



Snake behavior and seasonal variation in nest survival of northern cardinals *Cardinalis cardinalis*

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Seasonal variation in nest success is well documented for many bird species. Predator behavior has been suggested as a mechanism behind these seasonal patterns, but this hypothesis has received little attention. Here we test the hypothesis that predator behavior produces seasonal patterns of nest success by relating nest success of northern cardinals *Cardinalis cardinalis* to the activity of Texas rat snakes *Elaphe obsoleta*. Cardinal nest survival varied over the season and was lower when rat snakes were more active. The probability that a nest survived was associated both with when cardinals nested and with nest height, indicating that both temporal and habitat factors affected predation risk. The increased success of higher nests could be associated with some aspect of rat snakes' climbing ability. In combination with results for two other species studied previously at the same location, our results for cardinals suggest that the specific seasonal pattern of nest success expected for a given bird species will depend on how its nesting season coincides with predator activity. Determining the generality of seasonal variation in predator behavior as a mechanism for producing seasonal patterns of avian nest success will require additional studies that investigate birds and their nest predators simultaneously.

Nest success of many temperate bird species declines as the season progresses (Perrins 1970, Price et al. 1988, Peak 2007). Because predation is the primary cause of nest failure for songbirds (Ricklefs 1969, Martin 1993), variation in predator behavior has been suggested as a mechanism responsible for seasonal patterns of nest survival (Burhans et al. 2002, Wilson et al. 2007). Snakes have been shown to be primary predators on the eggs and nestlings of many bird species (Weatherhead and Blouin-Demers 2004a). Because snakes can exhibit substantial seasonal variation in activity (Sperry et al. 2008), it is therefore possible that variation in snake activity can account for seasonal patterns of nest success of the birds on which they prey. The two studies that have examined the association between snake activity and nest survival have produced mixed results, however, with nest survival highly correlated with snake activity for some species, but only weakly correlated for others (Sperry et al. 2008, Weatherhead et al. 2010). It is unclear why bird species vary in the degree to which their reproductive success is tied to snake activity, but this difference may result from differences in their timing of breeding or choice of nesting habitat. Here we take advantage of the long breeding season and broad nest site selection of northern cardinals *Cardinalis cardinalis* to test this hypothesis.

Sperry et al. (2008) found that the seasonal pattern of nest survival of black-capped vireos *Vireo atricapilla* was

tightly linked to seasonal variation in the activity of rat snakes *Elaphe obsoleta*, but the rate of nest survival for golden-cheeked warblers *Dendroica chrysoparia* was only weakly related to rat snake activity, even though rat snakes are an important nest predator for both species (Stake and Cimprich 2003, Stake et al. 2004, Reidy et al. 2008). Black-capped vireos nest later in the spring (April–July [Grzybowski 1995]) than golden-cheeked warblers (March–June [Peak 2007]), which could explain why their respective associations with snake activity differed. Rat snakes are relatively inactive during the first part of warblers' nesting season, whereas throughout the vireo nesting season rat snake activity is dynamic, rising to a peak and then falling (Sperry et al. 2008). Greater variation in snake activity over the vireo nesting season may provide more opportunity to detect a seasonal pattern between predator activity and nest success. If so, then we should expect a strong seasonal pattern of nest success corresponding with rat snake activity in a bird species with a nesting season that includes the full range of snake activity. In Texas where the vireos and warblers were studied, cardinals nest from March through August, and are therefore ideal for testing this prediction.

In addition to an extended nesting season, cardinal's use of a wide range of nesting habitats allows novel tests of hypotheses addressing the effects of snake habitat use on nest

predation risk. Black-capped vireos and golden-cheeked warblers nest in early and late successional oak/juniper habitats, respectively (Graber 1961, Ladd and Gass 1999). Differences between these habitats in factors such as temperature or concealment could potentially affect nest predation in a way that accounts for the difference in how seasonal patterns of nest predation are related to rat snake behavior. Using cardinals in this study allowed us to account for any confounding effect of habitat on seasonal patterns of predation because their nesting habitat encompasses the range of habitats used by both black-capped vireos and golden-cheeked warbler. A final advantage of using cardinals is that in a recent study in Illinois, Weatherhead et al. (2010) found that cardinal nest success varied with ratsnake activity. Because neither nest success nor snake activity varied seasonally in that study, however, that study did not provide a test of the hypothesis that predator activity explains seasonal patterns of nest success. Elsewhere, cardinal nest survival has been found to vary seasonally (Best and Stauffer 1980, Filliater et al. 1994), and Kinser (1973) hypothesized that snake predation contributed to seasonal patterns of nest success in cardinals.

Our objectives were to 1) determine if nest survival of northern cardinals varied seasonally and, if so, whether that pattern was related to seasonal variation in activity of Texas rat snakes studied simultaneously in the same location; 2) determine if cardinal nest survival was related to the similarity of nest site attributes known to be associated with rat snake microhabitat use; 3) determine the relative importance of temporal versus habitat variables on cardinal nest survival; 4) compare results of this study using an avian species that is a habitat generalist with a long reproductive season with those of Sperry et al. (2008), which focused on habitat specialists with relatively short reproductive seasons.

Because we did not identify nest predators, our study is predicated on the assumption that rat snakes are important predators of cardinal nests. There are several reasons to consider this a valid assumption. In nearly all studies in which cameras have been used to identify nest predators within the geographic range of rat snakes, these snakes are common predators (Carter et al. 2007, Thompson 2007, Benson et al. 2010). Rat snakes are the primary predators for black-capped vireos and golden-cheeked warblers, both of which, like cardinals, are open-cup nesting passerines that collectively overlap with cardinals in nest height and habitat (Stake and Cimprich 2003, Stake et al. 2004). In addition, rat snakes have been observed preying on cardinal nests at our study location in Texas (Reidy et al. 2008, Barron unpubl.) and elsewhere (Halkin and Linville 1999). If we fail to find an association between rat snake activity and cardinal nest failure it could be because this assumption is wrong. Evidence of such an association, however, would suggest the assumption was sound.

Methods

Study area

We conducted our study in 2007 and 2008 at Fort Hood, an 87 890-ha military installation in central Texas (30°10'N,

97°45'W). Habitat at Fort Hood is comprised primarily of oak–juniper (*Quercus* spp. and *Juniperus ashei*) woodlands and oak savannahs. Northern cardinals in this area nest in both woodlands and savannah. We had two study sites in 2007 and 12 in 2008, varying in size from 10.8 to 159.6 ha (mean = 46.8 ha). Because both focal species are habitat generalists, we chose sites that were generally representative of the habitat available at Fort Hood. We did choose sites that varied in the amount of military training activity, although military training did not affect cardinal breeding biology (Barron et al. 2012).

Nest monitoring

To investigate patterns of nest survival we located cardinal nests at each site using parents' behavior. Once located, we monitored nests every 2 to 4 d until fledging or failure. Nests were considered successful if at least one nestling fledged and failed if there was evidence of predation/failure (e.g. egg fragments, nest destroyed) or if nest contents were removed prior to the expected fledging date.

Snake monitoring

To quantify snake activity we opportunistically caught rat snakes in the same study areas where cardinal nests were located and monitored and surgically implanted radio transmitters in snakes for which transmitters weighed < 3% total body mass (Weatherhead and Blouin-Demers 2004b). Transmitters weighed 9 or 13 g and lasted 12 and 24 months, respectively (Model SI-2T, Holohil Systems, ON). We released snakes at their capture locations and then relocated them approximately every 48 h. Each time we relocated a snake we recorded date and location (UTM coordinates). Details of the snake telemetry methods are available in Sperry et al. (2009). Note that although the telemetry methods were the same as those used previously, we tracked different snakes for this study so that the snake activity data used here were collected concurrently with the nest predation data.

Habitat measurements

Habitat measurements were taken to determine whether variables important for snakes were associated with cardinal nest survival. Measurements at snake and random sites were taken in 2005–2007 as part of a study at the same location examining snake habitat preference (Sperry and Weatherhead 2009). We used those data here, but restricted analyses to data collected only during the cardinal breeding season (April–August). Sperry et al. (2009) also used these data in their study of nest survival of golden-cheeked warblers and black-capped vireos. However, Sperry et al. (2009) limited their analyses to the habitats in which warblers and vireos nested. Because cardinals nest in all habitats with suitable nest substrates at Fort Hood, our analyses here include additional random and snake-selected sites that were omitted from Sperry et al. (2009). Thus, our results differ somewhat from those of Sperry et al. (2009). In using the habitat data collected by Sperry et al. (2009), we assumed that rat snake habitat preference is

relatively unchanged from year to year, which was confirmed by an insignificant effect of year in our analyses (Results). Furthermore, four separate studies in different locations all found that rat snakes showed a significant preference for edge habitat (Durner and Gates 1993, Blouin-Demers and Weatherhead 2001, Carfagno and Weatherhead 2006, Sperry and Weatherhead 2009), suggesting that some aspects of rat snake habitat preferences are predictable even among locations.

We quantified habitat at every second snake location, and at every other snake location where habitat was quantified (i.e. every fourth location) we also measured habitat at a random site. Random sites were chosen by selecting a UTM coordinate at a random distance (10–200 m) and bearing from the snake location. Locations of snakes that were moving when found (12% of locations) were not included in habitat analyses because rat snakes have been observed retreating from approaching observers (Sperry unpubl.) and therefore these observations may represent habitat the snakes would not normally have selected.

We recorded microhabitat variables that are important for rat snakes in Texas (Sperry and Weatherhead 2009) at snake and random sites (Table 1). We recorded the same variables at cardinal nests as well as three variables specific to nests: nest height, nest concealment, and diameter of supporting branch. Nest height was estimated using a measuring tape or clinometer, depending on the height. Nest concealment was visually estimated as the mean percent of a nest concealed by vegetation when viewed from 1 m away in each of the four cardinal directions and from directly above. We used a mirror pole to estimate concealment for nests that were too high to allow direct visual estimation. Diameter of the supporting branch was measured at the nest. If the nest was supported by several branches we used the mean

diameter of all those branches as our measurement. Results were qualitatively unchanged if we used the sum of the diameters instead of the mean.

We measured features of both 2007 and 2008 nests at the end of the 2008 nesting season. Including nests from 2007 allowed us to increase our sample size and many of the attributes measured (e.g. nest height, distance to nearest tree, canopy cover) were unlikely to change from year to year. A total of 43 nests, across both years of the study, were no longer present at the time of measurements and therefore were not included in the nest site analysis. We acknowledge that restricting our analyses to intact nests may produce a bias favoring nests that were less exposed to inclement weather or predators. If present, this bias could reduce our ability to detect differences in nest survival associated with predator habitat use. Although documenting nest site attributes prior to nest completion would have reduced this bias, we chose instead to minimize disturbance to the nest by conducting assessments after completion of nesting.

Statistical analyses

We used an information-theoretic approach to examine the relative support for candidate models potentially affecting daily nest survival (Burnham and Anderson 2002). We used the logistic exposure method (Shaffer 2004) and PROC GENMOD in SAS (SAS Enterprise ver. 4.3, SAS Inst., Cary, NC) to model nest survival in terms of explanatory variables and to determine model-averaged estimates of nest survival. We ran two separate survival analyses, one with snake activity and temporal variables and another with snake activity and nest site variables. We conducted two analyses because we had nest site information for only a subset of our total nests (116 of 159) and the separate temporal analysis allowed us to use data from all nests.

For our temporal analysis, models were developed to include snake activity (mean daily distance traveled by a snake, averaged across all snakes), nest stage (incubation or nestlings), day of breeding season, quadratic effect of day of breeding season, cubic effect of day of breeding season, year, all two-way combinations of these variables, constant survival (intercept only), and a global model (all variables). Thus, for each nest observation day, in addition to the year and day of year of the observation, we had a corresponding snake distance traveled for that day and current nest stage. Daily distance traveled by a snake was calculated as the straight-line distance traveled between successive observations, divided by the number of days between observations. Although a straight line distance may not accurately reflect actual distances traveled, snake daily distance moved is strongly, positively correlated with frequency of movement (Sperry and Weatherhead 2009) and thus is an appropriate index of snake activity. We included quadratic and cubic effects of day of breeding season because these have been shown to be important for other species (Dinsmore et al. 2002, Grant et al. 2005) and because we know that the seasonal pattern of snake activity is nonlinear (Sperry et al. 2008). To graphically display seasonal patterns of nest survival and snake activity (Fig. 1), we used logistic exposure to calculate daily survival

Table 1. Habitat variables measured at snake-selected, random, and northern cardinal nest sites at Fort Hood, Texas.

Variable	Description
AVGCONC	Concealment (%) over the nest, averaged across 4 directions and directly above, from 1 m radius
NESTHT	Height (m) of nest
DIAMSUPP	Diameter (cm) of branch supporting nest
HCAN	Height (m) of canopy directly above
CANCLO	Canopy closure (%) directly above
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
NUNDER	Number of understory trees (≤ 7.5 cm dbh) in 5 m radius
LITTER	Average litter depth (cm) from 4 measurements taken at 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
DEGE	Distance (m) to nearest canopy opening (> 3 m diameter opening)

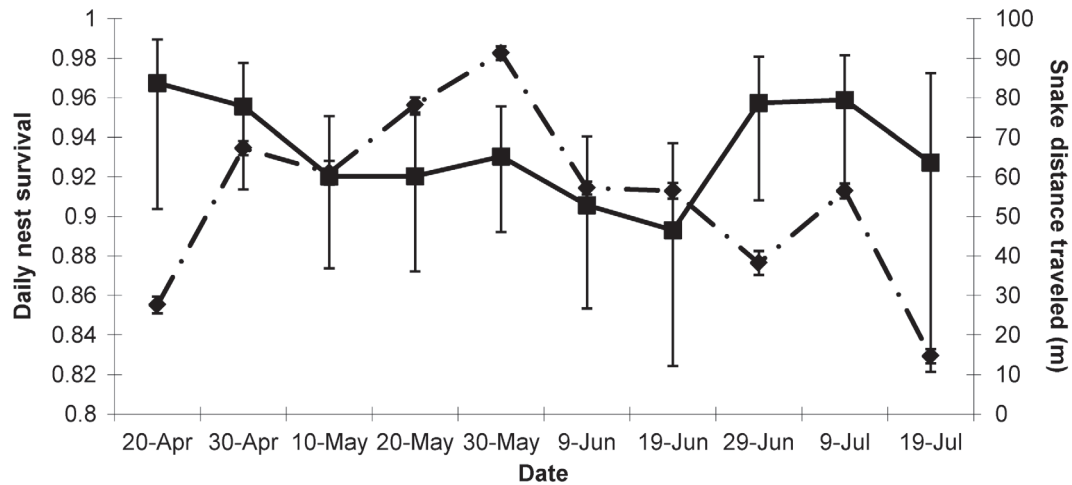


Figure 1. Northern cardinal daily nest survival, calculated at 10-d intervals across the nesting season, with 95% confidence intervals and daily distance traveled by snakes (averaged across all snakes, $\pm$ SE) at Fort Hood, Texas, 2007–2008. Solid line indicates daily nest survival and dashed line indicates snake distance. Number of observation days 10 d⁻¹ interval ranged between 17 observation days in the last interval and 261 observation days in the 30 May to 9 June interval (mean = 136.00 ± 21.86 observation days). Number of snakes included per interval ranged from 30 to 45 (mean = 40.30 ± 1.35 snakes per interval).

rate (DSR) at 10 d intervals across the nesting season. Season interval was the only variable included in the model used to calculate DSR.

We used a two-step approach to determine whether measured habitat attributes affected nest survival. First, we determined which habitat variables were important in differentiating snake-selected and random sites to characterize snake habitat preference. Second, we conducted cardinal nest survival analyses using those variables that differed between snake-selected and random sites to determine if the variables that influence snake habitat use also influence nest survival rates. To determine snake habitat preferences, we compared snake-selected and random sites using PROC MIXED in program SAS (SAS Enterprise ver. 4.3, SAS Inst., Cary, NC). To control for pseudo replication due to multiple observations per individual, we included individual as a random effect. We also included year as a random effect to control for any yearly variation. Correlations among variables were examined using a Pearson correlation matrix. Canopy closure and distance to nearest overstory tree were highly correlated with other variables (Pearson coefficients > 0.60) and so were removed from analyses. Some data were log-transformed to improve normality, although non-transformed data are presented in text and tables. To address the hypothesis that nests in habitats with features preferred by snakes 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 minimize the number of candidate models included in our nest survival analyses while maintaining all nest site variables, we examined single variable candidate models with variables (nest height and distance to habitat edge) that have been shown to be important in previous studies (Sperry et al. 2009, Weatherhead et al. 2010) and then combined the remaining variables into three models based on similarity of variables and location of variables

relative to the nest or snake location: 1) a nest-tree model that included substrate height, nest concealment, and diameter of supporting branch, 2) a ground-cover model that included distance to nearest cover object, litter depth, and percent of each ground cover type, and 3) a canopy model that included canopy height, distance to nearest understory tree, number of trees, and number of understory trees (see Table 1 for description of variables). We also included snake activity to determine the relative support for temporal vs. habitat variables. For both survival analyses, 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 and Anderson 2002). We examined the relationships between nest habitat variables and the day of the breeding season in which the nest fledged or failed using linear regression to determine whether habitat varied seasonally. All analyses were conducted using Program SAS (SAS Enterprise ver. 4.3, SAS Inst., Cary, NC). In text, means are presented ± 1 SE.

Results

We monitored 56 nests for 568 observation days in 2007 and 103 nests for 1096 observation days in 2008. Of 159 nests monitored, 51 were successful, 96 were depredated, 10 were abandoned, and the fate of two was unknown. Nest site characteristics were measured for 116 nests that were monitored for a total of 1239 observation days (295 observation days in 2007 and 944 observation days in 2008). For the snake habitat component of this study, we tracked a total of 53 snakes from 2005 to 2007 and conducted habitat assessments at 446 snake-selected sites (90 in 2005, 217 in 2006 and 139 in 2007) and 251 random sites (47 in 2005, 125 in 2006 and 79 in 2007). For the temporal component (to coincide with daily nest survival data), we

tracked 38 snakes during 2007 resulting in 1673 locations (mean = 44.0 ± 10.9 per snake) and 16 snakes during 2008 resulting in 550 locations (mean = 34.4 ± 3.4 per snake).

For both the temporal and habitat nest survival analyses, our data met the criteria for the analyses. Overdispersion parameters ($\hat{c}$) were 1.03 for the temporal analysis and 1.08 for the habitat analysis, and the Hosmer and Lemeshow (2000) goodness-of-fit test indicated that the global models fit the observed values ($\chi^2 = 1.32$, $DF = 8$, $p = 0.86$ for temporal and $\chi^2 = 5.2$, $DF = 8$, $p = 0.27$ for habitat).

Seasonal variation in cardinal nest survival was negatively associated with rat snake activity, which was low early and late in the season but rose to a mid-season peak (Fig. 1). In the temporal analysis, the model with snake activity alone received the most support and snake activity was included in the top six competing models ($\Delta AIC_c < 2$; Table 2). The model-averaged coefficient for snake activity was -0.009 and the 95% confidence intervals did not encompass zero (-0.017 , -0.001), indicating a negative relationship between daily nest survival and snake activity. The 95% confidence intervals for all other variables encompassed zero and the constant survival model ranked above all other individual models, indicating little support for any of the other variables.

For the snake habitat analysis, snake-selected and random sites differed for all variables (all $F > 11.80$ and all $p < 0.01$), with snake-selected sites in areas with more habitat structure (e.g. more trees, leaf litter, canopy, and retreat sites such as rocks and logs; Table 3). Results for cardinal nests were more ambiguous, with nest sites similar to random sites for seven variables, similar to snake-selected sites for three variables and different from both for two

Table 2. Model selection results from logistic exposure analysis examining temporal factors affecting northern cardinal nest survival at Fort Hood, Texas (2007–2008). 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. See text for a description of model variables. Effective sample size (Rotella et al. 2004) for observation days was 1532.

Model	K	AIC_c	ΔAIC_c	w_i
Snake	2	607.21	0.00	0.26
Snake and year	3	607.98	0.77	0.18
Snake and season	3	608.97	1.75	0.11
Snake and stage	3	609.11	1.90	0.10
Snake and season ³	3	609.13	1.92	0.10
Snake and season ²	3	609.22	2.01	0.10
Global model	6	609.54	2.32	0.08
Constant survival	1	613.22	6.00	0.01
Year	2	613.87	6.66	0.01
Season ³	2	614.77	7.56	0.01
Season	2	614.79	7.57	0.01
Stage	2	615.16	7.95	0.00
Season ²	2	615.20	7.99	0.00
Season and year	3	615.30	8.09	0.00
Year and season ³	3	615.56	8.35	0.00
Stage and year	3	615.83	8.62	0.00
Year and season ²	3	615.88	8.67	0.00
Season and stage	3	616.69	9.48	0.00
Stage and season ³	3	616.75	9.54	0.00
Stage and season ²	3	617.16	9.94	0.00

Table 3. Mean, standard errors, and range of habitat variables used in nest survival analysis from snake-selected, random, and northern cardinal nest sites on Fort Hood, Texas. Mean estimates and standard errors were calculated from PROC Mixed in Program SAS (SAS Enterprise ver. 4.3, SAS Inst., Cary, NC). Bold text indicates a group that significantly ($p < 0.05$) differed from the other two groups. See Table 1 for explanation of variables.

Variable	Snake		Cardinal nest (n = 116)
	Use (n = 458)	Random (n = 261)	
HCAN	6.51 $\pm$ 0.37 (0.00–22.00)	3.62 $\pm$ 0.40 (0.00–14.00)	6.32 $\pm$ 0.53 (2.07–22.64)
DCOVER	2.25 $\pm$ 0.69 (0.00–30.00)	5.62 $\pm$ 0.74 (0.00–30.00)	5.02 $\pm$ 0.95 (0.00–30.00)
DUNDER	2.06 $\pm$ 0.46 (0.00–30.00)	6.93 $\pm$ 0.52 (0.00–30.00)	1.81 $\pm$ 0.66 (0.00–14.10)
TREES	9.23 $\pm$ 0.90 (0.00–53.00)	6.11 $\pm$ 0.95 (0.00–37.00)	4.64 $\pm$ 1.56 (0.00–60.00)
NUNDER	14.22 $\pm$ 2.13 (0.00–80.00)	7.38 $\pm$ 2.19 (0.00–76.00)	13.61 $\pm$ 2.57 (0.00–51.00)
LITTER	31.72 $\pm$ 2.27 (0.00–145.75)	11.05 $\pm$ 2.44 (0.00–110.25)	14.37 $\pm$ 3.22 (0.00–55.00)
%GRASS	9.24 $\pm$ 1.43 (0.00–90.00)	29.18 $\pm$ 1.66 (0.00–100.00)	28.62 $\pm$ 1.97 (0.00–94.00)
%BARE	5.24 $\pm$ 0.78 (0.00–66.00)	18.71 $\pm$ 1.01 (0.00–100.00)	2.26 $\pm$ 1.43 (0–38.00)
%WOOD	15.83 $\pm$ 1.00 (0.00–100.00)	5.16 $\pm$ 1.20 (0.00–64.00)	3.89 $\pm$ 1.62 (0.00–34.00)
%ROCK	7.25 $\pm$ 0.89 (0.00–100.00)	11.49 $\pm$ 1.10 (0.00–100.00)	3.66 $\pm$ 1.45 (0.00–50.00)
%HERB	8.81 $\pm$ 2.58 (0.00–44.00)	13.45 $\pm$ 2.61 (0.00–66.00)	16.78 $\pm$ 2.70 (0.00–98.00)
DEDGE	7.57 $\pm$ 1.36 (0.00–123.83)	13.07 $\pm$ 1.53 (0.00–134.09)	1.80 $\pm$ 2.01 (0.00–5.78)

variables (Table 3). Because all habitat variables differed significantly between snake-selected and random sites, we included all of them in the nest survival analysis.

For the habitat nest survival analysis, the top models included nest height and nest height in combination with snake activity (Table 4). Nest height was positively related to nest survival (model averaged estimate = 0.39) although the 95% confidence interval encompassed zero (-0.09 , 0.87). The 95% confidence intervals for the model-averaged coefficient estimates encompassed zero for all other variables.

Discussion

Northern cardinal nest survival varied seasonally in a way that appeared to reflect variation in rat snake activity. Although the pattern of nest survival over the course of the season was not straightforward (e.g. nest success did not simply decline over the season), the general feature that emerged was that success was lowest in the middle of the season when rat snakes were most active. Because snake activity was present in competing nest survival models, it therefore seems reasonable that our assumption is correct that rat snakes are important predators of cardinal nests. It is possible that another important nest predator had seasonal activity patterns similar to those of rat snakes and thereby contributed to the apparent importance of rat snakes. Because no other single species of nest predator in the study area is likely to account for a substantial proportion

Table 4. Model selection results from logistic exposure analysis examining snake activity ('Snake') and habitat factors affecting northern cardinal nest survival at Fort Hood, Texas (2007–2008). 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. Effective sample size (Rotella et al. 2004) for observation days was 1157.

Model	K	AIC_c	ΔAIC_c	w_i
Nest height and snake activity	3	476.37	0.00	0.41
Nest height	2	477.15	0.78	0.28
Nest height and edge distance	3	478.66	2.29	0.13
Snake activity	2	481.02	4.65	0.04
Constant survival	1	481.92	5.55	0.03
Nest height and canopy	6	482.03	5.65	0.02
Edge distance and snake activity	3	482.12	5.75	0.02
Nest height and nest tree	5	482.82	6.44	0.02
Edge distance	2	482.84	6.47	0.02
Nest tree and snake activity	5	484.85	8.47	0.01
Nest height and ground	8	485.26	8.89	0.00
Nest tree	4	486.13	9.75	0.00
Snake activity and canopy	6	486.81	10.44	0.00
Nest tree and edge distance	5	486.85	10.48	0.00
Canopy	5	487.55	11.17	0.00
Ground	7	487.59	11.22	0.00
Snake activity and ground	8	488.01	11.64	0.00
Edge distance and ground	8	488.20	11.83	0.00
Edge distance and canopy	6	489.25	12.88	0.00
Canopy and ground	11	490.47	14.10	0.00
Nest tree and canopy	8	490.61	14.23	0.00
Nest tree and ground	10	492.63	16.26	0.00
Global model	16	495.15	18.77	0.00

of nest predation (Stake and Cimprich 2003, Stake et al. 2004), however, this possibility seems unlikely. Therefore, our results support the hypothesis that variation in predator activity can account for seasonal patterns of nest success in individual bird species. Furthermore, because cardinals' unusually prolonged breeding season and broad habitat preferences overlap with most other species in the area, it is likely that the broader passerine community is similarly affected by rat snake activity patterns.

Unlike black-capped vireos and golden-cheeked warblers (Sperry et al. 2008), cardinals nested well into the summer when rat snakes became less active. As predicted, this decline in snake activity was associated with increased nest survival. Although a mid-season peak in nest predation is not the most common seasonal pattern of nest failure (Perrins 1970, Price et al. 1988), a late season increase in nest survival has been observed previously for cardinals (Best and Stauffer 1980, Filliater et al. 1994). Together with Sperry et al.'s (2008) results for black-capped vireos and golden-cheeked warblers, our results for cardinals suggest that the specific seasonal pattern of nest success expected for a given bird species will depend on how its nesting season coincides with predator activity. When the overlap between nesting and predator activity is extensive (i.e. vireos and cardinals), seasonal patterns of nest success should occur, whereas reduced overlap (i.e. warblers) can reduce seasonal patterns even if the predator still accounts for a substantial proportion of nest failures.

Given that snakes are the primary predator of birds' nests in many geographic areas (Weatherhead and Blouin-Demers 2004a), our results may provide insight into the

seasonal patterns of nest survival of birds in other locations. Other than in the tropics, seasonality is primarily a thermal phenomenon, and because snakes are ectotherms, a general association between seasonality, snake activity and nest predation seems plausible. In Texas, rat snake activity during the period when birds are nesting is strongly correlated with temperature (Sperry et al. 2008), consistent with this hypothesis. In Illinois, however, snake activity was not significantly correlated with temperature when birds were nesting (Weatherhead et al. 2010), challenging the generality of this pattern.

Our habitat analyses indicated that Texas rat snakes were found in areas with more structure (e.g. larger trees, more litter, less grass) compared to what was available. In contrast, northern cardinals nests were found in relatively open habitats, with few trees and a higher percentage of grass ground cover. Although it is possible that differences in habitat use indicate that cardinals actively select nest sites different from snake-preferred areas, we found that most nest site attributes had little influence on nest survival, suggesting that if cardinals are attempting to avoid rat snakes they realize little benefit from doing so. Similar to what was seen with golden-cheeked warblers and black-capped vireos at the same study sites (Sperry et al. 2009), our results with cardinal nesting habitat and nest survival were less clear than our temporal analyses. Nest height was included in all competing nest survival analysis models, with higher nests experiencing higher survival. However, the model-averaged estimates for nest height did not significantly differ from zero, indicating a weak effect. Weatherhead et al. (2010) also found evidence that higher nests were more successful in the bird community they studied. Whether this reflects something about rat snake climbing behavior remains to be determined.

It is encouraging that we can start to explain patterns of nest predation by studying nest predators, particularly given the limitations of the data used to date. Although rat snakes have been documented to be the most important nest predators in this area, other predators undoubtedly account for some nest failures (Stake and Cimprich 2003, Stake et al. 2004, Benson et al. 2010). Benson et al. (2010) recently demonstrated that identifying nest predators allows detection of patterns that are masked when nests with different predators are examined together. This suggests that predator-driven seasonal patterns of nest success may be more apparent when a single type of predator accounts for most of the predation. Therefore, the patterns of nest success associated with rat snake behavior in this study would presumably be even clearer if we could restrict analyses only to nests known to have been preyed on by rat snakes. In addition, depending on the primary predator, simple measures of predator activity may not be positively correlated with predation risk if other activities, such as mate searching, are mutually exclusive from activity associated with foraging. For predators such as ratsnakes that appear to be opportunistic foragers (Weatherhead et al. 2003), however, an increase in activity, regardless of the primary function of the activity, would be expected to result in increased predation risk for nesting birds.

The ultimate goal of understanding seasonal or other patterns of nest predation is to be able to predict how the

risk of nest predation varies for nesting birds, and thereby to understand how natural selection affects how individual birds choose when and where to nest and how to behave once a nest has been initiated. Although this study provides additional evidence that variation in nest success is primarily driven by predator behavior, to understand the selective forces on nesting songbirds we need more studies that identify nest predators while simultaneously studying the behavior of both those predators and the nesting birds on which they prey.

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