Effects of Tornado Disturbance on Bat Communities in Southern Illinois

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Abstract - On 6 May 2003, a tornado severely damaged 284 ha of Mermet Lake State Forest and Wildlife Area in southern Illinois. We used mist nets and Anabat ultrasonic detectors to determine if community composition and habitat use of bats differed between the tornado-disturbed forest and surrounding undisturbed forest during the summers of 2004 and 2005. Ten species of bats (118 individuals) were caught using mist nets on sites in undisturbed forest; 4 species (11 individuals) were mist-netted on disturbed sites ($\chi^2 = 34.24$, df = 1, $P < 0.0001$). The Anabat system documented six species on both habitat types with no difference in the number of bat passes detected acoustically. We suspect that apparent differences in mist-net data reflect the greater ability of bats on the disturbed sites to avoid nets. Telemetry data and field observations confirmed bats used disturbed and undisturbed areas for roosting and foraging. Unless precluded by higher fire danger, we suggest that tornado-disturbed areas remain non-salvaged because they provide additional roosting and foraging habitat for many bat species.

Introduction

Forest structure, dynamics, and associated biotic communities are altered by the scale, intensity, and frequency of natural and anthropogenic disturbances (Petraitis et al. 1989, Pickett and White 1985). Wind is a major form of disturbance in forests and can create significant immediate and longer-term structural and compositional changes to the community (Battaglia and Sharitz 2005, Battaglia et al. 1999, Peterson 2000a, Putz and Sharitz 1991). Wind disturbance can result in high mortality of canopy trees and affect subsequent patterns of forest regeneration (Harrington and Bluhm 2001, Nelson et al. 2008, Peterson 2000b, Peterson and Rebertus 1997), creating a shifting mosaic of forest patches of different successional stages. For bat populations, immediate impacts of wind may be manifested in individual mortality or dispersal to new areas; long-term effects may include changes (negative or positive) in reproduction and population size.

Changes in forest structure that result from these disturbances influence the temperature regime, light availability, and forage quantity and quality

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for all wildlife. These shifts in resource availability can have positive effects on some wildlife species, but negative impacts on others (Fenton et al. 1998, Prather and Smith 2003, Rowan et al. 2005, Will 1991). Many small mammals have short life spans, mature early, produce many offspring in a litter, have little maternal care, and die at an early age (Barclay and Harder 2003). Although the initial impacts of wind disturbance on individuals may be negative, with an increase in snags and herbaceous plant cover associated with the disturbance, rodent populations may quickly respond favorably to increased nesting habitat and forage because of their high reproductive potential (Carey and Johnson 1995). Bats, however, are small mammals that are long-lived, mature late, and have low fecundity (Kunz and Fenton 2003). Within temperate regions, most vespertilionid bats produce a litter comprised of a single pup, although *Perimyotis subflavus* Cuvier (Eastern Pipistrelle) and *Lasiurus borealis* Müller (Red Bat) are exceptions. Because of their low fecundity, bats may be susceptible to the initial negative impacts of disturbances that result in dramatic, immediate habitat change (Bright and Morris 1996, Law 1996, Tuttle and Stevenson 1982), but may be slower to respond to positive effects than other small mammals.

Many North American bats rely on forest habitat for both food and shelter (Barclay and Brigham 1995, Crampton and Barclay 1998, Fenton et al. 1998, Patriquin and Barclay 2003). Because tornadoes reduce density and basal area of canopy trees (Glitzenstein and Harcombe 1988, Held and Winstead 1976), species that roost under tree canopies, such as Red Bats, may have less roosting habitat available after a tornado. Conversely, *Myotis septentrionalis* Trouessant (Northern Long-eared Myotis) and *M. sodalis* Miller and Allen (Indiana Myotis) may find new roosts under the sloughing bark of dead trees or within newly formed splinters (Carter and Feldhamer 2005). As long as roosting requirements are met, the insects that dead and dying trees attract and the increased habitat heterogeneity should provide long-term benefits to all species of insectivorous bats.

Most studies on the effects of high-intensity wind disturbance on bat communities involved hurricanes or cyclones. Yih et al. (1991) reported that bat populations declined, at least initially, following Hurricane Joan in southeast Nicaragua. Similarly, Gannon and Willig (1994) found that bat richness in Puerto Rico declined after Hurricane Hugo, as did bats on Montserrat (Pedersen et al. 1996). Jones et al. (2001) reported significant declines in abundance and species richness of bats following Hurricane Georges. Similar results have been reported for fruit bats on Pacific islands following cyclones (Carroll 1984, Pierson et al. 1996). The effects of tornado disturbance have received less attention than other windstorms such as hurricanes. Tornadoes are highly intense events accompanied by strong winds (64–512 km/h, F0–F5 as measured on the Fujita scale) that travel over relatively short distances (4.84 km on average) compared to hurricanes. Because tornadoes are sudden and spatially unpredictable, pre-existing data on the characteristics of flora and fauna in tornado-disturbed areas usually are unavailable (Everham and Brokaw 1996, Foster and Boose 1995, Peterson 2000b). We are unaware of any studies that have investigated the effects of tornado disturbance on bats. Our objective was to compare bat community composition and habitat use in bottomland hardwood forest sites impacted by tornado disturbance to those in an adjacent undisturbed area through the use of mist nets and acoustic surveys. We also used radio transmitters to document bats roosting and foraging on the study area and to determine use of roost tree species as well as foraging habitat.

Materials and Methods

Study area

Our study site was Mermet Lake State Forest and Wildlife Area (MLSFWA) located in southern Illinois about 9.4 km north of the Ohio River (37°15'22" N, 88°50'44" W) in Massac County, IL. The area is primarily bottomland hardwood forest dominated by *Quercus palustris* Muenchh. (Pin Oak), *Q. phellos* L. (Willow Oak), *Acer rubrum* L. (Red Maple), *A. saccharum* Marsh. (Sugar Maple), *Liriodendron tulipifera* L. (Tulip Poplar), *Ulmus rubra* Muhl. (Slippery Elm), and *U. americana* L. (American Elm), with some *Taxodium distichum* (L.) Rich. (Bald Cypress) in low-lying sloughs (Nelson et al. 2008). The area covers 1064.3 ha, of which 279.2 ha is permanent water, including a centralized 182.9-ha lake. The site is one of several forest fragments that are embedded in an agricultural landscape dominated by corn and soybeans; these patches function as habitat oases for bats and other wildlife (Vessey and Cummings 1994).

On 6 May 2003, an F4-class tornado with wind speeds estimated at 333–419 km/h caused damage to 283.3 ha in the southern part of MLSFWA. In the summer of 2003, approximately 20.2 ha of disturbed timber were cleared from the southeastern section of the area. However, most of the coarse woody material in the disturbed area was not salvaged.

Data collection

Mist-netting. We used standard mist-netting techniques (Kunz and Kurta 1988) at 19 sites for a total of 885 net nights from 18 June through 16 August 2004, and from 9 April through 25 September 2005. Black monofilament mist nets were stacked between interlocking aluminum antenna masts, as described by Gardner et al. (1989). Single net sets had a height of 2.6 m and doubles were 5.2 m; net-height selection depended on the extent of overhanging branches. Potential netting sites were assessed based on water availability and tree canopy cover. Generally, three net sets were placed over or near a water source large enough for bats to come to drink or capture aquatic insects, along vegetation next to the water's edge, or in potential flight corridors in the interior of undisturbed or disturbed forest (e.g., roads, streambeds, and trails where the canopy formed a "tunnel"). A net site was surveyed for two consecutive nights, and each net was checked every 10 minutes for the first hour and then every 20 minutes thereafter. Nets were opened 30 minutes before sunset and remained open until 2400 h. Species, sex, age (juvenile vs. adult), reproductive status (pregnancy, lactation, or scrotal testes), weight, and forearm length (mm) were recorded for all captured bats. Bats were weighed to the nearest 0.5 g and then released at the site of capture.

Acoustic monitoring. Two Anabat II bat-detector systems (Titley Electronics, Ballina, NSW, Australia) were used to record echolocation calls of bats in disturbed and undisturbed sites. Detectors were set to passively record bat echolocation calls at a sensitivity of 8. Each detector was linked to a Zero Crossing Analysis Interface Module (Titley Electronics, Ballina, NSW, Australia) that transferred the echolocation calls onto an IBM Thinkpad 755CX laptop computer (International Business Machines Corporation, Armonk, NY). Anabat software (version 6.3g) saved calls to the hard drive for later analysis (Murray et al. 2001). Bat activity and species identification were determined acoustically from randomly selected sites in disturbed and undisturbed forest stands. Random drawings (without replacement) were made for each night to determine site placement of the detectors.

Every night at each site, bat sampling commenced 30 minutes before sunset and ended approximately 5 hours later. Timing of the sampling period ensured that it corresponded with peak activity of foraging bats. Detectors were operated a total of 50 sample nights. The detectors were placed at a 45° angle oriented either over water, open fields, or in flight corridors. Detectors were placed so that the microphone would not be obstructed by vegetation.

After recording, Anabat files were then visually examined using the software Analook, version 4.9j (Titley Electronics, Ballina, NSW, Australia) to remove those that failed to contain echolocation calls of bats. All files containing only one bat call or extraneous noise, such as insects or set-up noise, were discarded. Acoustic identification of bats was conducted using techniques discussed by Britzke (2003). Discriminate function analysis (DFA; Minitab® version 14) was used to identify individual species. Bat detectors were only used for species identification, not to count individual bats (Thomas and LaVal 1988, Wickramasinghe et al. 2003). Because identification using DFA is probabilistic, species presence at a site was based on the majority of files being identified as that species (Britzke et al. 2002).

Roost trees and foraging sites. To determine roost sites and foraging areas, five bats (one *Nycticeius humeralis* Rafinesque [Evening Bat], two Red Bats, one Northern Long-eared Myotis, and one Indiana Myotis) that were captured on the study site were fitted with radio transmitters that weighed 0.5 g (Holohil, Woodlawn, ON, Canada, and Wildlife Materials, Murphysboro, IL). A small patch of hair was removed from the mid-dorsal region of the bat using scissors. Transmitters were then affixed with Skin-Bond® latex cement (Pfizer, Inc. New York, NY). Bats were retained for 30 minutes prior to release to ensure proper transmitter attachment. Bats were tracked using a TRX-1000S receiver (Wildlife Materials, Murphysboro, IL) and a 3-element Yagi antenna daily for the life of the transmitters, about 14 days. A 7- to 12-

night duration was used to determine locations for each individual. Roost trees within disturbed or undisturbed forest were identified and marked with a numbered aluminum tag, and their locations were recorded using a Garmin e-trex GPS unit.

Starting at 1600 h, tracking was done with the receiver and antenna—first by vehicle and then on foot. All roost trees were located by homing in on the signal. Roost trees were confirmed by observation of exiting bats (exit counts). Tracking of foraging bats was done after mist-netting, starting at 0030 hrs. Tracking was done by vehicle, with stops at 0.4-km intervals to listen for all tagged bats. Continual changes in both signal strength and direction were used to determine foraging activity for an individual. Foraging locations were assigned to disturbed or non-disturbed forest based on consecutive fixes.

Results

Mist-netting

During 596 net nights in undisturbed habitat and 289 in disturbed sites, we mist-netted 129 vespertilionid bats of 10 species (Table 1). We caught 65 bats in 2004, and 64 bats in 2005. Of the total bats captured, 93 (72.6%) were of three species: Red Bat (*n* = 55), Eastern Pipistrelle (*n* = 23), and Evening Bat (*n* = 15). One hundred eighteen individual bats were caught in the undisturbed habitat compared to 11 caught within the disturbed habitat (Table 1). Accounting for the uneven sampling effort (307 more net nights in undisturbed habitat), this remained a highly significant difference (χ^2 = 34.24, df = 1, $P < 0.0001$).

Acoustic monitoring

A total of 136 hours of acoustic monitoring was conducted during 29 nights in undisturbed habitats (24 sites) and 21 nights in disturbed habitats (10 sites). Individual sites were not sampled evenly because of technical and weather-related problems, and disturbed vs. undisturbed sites could

Table 1. Numbers of bats captured within undisturbed and disturbed bottomland hardwood forest stands during 885 mist-net nights. Numbers in parentheses represent [captures/net-night] x 100.

Species	Undisturbed forest (596 net-nights)	Disturbed forest (289 net-nights)	Total
Red Bat	49 (8.22)	6 (2.08)	55
Eastern Pipistrelle	22 (3.69)	1 (0.35)	23
Evening Bat	15 (2.52)	0	15
Eptesicus fuscus (Beauvois) (Big Brown Bat)	13 (2.18)	0	13
Northern Long-eared Myotis	9 (1.51)	3 (1.04)	12
Southeastern Myotis	5 (0.84)	1 (0.35)	6
Little Brown Myotis	2 (0.34)	0	2
Hoary Bat	1 (0.17)	0	1
Indiana Myotis	1 (0.17)	0	1
Silver-haired Bat	1 (0.17)	0	1
Total	118 (19.79)	11 (3.81)	129

not always be monitored the same night. A total of six species was detected during the acoustic survey in both disturbed and undisturbed habitats (Table 2). Consistent with the mist-net capture data, Eastern Pipistrelles, Red Bats, and Evening Bats were the most commonly detected species in both disturbed and undisturbed forest. Contrary to the mist-net results, however, when corrected for the number of sites and nights monitored in each forest type, the numbers of bat passes detected acoustically on the two forest types were not different ($F = 1.79$, df = 10, $P = 0.108$).

Roost trees and foraging sites

Telemetry data and field observation confirmed that bats roosted and foraged in disturbed and undisturbed areas. The Evening Bat was caught over a small waterway in undisturbed forest. It maintained roost fidelity to a *Gleditsia aquatica* Marsh. (Water Locust) tree located in an undisturbed bottomland hardwood stand. It was the only bat present at the exit count, and it foraged within the same forested area.

One Red Bat was netted and radiotagged in disturbed habitat, but roosted in a *Populus deltoides* Bartr. ex Marsh. (Eastern Cottonwood) in undisturbed habitat. Foraging included an off-site agricultural field adjacent to the forest edge. The second Red Bat was radiotagged in undisturbed habitat. It roosted under the foliage of a *Catalpa speciosa* Scop. (Catalpa Tree) with four pups at the forest edge close to the initial capture site and foraged along the forested edge adjacent to a road.

The Northern Long-eared Myotis was caught in disturbed habitat. It moved its roost site every two to three days within mostly flooded disturbed habitat. The first roost tree was a young Sugar Maple with a decaying limb where the bat entered and exited. The second roost tree, a *Fraxinus profunda* Bush (Pumpkin Ash), was in water approximately 0.5 m deep with the top splintered off from the tornado. A third roost tree was in water approximately 0.4 m deep and also had the main stem damaged by the tornado. Foraging occurred off-site over fields and within undisturbed forested bottomlands.

The Indiana Myotis was caught over a seasonal waterway in undisturbed forest. It roosted under the exfoliating bark of a snag in undisturbed forest and foraged over cornfields off-site. Exit counts consisted of one bat except on the last day of telemetry, when three bats left the tree.

Table 2. Number of undisturbed and disturbed bottomland forest sites in which 6 species of bats were detected using Anabat ultrasonic detectors. For more meaningful comparisons, numbers in parentheses represent given values x 100 / [number of sites in each forest type x nights sampled in each forest type].

Species	Undisturbed forest (n = 24 sites and 29 nights)	Disturbed forest (n = 10 sites and 21 nights)
Eastern Pipistrelle	18 (2.58)	7 (3.33)
Red Bat	12 (1.72)	6 (2.86)
Evening Bat	6 (0.86)	9 (4.28)
Big Brown Bat	9 (1.29)	2 (0.95)
Silver-haired Bat	4 (0.57)	2 (0.95)
Indiana Bat	1 (0.14)	1 (0.48)

Discussion

The mist net vs. acoustic detector sampling differed in terms of bat detectability. There appeared to be striking differences in species richness and number of individual bats mist-netted on disturbed vs. undisturbed habitats following the tornado on MLSWFA. We feel this was an artifact of mist-netting rather than a reflection of relative use of the two forest types. Undisturbed habitats provided the structural corridors of overstory canopy necessary to "funnel" bats into nets, whereas disturbed areas had relatively low canopy cover—or none at all—allowing bats to avoid the nets. Thus, bats in disturbed (open) areas were less likely to be caught relative to those in undisturbed forest. Conversely, the acoustic data showed bats used the disturbed sites to the same extent as undisturbed sites for foraging. Grindal and Brigham (1998) found similar patterns of bat activity between small areas of harvested and unharvested timber, which they attributed to equivalent insect availability. Likewise, Fenton et al. (1998) found that lack of canopy trees did not reduce insects available to bats in African woodlands. We believe a similar situation existed in our study because MLSWFA is a relatively small area and insects were abundant throughout. Many insects were consistently entangled within the mist nets in both habitats.

In undisturbed sites, mist-netting resulted in the capture of four more species of bats than detected by acoustic surveys: Northern Long-eared Myotis, *M. austroriparius* Rhoads (Southeastern Myotis), *M. lucifugus* LeConte (Little Brown Myotis), and *Lasiurus cinereus* Beauvois (Hoary Bat). These species were captured in low numbers during the study, and likely represented a small component of the bat community at the site. It is possible that these species would have been detected with additional acoustic sampling. Acoustic detectors documented *Lasionycteris noctivagans* LeConte (Silver-haired Bat) at six sites even though only one individual was captured. Both techniques have advantages and disadvantages and are complementary for an accurate assessment of the bat community at sites such as our study area.

We do not know if the tornado reduced reproductive potential or population size on the study area because no pre-tornado baseline data are available. Previous studies of Caribbean and South Pacific bats (see Jones et al. 2001) suggest that wind disturbances create greater long-term negative effects on frugivorous and nectarivorous bats—those that depend on plants—than on insectivorous species. Following immediate negative impacts of wind and rain from the tornado, we suspect most insectivorous bat species on our study area experienced minimal longer-term impacts either to roosting or foraging. This study was initiated one year after the tornado struck MLSFWA, when many of the trees in the disturbed area had not had sufficient time to reach the levels of decay where bark exfoliated. Thus, the total long-term benefits of this disturbance to exfoliating-bark roosting bats may not have occurred. Species such as the Indiana Myotis and Northern

Long-eared Myotis should benefit from the new roosting resources available. Snags, shattered trunks, and exfoliating bark offer ideal conditions for maternity colonies (Carter and Feldhamer 2005). Unless precluded by unacceptable fire hazard, we recommend that disturbed forest areas remain non-salvaged to maintain the potential for enhanced density and diversity of bats.

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Literature Cited

Barclay, R.M.R., and R.M. Brigham (Eds.). 1995. Bats and Forests Symposium. British Columbia Ministry of Forests Research Program, Victoria, BC, Canada. 292 pp.

Barclay, R.M.R., and L.D. Harder. 2003. Life history of bats: Life in the slow lane. Pp. 209–253, *In* T.H. Kunz and M.B. Fenton (Eds.). Bat Ecology. University of Chicago Press, Chicago, IL. 798 pp.

Battaglia, L.L., and R.R. Sharitz. 2005. Effects of natural disturbance on bottomland hardwood regeneration. Pp. 121–136, *In* L.H. Fredrickson, S.A. King, and R.M. Kaminski (Eds.). Ecology and Management of Bottomland Hardwood Ecosystems: The State of our Understanding. University of Missouri-Columbia, Gaylord Memorial Laboratory Special Publication No. 10, Puxico, MO. 542 pp.

Battaglia, L.L., R.R. Sharitz, and P.R. Minchin. 1999. Patterns of seedling and overstory composition along a gradient of hurricane disturbance in an old-growth bottomland hardwood community. Canadian Journal of Forest Research 29:144–156.

Bright P.W., and P.A. Morris. 1996. Why are dormice rare? A case study in conservation biology. Mammal Review 26:157–187.

Britzke, E.R. 2003. Use of ultrasonic detectors for acoustic identification and study of bat ecology in the eastern United States. Ph.D. Dissertation. Tennessee Technological University, Cookeville, TN.

Britzke, E.R., K.L. Murray, J.S. Heywood, and L.W. Robbins. 2002. Acoustic identification. Pp. 220–224, *In* A. Kurta and J. Kennedy (Eds.). The Indiana Bat: Biology and Management of an Endangered Species. Bat Conservation International, Austin, TX. 253 pp.

Carey, A.B., and M.L. Johnson. 1995. Small mammals in managed, naturally young, and old-growth forests. Ecological Applications 5:336–352.

Carroll, J.B. 1984. The conservation and wild status of the Rodrigues Fruit Bat, *Pteropus rodricensis*. Myotis 21–22:148–154.

Carter, T.C., and G.A. Feldhamer. 2005. Roost-tree use by maternity colonies of Indiana Bats and Northern Long-eared Bats in southern Illinois. Forest Ecology and Management 219:259–268.

Crampton, L.H., and R.M.R. Barclay. 1998. Selection of roosting and foraging habitat by bats in different-aged Aspen mixed-wood stands. Conservation Biology 12:1347–1358.

Everham, E.M., and N.V.L. Brokaw. 1996. Forest damage and recovery from catastrophic wind. Botany Review 62:113–185.

Fenton, M.B., D.H.M. Cumming, I.L. Rautenbach G.S. Cumming, M.S. Cumming, G. Ford, R.D. Taylor, J. Dunlop, M.D. Hovorka, D.S. Johnston, C.V. Portfors, M.C. Kalcounis, and Z. Mahlanga. 1998. Bats and the loss of tree canopy in African woodlands. Conservation Biology 12:399–407.

Foster, D.R., and E.R. Boose. 1995. Hurricane disturbance regimes in temperate and tropical forest ecosystems. Pp. 305–339, *In* M.P. Coutts and J. Grace (Eds.). Wind and Trees. Cambridge University Press, Cambridge, UK. 504 pp.

Gannon, M.R., and M.R. Willig. 1994. The effects of Hurricane Hugo on bats of Luquillo Experimental Forest of Puerto Rico. Biotropica 26:320–331.

Gardner J.E., J.D. Garner, and J.E. Hofmann. 1989. A portable mist-netting system for capturing bats with emphasis on *Myotis sodalis* (Indiana Bat). Bat Research News 30:1–8.

Glitzenstein, J.S., and P.A. Harcombe. 1988. Effects of the December 1983 tornado on forest vegetation of the Big Thicket, southeast Texas. Forest Ecology and Management 25:269–290.

Grindal, S.D., and R.M. Brigham. 1998. Short-term effects of small-scale habitat disturbance on activity by insectivorous bats. Journal of Wildlife Management 62:996–1003.

Harrington, T.B., and A.A. Bluhm. 2001. Tree regeneration responses to microsite characteristics following a severe tornado in the Georgia Piedmont, USA. Forest Ecology and Management 140:265–275.

Held, M.E., and J.E. Winstead. 1976. Structure and composition of a climax forest system in Boone County, Kentucky. Transactions of the Kentucky Academy of Science 37:57–67.

Jones, K.E., K.E. Barlow, N. Vaughan, A. Rodríguez-Durán, and M.R. Gannon. 2001. Short-term impacts of extreme environmental disturbance on the bats of Puerto Rico. Animal Conservation 4:59–66.

Kunz, T.H., and M.B. Fenton (Eds.). 2003. Bat Ecology. University of Chicago Press, Chicago, IL. 779 pp.

Kunz, T.H., and A. Kurta. 1988. Capture methods and holding devices. Pp. 1–29, *In* T.H. Kunz (Ed.). Ecological and Behavioral Methods for the Study of Bats. Smithsonian Institution Press, Washington, DC. 533 pp.

Law, B.S. 1996. The ecology of bats in south-east Australian forests and potential impacts of forestry practices: A review. Pacific Conservation Biology 2:363–374.

Murray, K.L., E.R. Britzke, and L.W. Robbins. 2001. Variation in search-phase calls of bats. Journal of Mammalogy 82:728–737.

Nelson, J.L., J.W. Groninger, L.L. Battaglia and C.M. Ruffner. 2008. Bottomland hardwood forest vegetation and soils recovery following a tornado and salvage logging. Forest Ecology and Management 256:388–395.

Patriquin, K.J., and R.M.R. Barclay. 2003. Foraging by bats in cleared, thinned, and unharvested boreal forest. Journal of Applied Ecology 40:646–657.

Pedersen, S.C., H.H. Genoways, and P.W. Freeman. 1996. Notes on bats from Montserrat (Lesser Antilles) with comments concerning the effects of Hurricane Hugo. Caribbean Journal of Science 32:206–213.

Peterson, C.J. 2000a. Catastrophic wind damage to North American forests and the potential impact of climate change. The Science of the Total Environment 262:287–311.

Peterson, C.J. 2000b. Damage and recovery of tree species after two different tornadoes in the same old growth forest: A comparison of infrequent wind disturbances. Forest Ecology and Management 135:237–252.

Peterson, C.J., and A.J. Rebertus. 1997. Tornado damage and initial recovery in three adjacent, lowland, temperate forests in Missouri. Journal of Vegetation Science 8:559–564.

Petraitis, P.S., R.E. Latham, and R.A. Niesenbaum. 1989. The maintenance of species diversity by disturbance. Quarterly Review of Biology 64:393–418.

Pickett, S.T.A., and P.S. White (Eds.). 1985. The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, Orlando, FL. 472 pp.

Pierson, E.D., T. Elmqvist, W.E. Rainey, and P.A. Cox. 1996. Effects of tropical cyclone storms on Flying Fox populations on the South Pacific Islands of Samoa. Conservation Biology 10:438–451.

Prather, J.W., and K.G. Smith. 2003. Effects of tornado damage on forest bird populations in the Arkansas Ozarks. Southwestern Naturalist 48:292–297.

Putz, F.E., and R.R. Sharitz. 1991. Hurricane damage to old-growth forest in Congaree Swamp National Monument, South Carolina, USA. Canadian Journal of Forest Research 21:1765–1770.

Rowan, E.L., W.M. Ford, S.B. Castleberry, J.L. Rodrigue, and T.M. Schuler. 2005. Response of Eastern Chipmunks to single application spring prescribed fires on the Fernow Experimental Forest. Research Paper NE-727. US Department of Agriculture, Forest Service, Northeastern Station, Newton Square, PA.

Thomas, D.W., and R.K. LaVal. 1988. Survey and census methods. Pp. 77–89, *In* T.H. Kunz (Ed.). Ecological and Behavioral Methods for the Study of Bats. Smithsonian Institution Press, Washington, DC. 533 pp.

Tuttle M.D., and D. Stevenson. 1982. Growth and survival of bats. Pp. 105–150, *In* T.H. Kunz (Ed.). Ecology of Bats. Plenum Press, New York, NY. 425 pp.

Vessey, S.H., and J.R. Cummings. 1994. Agricultural influences on movement patterns of White-footed Mice (*Peromyscus leucopus*). American Midland Naturalist 132:209–218.

Wickramasinghe, L.P., S. Harris, G. Jones, and N. Vaughan. 2003. Bat activity and species richness on organic and conventional farms: Impact of agricultural intensification. Journal of Applied Ecology 40:984–993.

Will, T. 1991. Birds of a severely hurricane-damaged Atlantic Coast rain forest in Nicaragua. Biotropica 23:497–507.

Yih, K., D.H. Boucher, J.H. Vandermeer, and N. Zamora. 1991. Recovery of the rain forest of southeastern Nicaragua after destruction by Hurricane Joan. Biotropica 23:106–113.