0.00
Snake	-1794.38	2	3592.76	42.62	0.00
Year	-1801.85	3	3609.71	59.56	0.00
Constant survival	-1805.52	1	3613.04	62.90	0.00

activity and minimum daily temperature for both vireo and warbler nesting seasons show that the relationship was stronger during the vireo nesting season ($R^2 = 0.30$ and 0.16 , $F = 91.56$ and 56.38 , respectively, both $P < 0.001$).

Discussion

We found clear evidence that variation in nest success of two bird species was associated with activity of Texas ratsnakes, and thus that seasonal variation in avian nest success can be driven by seasonal changes in predator activity. In the case of black-capped vireos, the association was striking. Relatively high nest success occurred early and late in the season when ratsnakes were least active, whereas much lower nest success in mid-season corresponded with high snake activity. Attributing causation to correlation requires caution, but in this case it may be justified because nest success and snake activity patterns were not simple monotonic trends across the season. Rather, the more complex pattern of nest success falling, rising and then falling again as snake activity increased, declined and then increased in concert makes a causative relationship seem more likely. Results for golden-cheeked warblers were less straightforward. Although nest success was associated with snake activity, the pronounced increase in snake activity over the warbler breeding season was not matched by a simple decline in nest success.

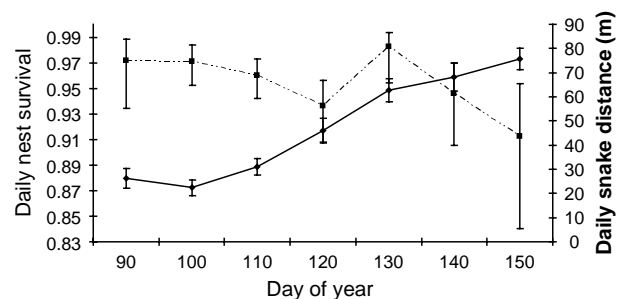


Figure 2. Mean golden-cheeked warbler daily nest survival rates (with 95% CI) over 10-d intervals and daily distance traveled by snakes (averaged across all snakes, \pm SE) through the warbler nesting season at Fort Hood, Texas, 2005–2007. Dashed lines indicate daily nest survival and solid indicates snake distance. Number of observation days for each interval varied from 80 to 396.

Table 2. Model selection results from logistic exposure analysis examining temporal factors effecting golden-cheeked warbler daily nest survival at Fort Hood, Texas, 2005–2007. $\text{Log}_e(L)$ is maximized log-likelihood, K is number of parameters in each model including the intercept, ΔAIC_c is difference between each model and the model with the lowest AIC_c score, and w_i describes relative support for each model. Effective sample size is 2,214.

Model	$\text{Log}_e(L)$	K	AIC_c	ΔAIC_c	w_i
Season	-340.39	2	684.78	0.00	0.494
Snake+season	-340.34	3	686.68	1.90	0.191
Snake	-341.77	2	687.55	2.76	0.124
Constant survival	-343.21	1	688.43	3.64	0.080
Season+year	-340.28	4	688.58	3.80	0.074
Snake+year	-341.36	4	690.73	5.95	0.025
Year	-343.21	3	692.44	7.65	0.011

Even though ratsnakes account for a higher percentage of warbler nest predation (Stake and Cimprich 2003, Stake et al. 2004), snake activity was more strongly correlated with vireo nest success. This could be a consequence of both snake habitat selection, and differences in snake behavior in different habitats. Higher predation on warbler nests seems likely to result from ratsnakes spending more time in warbler habitat than in vireo habitat (J. H. Sperry unpubl. data). Warbler habitat provides snakes with more retreat sites such as tree cavities, so in addition to active foraging, snakes may also use warbler habitat for other activities (e.g. digestion, thermoregulation), but also prey on warbler nests opportunistically. Conversely, if ratsnakes only use vireo habitat when foraging, that could cause vireo nest predation to be more closely linked to snake activity. Testing this hypothesis will require detailed information of snake behavior in different habitats. Such data would provide a much higher resolution picture of snake activity than what is obtained by locating snakes once every other day as we did in this study.

The tight association between ratsnake activity and vireo nest success is noteworthy because there are several factors that one might expect to weaken the association. First, although ratsnakes were the principal predator for vireos, both avian and mammalian predators were also documented (Stake and Cimprich 2003). Second, ratsnakes are generalist predators that do not specialize on birds during the breeding season (Weatherhead et al. 2003). Thus, birds in general and vireos specifically are likely to constitute a relatively small part of the snakes' diet. Third, annual

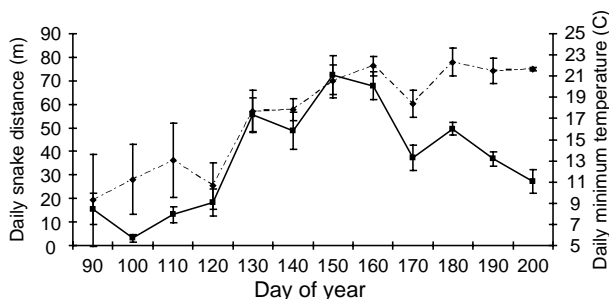


Figure 3. Daily snake distance traveled (averaged across all snakes, \pm SE) and average minimum daily temperature (\pm SE) across 10-d intervals of the avian nesting season at Fort Hood, Texas in 2005. Dashed line indicates temperature and solid indicates snake distance.

variation in weather seems likely to affect not only snake activity, but also the availability of other prey for snakes, food availability for birds, and nest site quality. Over the course of the study central Texas experienced one year with typical weather, one extreme drought year and one of the wettest springs on record. Remarkably, we found no year effects in the analysis indicating that snake activity had a constant effect on vireo nest survival.

Despite the overall increase in snake activity with warmer temperatures, the relationship was actually reversed later in the avian nesting season. Reduced activity in early spring and again in late summer is consistent with snakes avoiding cool and hot temperatures, respectively, a seasonal pattern that has been reported for other snake species (Dalrymple et al. 1991, Krysko 2002). Temperature does not explain all changes in activity, however, because the sharp decrease in snake activity late in the season occurred despite temperatures remaining relatively stable. Mating behavior may also have been involved. Ratsnakes mate in spring and both males and females become more active at that time (Blouin-Demers and Weatherhead 2002). Therefore, the increase in activity early in the season is likely to be a function of both rising temperatures and mating behavior causing snakes to take advantage of all thermal conditions that allow them to be active. Once mating ends, however, activity declines and warm conditions may largely disconnect movement from ambient temperature.

Our results provide support for the hypothesis that predator behavior can drive seasonal patterns of bird nest success. However, our study also provides a note of caution regarding generality of that hypothesis. Texas ratsnakes are the primary predator for both black-capped vireos and golden-cheeked warblers (Stake and Cimprich 2003, Stake et al. 2004), yet snake activity and seasonal nest success were closely matched only for vireos. Given the likelihood that the strength of the relationship between predators and birds depends to some extent on nesting ecology of the birds, this relationship is also likely to vary for other bird species nesting in the same community. More broadly, in other communities in which snakes are important predators, seasonal variation in temperature could affect snake activity and produce seasonal patterns of avian nest success. When the important predators are homeotherms, however, influence of temperature on activity is likely to be less pronounced. If other factors such as mating do not produce strong seasonal variation in predator activity, predator-mediated seasonal changes in nest success would seem unlikely. Testing these ideas will require simultaneously documenting activity of a variety of predators and nest success of birds on which they prey.

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and animal care followed all institutional animal care regulations (IACUC) as well as all state and federal regulations.

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