# Barking up the wrong tree: climbing performance of rat snakes and its implications for depredation of avian nests

# Stephen J. Mullin and Robert J. Cooper

Abstract: Nest depredation is the leading cause of nest failure in Neotropical–Nearctic migratory birds, which are of interest because of their declining populations. In a recent study in a bottomland hardwood forest, Acadian Flycatchers (*Empidonax virescens*) experienced higher nest success in Nuttall oak (*Quercus nuttallii*), a tree species with relatively smooth bark at maturity. To determine if variation in bark-surface irregularities may influence the ability of a predator species to access the contents of avian nests, we examined the climbing abilities of rat snakes (*Elaphe obsoleta*) on trees having three different bark types. None of the subjects was able to ascend large Nuttall oaks in the absence of vines; with vines present, subjects still required more time to climb Nuttall oaks than to climb other species. A few of the subjects successfully climbed smaller Nuttall oaks lacking vines, but ascent time was longer and climbing behavior was modified from that observed in the other trials. Our results indicate that the likelihood of nest predation by rat snakes decreases in this forest when birds nest in trees with smooth bark and without vines. Investigators need to consider differences among nest substrates that are important to both the prey and the predator.

**Résumé**: Le pillage des nids est la principale cause des nidifications ratées chez les oiseaux migrateurs néotropicaux– néarctiques qui prennent un intérêt particulier parce que leurs populations sont en déclin. Au cours d'une étude récente dans une forêt de feuillus des terres basses, des moucherolles verts (*Empidonax virescens*) qui ont niché dans des chênes de Nuttall (*Quercus nuttallii*), à l'écorce relativement lisse à maturité, ont eu plus de succès à la reproduction. Pour déterminer si la variation dans les irrégularités de surface de l'écorce peut influencer la capacité d'une espèce prédatrice d'accéder au contenu de nids d'oiseaux, nous avons évalué l'aptitude de serpents ratiers (*Elaphe obsoleta*) à grimper à des arbres présentant trois types d'écorce. Aucun des serpents n'a réussi à faire l'ascension de gros chênes de Nuttall en l'absence de lianes; cependant, à l'aide de lianes, les serpents grimpaient aux chênes de Nuttall dépourvus de lianes, mais de plus petite taille, et dans ces cas, l'ascension était plus lente et le comportement au cours de la montée était distinct de celui observé pendant les autres essais. Nos résultats indiquent que la probabilité de pillage des nids par les serpents ratiers est moins élevée dans cette forêt lorsque les oiseaux nichent dans des arbres à écorce lisse et sans liane. Il est donc essentiel de tenir compte des différences de substrats qui sont importantes tant pour les prédateurs que pour les proies.

[Traduit par la Rédaction]

## Introduction

Recent declines in many species of Neotropical–Nearctic migratory birds have prompted researchers to investigate factors that limit populations (e.g., Martin and Finch 1995; Rappole 1995). Of considerable interest is nest depredation, the leading cause of nest failure for most passerine birds (Ricklefs 1969). Natural selection should favor open-nesting birds that choose nest sites which minimize the likelihood of depredation. The characteristics of nest sites that deter depredation are unclear. Sometimes visual concealment was greater around successful nests than around depredated nests (Martin

Received 6 September 2001. Accepted 27 February 2002. Published on the NRC Research Press Web site at http://cjz.nrc.ca on 19 April 2002.

S.J. Mullin.<sup>1</sup> Department of Biological Sciences, Eastern Illinois University, Charleston, IL 61920-3099, U.S.A.
R.J. Cooper. Daniel B. Warnell School of Forest Resources, University of Georgia, Athens, GA 30602, U.S.A.

<sup>1</sup>Corresponding author (e-mail: cfsjm@eiu.edu).

1992; Howlett and Stutchbury 1996; Burhans and Thompson 1998 and references therein). More often, however, concealment and other habitat measurements did not differ between successful and depredated nests (Howlett and Stutchbury 1996; Burhans and Thompson 1998 and references therein).

In a southeastern U.S. bottomland hardwood forest, Wilson and Cooper (1998*a*) found that one species of Neotropical– Nearctic migratory songbird, the Acadian Flycatcher (*Empidonax virescens*), nested preferentially in Nuttall oak (*Quercus nuttallii*), one of the red oak group. Furthermore, birds usually were more successful in Nuttall oak than in other tree species on the study site (Wilson and Cooper 1998*a*; Cooper et al. 1999). We knew that rat snakes depredate Acadian Flycatcher nests (R.J.C., personal observation) and are capable of leading an arboreal existence (Mullin et al. 2000). We hypothesized that the smooth bark on mature Nuttall oaks would deter important reptilian nest predators, like rat snakes, from climbing them, thus providing nest locations that were safe from these predators.

Saenz et al. (1999) documented the effectiveness of shaving tree bark with a forester's drawknife to deter predation of woodpecker nests by rat snakes. Shaving removes the surface irregularities on the trunk that snakes use as purchase points when ascending trees. Substrate irregularities facilitate movement of snakes in general (Cundall 1987), and are particularly useful when rat snakes climb the vertical surfaces of trees (Lillywhite and Henderson 1993).

In the present study, we continue the approach of Mullin and Cooper (1998) of using predator foraging trials under controlled conditions to evaluate rat snakes' climbing behavior. Specifically, we consider the climbing performance of rat snakes on different tree species in a natural setting and discuss our results as they pertain to nesting success of bird species in bottomland hardwood forests. In addition to describing the snake climbing behavior, we address the following questions: (*i*) Does rat snake climbing performance differ on tree species having different bark characteristics? (*ii*) Does the presence of vines along the trunk affect snake climbing performance on these tree species? (*iii*) Does climbing performance on these tree species vary by subject size or gender? (*iv*) Does climbing performance vary on trees of different sizes?

## Materials and methods

## Study site and subjects

The White River National Wildlife Refuge (WRNWR) is a 60 000-ha tract of mostly bottomland hardwood forest that extends 104 km along the White River in southeastern Arkansas. We conducted our study in a 50-ha plot that is part of a 1376-ha management compartment of contiguous homogeneous habitat within WRNWR. The dominant overstory tree species in the plot were sugarberry (*Celtis laevigata*), overcup oak (*Quercus lyrata*), Nuttall oak, green ash (*Fraxinus pennsylvanica*), and bitter pecan (*Carya aquatica*). Other tree species found at the site and additional description of WRNWR habitat are found in Wilson and Cooper (1998*a*) and Wilson (1997).

We collected rat snakes at WRNWR as well as in Shelby County, Tennessee (Tennessee Wildlife Resources Agency permit No. 684), Faulkner County, Arkansas, and Alexander, Coles, and Johnson counties in Illinois (Illinois Department of Natural Resources Scientific Permit No. A00.0506). Of our 16 subjects (12 males and 4 females), 9 were collected from bottomland hardwood forest habitat; the other subjects were collected in old-field sites or early-succession ecotones with forest habitats. Subjects from the latter habitats were not inferior climbers on trees at our study plot (discussed below). None of the subjects used were in the process of ecdysis or, if female, gravid. A few of our subjects were used in previous studies and had been maintained in captivity for up to 7 years (Institutional Animal Care and Use Committee protocol No. A-9336). We acknowledge that prolonged captivity may influence behavior and (or) physiological performance, but we minimized handling of the subjects during their time in captivity to reduce any effects on their climbing ability (Warwick 1990; Ford 1995). We sexed all subjects with a cloacal probe and measured their mass  $(\pm 0.1 \text{ g})$ and snout-vent length (SVL; ±0.5 cm) within 24 h prior to beginning the study. Subject mass was recorded again at the conclusion of the study 3 days later. We provided subjects with access to water prior to, and between, the days they were used in the trials.

## **Climbing trials**

We conducted our study from 7 to 9 June 2000, a time period when several bird species inhabiting WRNWR, including Acadian Flycatchers, were breeding. Ambient temperatures during all trials ranged between 23.6 and 29°C. We used two trees of each of three species in which Acadian Flycatchers nest most frequently (sugarberry, overcup oak, and Nuttall oak) that were  $30 \pm 5$  cm diameter at breast height (DBH). This DBH range includes the mean tree size used by successfully nesting Acadian Flycatchers at our site (26 cm; Wilson and Cooper 1998a). Each of these species is characterized by a distinct bark type offering different levels of surface irregularities for purchase by a climbing snake. We categorized the bark of each tree species as smooth (Nuttall oak), rough (overcup oak), or bumpy (sugarberry). Specifically, the rough bark of overcup oak contains large irregular plates or ridges with longitudinal fissures in between, and the bumpy bark of sugarberry contains corky warts or ridges on otherwise smooth bark (Harlow and Harrar 1969).

The first lateral branch of all trees used in our study was at least 5 m above ground level. Subjects were therefore ascending vertical surfaces in all trials (all tree trunks used were within 3° of being vertically straight for the first 7.5 m of their height). Of the two trees chosen for each species, one had vines (poison ivy (*Toxicodendron radicans*), Virginia creeper (*Parthenocissus quinquifolia*), and (or) grape (*Vitis* sp.)) attached to the bark surface at least to the height of the first lateral branch; the other tree representing each species lacked vines. To illustrate that the presence of minor surface irregularities was sufficient to affect the climbing performance of rat snakes (discussed below), we chose trees where vines were few in number (2–4 per tree) and relatively small (0.2–3.5 cm DBH).

On each tree we marked the end-points of a 2-m vertical distance (beginning at least 1.5 m above the ground) by scoring the bark around the trunk with a carpenter's file. This distance exceeded the SVL of all subjects (see Results). We positioned a ladder against the tree that allowed us to retrieve a subject after it reached the top of the 2-m vertical distance, but not so close to that height as to allow the subject to extend over to the ladder prior to completing the ascent.

Subjects were individually placed on the tree trunk below the beginning of the 2-m vertical distance. When positioning subjects on trees with vines, we placed at least 30% of the subject's total length in contact with a vine; the starting position (around the tree trunk) was otherwise chosen haphazardly. Subjects usually began climbing immediately upon their release onto the tree. Some individuals hesitated, however, and were coaxed with gentle tail-tapping ( $\leq 1$  tap per 5 s) with a snake hook (Saenz et al. 1999). We recognize that tail-tapping the snakes may have influenced their climbing speed, but assume that differences in ascent time due to a subject's motivational state were negligible compared with the differences in treatment level (bark type and presence/ absence of vines). We recorded whether or not the subject completed the climb (repeated falls or refusal to ascend were recorded as unsuccessful attempts) and the time elapsed  $(\pm 0.5 \text{ s})$ 

**Table 1.** Masses  $(\pm 0.1 \text{ g})$  and snout–vent lengths (SVL;  $\pm 0.5 \text{ cm}$ ) of rat snakes (*Elaphe obsoleta*) used in climbing experiments at White River National Wildlife Refuge, Arkansas, 5–7 June 2000.

	Males $(n = 10)$	Females $(n = 4)$
Mass		
Mean $\pm 1$ SE	$517.3 \pm 104.2$	$573.6 \pm 147.0$
Range	248.6 - 1112.9	161.2 - 847.3
SVL		
Mean $\pm 1$ SE	$119.4 \pm 6.9$	$112.5 \pm 10.6$
Range	97.0 - 157.0	81.0 - 125.0

**Note:** Differences in mass and SVL as a function of sex are absent (ANOVA,  $F \le 0.29$ ,  $p \ge 0.60$ ).

between the subject's snout tip crossing the end-points of the 2-m vertical distance.

#### **Statistics**

We randomized the order in which subjects climbed the trees in the different treatments. Of our 16 snakes, we used 14 in a complete-block design with all treatment levels (i.e., the individual snake was treated as a block). Differences in climbing time were assessed using a multiway analysis of variance (ANOVA) with a significance level of 0.05. Tukey's honestly significant difference (HSD) test (df = 1 in all comparisons) was used as a pairwise follow-up test to detect differences between treatment means (Zar 1999; Dowdy and Wearden 1991). All statistical analyses were performed using SuperANOVA (Abacus Concepts). We limited each subject to 3 climbs per day and allowed a minimum of 2 h to elapse between climbing attempts.

## Results

Neither subject mass nor SVL was a function of gender (Table 1; ANOVA,  $F \le 0.29$ ,  $p \ge 0.60$ ). Longer snakes were typically heavier (Pearson's correlation, r = 0.92, p = 0.001), but neither mass nor SVL influenced ascent time (Pearson's correlation,  $r \le 0.13$ ,  $p \ge 0.67$ ). The habitat type from which the snake was collected also did not influence ascent time (ANOVA,  $F_{[1,12]} = 0.42$ , p = 0.53). Subjects lost 23.4 ± 4.5 g (mean  $\pm$  SE) in mass during the 3-day experiment, but variation in climbing performance was not influenced by either fatigue or possible experience (ANOVA,  $F_{[5,59]} = 0.31$ , p =0.90). The temperature during the trials did not influence climbing performance (Pearson's correlation, r = 0.14, p =0.24). In all of our complete-block analyses, the block effect (that of the individual snake) was significant, with snakes taking longer to climb if they had spent more time in captivity prior to the start of the experiment (r = 0.82, p = 0.003).

None of our subjects were able to climb large ( $\geq 26.0$  cm DBH) Nuttall oaks in the absence of vines. This result necessitated our using two separate analyses. First, we used a completely randomized block design comparing the three tree species with vines present. When vines were present, ascent time varied with tree species (Table 2;  $F_{[2,26]} = 7.85$ , p = 0.002), with subjects requiring more time to ascend Nuttall oaks than to ascend the other tree species (Tukey's HSD test,  $F \geq 10.85$ ,  $p \leq 0.003$ ). Second, a two-way factorial design compared only overcup oak and sugarberry trees with

**Table 2.** Ascent times of 14 rat snakes (*Elaphe obsoleta*) on three tree species at White River National Wildlife Refuge, Arkansas, 5–7 June 2000.

	Ascent time (s)	
	Without vines	With vines
Nuttall oak	_	350.6 ± 79.2
Overcup oak	$222.8 \pm 53.3$	$170.1 \pm 36.3$
Sugarberry	$165.0 \pm 31.0$	$183.4 \pm 35.9$

**Note:** No subject successfully climbed Nuttall oaks in the absence of vines. Values are given as the mean  $\pm 1$  standard error. See the text for the results of statistical analyses.

and without vines. Ascent times did not differ according to tree species ( $F_{[1,39]} = 0.93$ , p = 0.34), presence or absence of vines ( $F_{[1,39]} = 0.56$ , p = 0.46), or their interaction ( $F_{[1,39]} = 2.38$ , p = 0.13). The interaction approached significance because vines decreased climbing time in overcup oak but increased climbing time in sugarberry (Table 2).

Following all trials, because none of the subjects climbed large Nuttall oaks lacking vines, snakes were allowed to climb smaller DBH trees of that species without vines. Of 14 attempts on each of two smaller DBH trees, 6 snakes ascended an 8 cm DBH tree (time =  $160.3 \pm 48.1$  s) and only 2 snakes ascended a 20 cm DBH tree (time =  $295.0 \pm 34.0$  s). Although ascent times during these trials were comparable to those in other treatment conditions, we tail-tapped snakes more often to encourage climbing and observed that subjects spent more time searching for irregularities on the bark surface that could be used as purchase points during their climb.

Our subjects used lateral undulation most often when climbing; however, a modified form of concertina locomotion was observed in those snakes climbing the 8.0 cm DBH Nuttall oak. With a posterior body coil encircling the entire trunk, the anterior portion of the body was extended and then wrapped around a higher point on the trunk. The posterior body was then drawn up the tree and the process repeated to further the ascent.

## Discussion

In addition to their keen vomeronasal sense (Halpern 1992), rat snakes also use visual cues to find avian nests in arboreal habitat (Mullin and Cooper 1998). Most Acadian Flycatcher nests are positioned in the midcanopy (mean height of 511 nests = 6.5 m; Wilson and Cooper 1998*a*), and provisioning behavior at the nest may provide specific locality information to potential predators on the ground (Mullin and Cooper 1998). Because substrate irregularities on tree trunks vary considerably in a mixed-species deciduous forest, access to those nests by rat snakes can be limited by the bark characteristics of the nest tree. We have demonstrated that rat snakes are incapable of climbing mature Nuttall oaks which lack purchase points for the snakes' ventral scales. We suggest that this may, in part, account for the higher nesting success observed for Acadian Flycatchers in this tree species (Wilson and Cooper 1998a).

In treatment conditions other than Nuttall oak without vines, subjects did not move, or fell, in only 5 out of 75

attempts when climbing. There was no relationship between these failed attempts and treatment condition, and the subjects later completed a climb for the treatment in which they had failed. We caution that, although rat snakes have been observed depredating Acadian Flycatcher nests (Wilson and Cooper 1998b), we have not quantified the amount or percentage of nests depredated by rat snakes. Therefore, the higher nest success in Nuttall oak than in the other tree species cannot necessarily be attributed to the inability of all snakes to climb the smooth bark.

Irregularities on the bark of various tree species often change with age and height (Harlow and Harrar 1969). In particular, young overcup oak and sugarberry have relatively smooth bark compared with older trees of these species, whereas the reverse occurs in Nuttall oak (personal observation). This may explain the differential climbing abilities of rat snakes on Nuttall oaks of different sizes. When climbing smaller Nuttall oaks having relatively rougher bark, rat snakes were less likely to use undulatory movements and more likely to use a variant of concertina locomotion (Lillywhite and Henderson 1993). Presumably, lateral undulation would be used if vines or lateral branches were present on these smaller trees.

The presence of vines allowed rat snakes to climb large Nuttall oaks, whose smooth bark might otherwise preclude climbing. The presence of vines also decreased climbing time in overcup oak, but not sugarberry, where climbing time was less on the tree without vines. Rat snakes used the bumps on sugarberry bark as purchase points, and obviously did not need the vines to successfully climb the tree. Climbing speed probably depends as much on the size and arrangement of the bumps, which are highly variable from tree to tree, as on the presence of vines. In habitats like bottomland hardwood forests, the presence and number of vines are potentially important variables in predicting nest success of tree-nesting bird species and should be measured in studies of nest-site selection when appropriate (Martin et al. 1996). We recommend testing the practice of removing vines from tree trunks, especially smooth ones, if the management objectives for a bottomland hardwood forest include the conservation of Neotropical-Nearctic migratory birds.

We acknowledge that the significant block effect in our analyses (due to differences between subjects) may be attributable to those snakes that took longer to climb trees if they had spent more time in captivity. We were not able to capture all of our subjects immediately prior to the experiment, however, and we minimized our handling of those subjects that were maintained in captivity for extended periods (Warwick 1990). All subjects held in captivity prior to this experiment did not lack climbing experience, as they had been used in previous studies involving arboreal habitat (e.g., Mullin and Cooper 1998, 2000). More importantly, time spent in captivity may have little bearing on the effects of substrate roughness on climbing speed (cf. Jackson 1976).

Rat snakes used in our study failed to climb large Nuttall oaks lacking vines, thus they were denied access to nests constructed in that tree type. However, our subjects also required nearly twice as long to climb that species when vines were present as to climb either overcup oak or sugarberry (with or without vines). Unless vines are dense enough to conceal a climbing snake beneath the foliage, the predator is relatively exposed on a surface offering little in the way of vantage points or retreat sites. If ascent time is viewed as time spent exposed to other predator species (e.g., raptorial birds), the risk associated with the time taken to ascend a vertical substrate may be an important factor to a foraging rat snake (Lima 1998). Therefore, Acadian Flycatchers' nest success in Nuttall oaks may be relatively high regardless of vine presence because the bark smoothness limits the rate at which rat snakes can ascend the tree. We suggest that avian and conservation biologists are more likely to obtain new insights into nest-site selection by studying the predator as well as the prey.

## Acknowledgments

We are grateful to J. Bois, H. Fraser, S. Reilly, J.B. Towey, and an anonymous reviewer for their comments on earlier drafts of the paper. Partial support for this study was provided by the Department of Biological Sciences at Eastern Illinois University and cost-share agreements of the Arkansas Game and Fish Commission and U.S. Fish and Wildlife Service with the University of Georgia (USDI Challenge Costshare Agreement No. 1448-40181-98-G-045).

## References

- Burhans, D.E., and Thompson, F.R. 1998. Effects of time and nestsite characteristics on concealment of songbird nests. Condor, 100: 663–672.
- Cooper, R.J., Wilson, R.R., Zenitsky, G.D., Mullin, S.J., DeCecco, J.A., Marshall, M.R., Wolf, D.J., and Pomara, L.Y. 1999. Does nonrandom nest placement imply nonrandom nest predation? A reply. Condor, **101**: 920–923.
- Cundall, D. 1987. Functional morphology. *In* Snakes: ecology and evolutionary biology. *Edited by* R.A. Seigel, J.T. Collins, and S.S. Novak. McGraw-Hill, Inc., New York. pp. 106–140.
- Dowdy, S., and Wearden, S. 1991. Statistics for research. 2nd ed. John Wiley and Sons, New York.
- Ford, N.B. 1995. Experimental design in studies of snake behavior. Herpetol. Monogr. No. 9. pp. 130–139.
- Halpern, M. 1992. Nasal chemical senses in reptiles: structure and function. *In* Biology of the Reptilia. Vol. 18. Physiology E. *Edited by* C. Gans and D. Crews. University of Chicago Press, Chicago. pp. 423–523.
- Harlow, W.M., and Harrar, E.S. 1969. Textbook of dendrology. 5th ed. McGraw-Hill, Inc., New York.
- Howlett, J.S., and Stutchbury, B.J. 1996. Nest concealment and predation in Hooded Warblers: experimental removal of nest cover. Auk, **113**: 1–9.
- Jackson, J.A. 1976. Relative climbing tendencies of gray (*Elaphe obsoleta spiloides*) and black rat snakes (*E. o. obsoleta*). Herpetologica, **32**: 359–361.
- Lillywhite, H.B., and Henderson, R.W. 1993. Behavioral and functional ecology of arboreal snakes. *In* Snakes: ecology and behavior. *Edited by* R.A. Seigel and J.T. Collins. McGraw–Hill, Inc., New York. pp. 1–48.
- Lima, S.L. 1998. Stress and decision making under risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. Adv. Study Behav. 27: 215–290.
- Martin, T.E. 1992. Breeding productivity considerations: what are the appropriate habitat features for management? *In* Ecology and conservation of Neotropical migrant landbirds. *Edited by*

J.M. Hagan III and D.W. Johnston. Smithsonian Institution Press, Washington, D.C. pp. 455–473.

- Martin, T.E., and Finch, D.M. (*Editors*). 1995. Ecology and management of Neotropical migratory birds. Oxford University Press, New York.
- Martin, T.E., Paine, C., Conway, C.J., and Hochachka, W.M. 1996. BBIRD field protocol. Montana Cooperative Wildlife Research Unit, Missoula.
- Mullin, S.J., and Cooper, R.J. 1998. The foraging ecology of the gray rat snake (*Elaphe obsoleta spiloides*)—visual stimuli facilitate location of arboreal prey. Am. Midl. Nat. **140**: 397–401.
- Mullin, S.J., and Cooper, R.J. 2000. The foraging ecology of the gray rat snake (*Elaphe obsoleta spiloides*). II. Influence of variable habitat structural complexity on snakes foraging for arboreal avian prey. Amphib.-Reptilia, **21**: 1–12.
- Mullin, S.J., Gutzke, W.H.N., Zenitsky, G.D., and Cooper, R.J. 2000. Home ranges of rat snakes (Colubridae: *Elaphe*) in different habitats. Herpetol. Rev. **31**: 20–22.
- Rappole, J.H. 1995. The ecology of migrant birds: a Neotropical perspective. Smithsonian Institution Press, Washington, D.C.

- Ricklefs, R.E. 1969. An analysis of nesting mortality in birds. Smithson. Contrib. Zool. 9: 1–48.
- Saenz, D., Collins, C.S., and Conner, R.N. 1999. A bark-shaving technique to deter rat snakes from climbing red-cockaded woodpecker cavity trees. Wildl. Soc. Bull. 27: 1069–1073.
- Warwick, C. 1990. Reptilian ethology in captivity: observations of some problems and an evaluation of their aetiology. Appl. Anim. Behav. Sci. 26: 1–13.
- Wilson, R.R. 1997. Breeding biology of Acadian Flycatchers in a bottomland hardwood forest. M.S. thesis, University of Memphis, Memphis, Tenn.
- Wilson, R.R., and Cooper, R.J. 1998a. Acadian Flycatcher nest placement: does placement influence reproductive success? Condor, 100: 673–679.
- Wilson, R.R., and Cooper, R.J. 1998b. Breeding biology of Acadian Flycatchers in a bottomland hardwood forest. Wilson Bull. 110: 226–232.
- Zar, J.H. 1999. Biostatistical analysis. 4th ed. Prentice Hall, Inc., Englewood Cliffs, N.J.