

ESCAPE BEHAVIOR OF NORTHERN LONG-EARED BATS (*MYOTIS SEPTENTRIONALIS*) FOLLOWING DIURNAL DISTURBANCE

Dale W. Sparks: Center for North American Bat Research and Conservation, Department of Biology, Indiana State University, Terre Haute, Indiana 47809 USA

ABSTRACT. Field observations of newly-banded bats led to the hypothesis that co-roosting northern long-eared bats (*Myotis septentrionalis*) fled to a single roost following diurnal disturbance. Five groups of co-roosting bats were used to test this hypothesis. Bats from each group were released in quick succession during daylight, and the direction of escape for each bat was noted. Direction of escape for four of five groups was oriented in one direction, while bats in a fifth group were bimodal in their escape paths. Contrary to prediction, bats from four groups entered at least eight total roosts, rather than one roost per group. A revised hypothesis was generated that predicted bats would flee to areas of dense cover in response to potential predation by diurnal raptors. When two groups of bats were released into fields adjacent to woodlands, the bats flew directly into the woods. Bats released in woodlots at night escaped in random directions.

Studies of roosting habits of bats have become common in the last 15 years (Barclay & Kurta 2007). Most of these studies, however, were aimed primarily at documenting and describing roost types. One discovery from these studies was that individuals of many species frequently switch roosts (Lewis 1995). Among hypothesized roles for this behavior is that frequent roost switching allowed bats to become familiar with multiple roosts, which may allow bats to change roosts efficiently should the one they are occupying be disturbed (Lewis 1995; Whitaker 1998). Rapid movement between roosts would be an important adaptation given the intense predatory pressure that diurnal raptors are able to exert upon bats (Sparks et al. 2000; Speakman 1990, 1991a, b, 1995; Speakman et al. 1994). Because many bats use large dead trees as roosts (Barclay & Kurta 2007), it is likely that these trees occasionally fall over while occupied which would expose escaping bats to potential predators. Also, given the many benefits that colonial species obtain from group living, one would expect co-roosting bats to have behavioral adaptations to relocate roost mates if separated. The most direct way of relocating roost mates would be for all of the bats in a roost to flee to one alternate roost following disturbance and such behavior is known in several Neotropical species (Allen 1939; Bradbury & Vehrencamp 1976).

As part of efforts to understand the effectiveness of artificial roosts as a management tool (Whitaker et al. 2006), newly-banded bats were observed fleeing to a single bat-box when banded and released during the late afternoon in 1998. Simultaneous work with other roosts also resulted in observations of bats fleeing in a single direction. These observations led to the hypothesis that roost mates flee to a single roost following disturbance, a behavior unknown among North American bats. The purpose of this paper was, first, to report results of an experiment that tested and rejected this “common-target” hypothesis. Observations made during this experiment led to the development of an alternative hypothesis: the “flight-to-cover” hypothesis. This hypothesis was that bats flee to areas of dense cover before selecting a roost, and this behavior was driven by the need to escape potential predation by diurnal raptors. The second purpose of this paper was to report the results of a series of experiments conducted to test the flight-to-cover hypothesis.

METHODS

Capturing and marking bats.—Between 1991 and 1996, a total of 3216 artificial roost structures was placed by a consulting firm on properties managed by the Indianapolis Airport Authority to help mitigate for loss of habitat for the federally-endangered Indiana myotis, *Myotis sodalis* (Sparks et al. 1998; Whitaker et al. 2004, 2006). Although largely unsuccessful in attracting Indiana myotis, these structures do

Correspondent: dsparks@isugw.indstate.edu

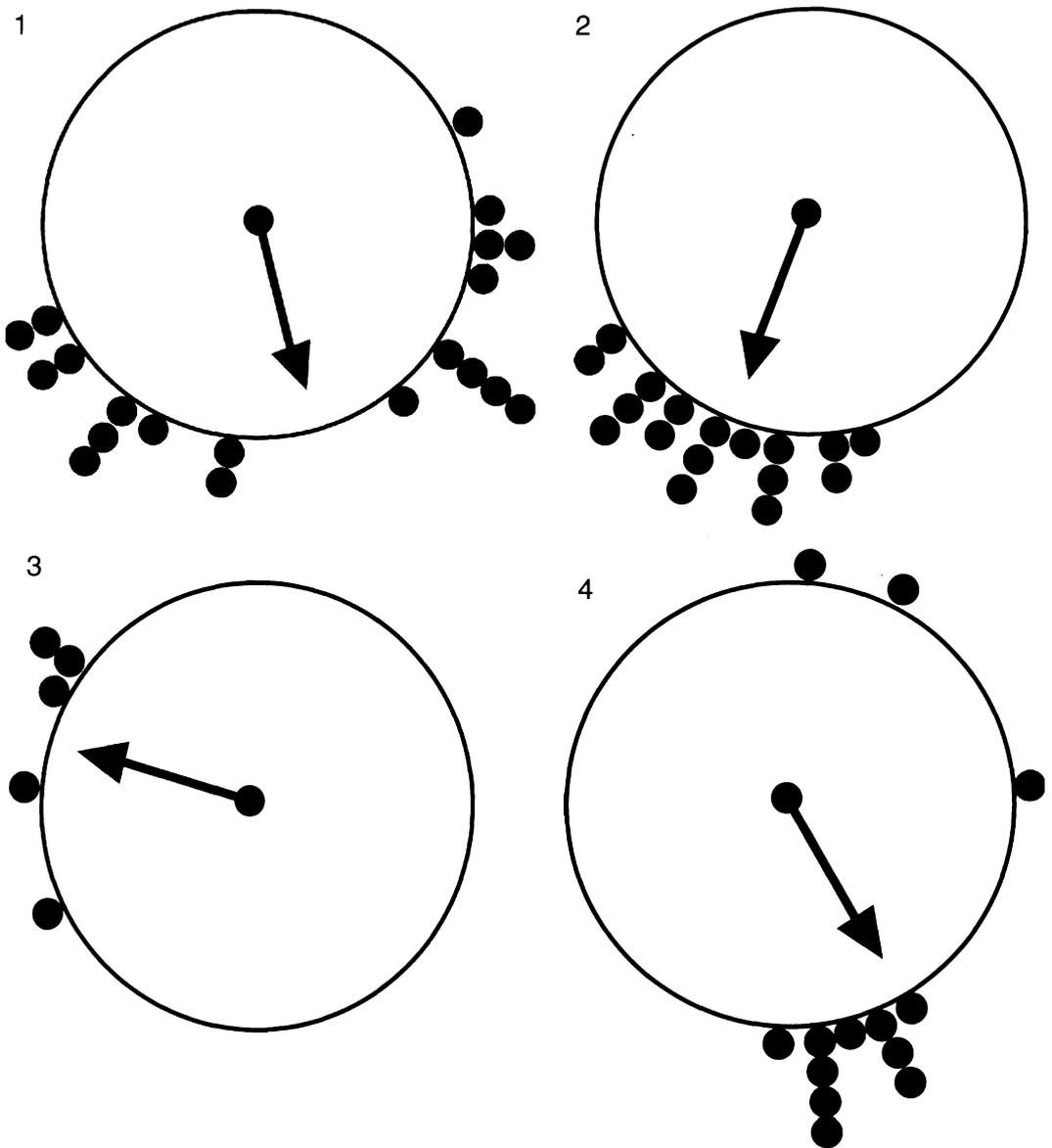


Figure 1.—Direction of escape for the first group of bats released into woodlots near the Indianapolis International Airport in 1998. The dot in the center of the figure represents the point where the bats were released, while the dots around the periphery of the circle represent the last observed heading for an individual bat. North is at the top of the figure. This group is significantly oriented to the southeast (Rayleigh Test, mean vector = 0.621, $n = 20$, $P < 0.001$).

Figure 2.—Direction of escape for the second group of bats released into woodlots near the Indianapolis International Airport in 1998. The dot in the center of the figure represents the point where the bats were released, while the points around the periphery of the circle represent the last observed heading for an individual bat. North is at the top of the figure. This group is significantly oriented to the southwest (Rayleigh Test, mean vector = 0.953, $n = 17$, $P < 0.001$).

Figure 3.—Direction of escape for a group of bats released into woodlots near the Indianapolis International Airport in 1998. The dot in the center of the figure represents the point where the bats were released, while the dots around the periphery of the circle represent the last observed heading for an individual bat. North is at the top of the figure. This group is significantly oriented to the west (Rayleigh Test, mean

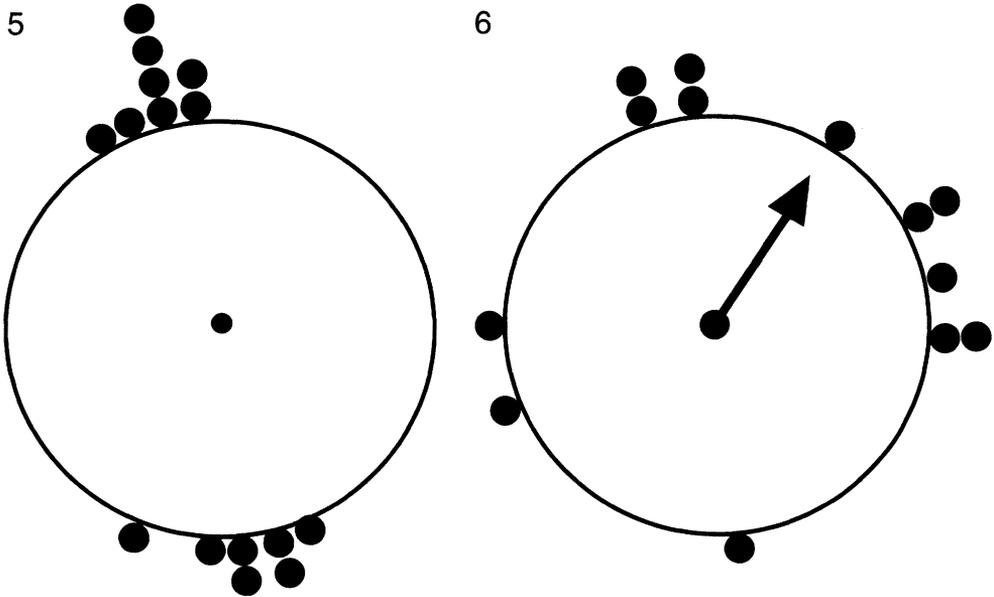


Figure 5.—Direction of escape for a group of bats released into woodlots near the Indianapolis International Airport in 1998. The dot in the center of the figure represents the point where the bats were released, while the dots around the periphery of the circle represent the last observed heading for an individual bat. North is at the top of the figure. This group was not significantly oriented in any one direction (Rayleigh Test, mean vector = 0.077, $n = 17$, $P > 0.865$), although a significant orientation along a north to south axis is present (Rayleigh Test, mean vector = 0.956; $P < 0.001$).

Figure 6.—Direction the bats from Fig. 4 went compared to the direction they were facing when released. The central dot represents the point of release, while dots along the edge of the circle represent the direction that a bat went relative to the direction of release (top of figure). Thus, if a bat went the direction of release it would be represented by a dot at the 12 o'clock position, while a bat that went the opposite direction would be represented by a dot at the six o'clock position. This group is significantly oriented in the direction of release (V-test: $n = 13$, $\mu = 1.80$, $P < 0.05$).

support several groups (i.e., multiple bats in a roost) of northern long-eared bats. As part of the monitoring effort aimed at determining the value of these artificial roosts to bats, each structure was examined at least once per year with a spotlight. When a structure contained bats the tree was climbed and the bats captured in order to allow the identification of the bats using the roost. For safety reasons, trees were climbed in late afternoon, and the bats were released after examination.

Between May and August 1998 and 1999, groups of northern long-eared bats were cap-

tured and used in the following experiments on eight different occasions. Subsequent observations indicated that these bats belonged to at least four, and possibly five, separate colonies based on patterns of movement between roosts by marked individuals (unpubl. data). Individual bats were used in a maximum of two trials per year. Bats were located by examining structures from the ground using Brinkman™ 2,000,000 candle-power spotlights (Forestry Supplies; Jackson, Mississippi). If present, bats were removed from the roost to determine the species, sex, age (juvenile or adult), forearm length,

vector = 0.903, $n = 5$, $P < 0.011$).

Figure 4.—Direction of escape for the fourth group of bats released into woodlots near the Indianapolis International Airport in 1998. The dot in the center of the figure represents the point where the bats were released, while the dots around the periphery of the circle represent the last observed heading for an individual bat. North is at the top of the figure. This group is significantly oriented to the southeast (Rayleigh Test, mean vector = 0.669, $n = 13$, $0.002 < P < 0.003$).

Table 1.—Number of bats observed entering roost structures following diurnal releases in 1998. In all cases, the majority of bats did not enter the roosts noted below.

Group	Number of bats	Number of bats seen entering structures	Number of structures entered
1	20	4	3
2	17	2	1
3	5	2	1
4	13	2	1
Total	55	10	6

reproductive condition, weight, band number, and cohabitants. Unbanded bats received a numbered plastic armband (National Band and Tag Company; Newport, Kentucky) either on the right (males) or left forearm (females).

Releasing bats.—All diurnal releases were conducted in late afternoon (1700–1900 h). Bats were not disturbed when nonvolant young were present (1 June–15 July), or if wind speed exceeded 6 km/hr. Prior to release, the area surrounding the release area was checked for evidence of predatory birds using both audio and visual scanning. Bats from a group were held in a Mumford cage (Barbour & Davis 1969) until the entire group was banded (approximately 1 min/bat). All bats in a group were released from a common location within 10 m of the roost. At the time of release a single bat would be held in a cupped hand 2 m above the ground, pointed in one of the cardinal directions (this was systematically rotated between bats). Observers were arranged around the release point in positions (within 15 m of the release point) where they could see the fleeing bats. The azimuth in which the bat was last seen flying (below referred to as vanishing direction) was recorded and treated as an indication of the direction that the bat fled (Akesson et al. 1996).

The release protocol above was subjected to three experimental manipulations. Two of these manipulations consisted of bats being released within woodlots. The first five releases were designed to test the common-target hypothesis, and consisted of bats released within woodlots during late afternoon (1700–1900 h) in 1998. Observations of bats used in the first three releases suggested that they were actually fleeing to areas of dense cover prior to selecting

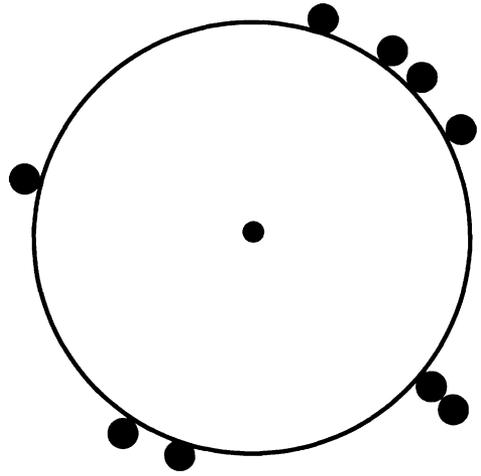
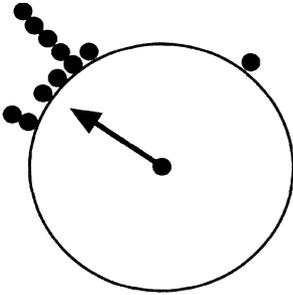


Figure 7.—Direction of escape for a group of bats released into a woodlot at night near the Indianapolis International Airport in 1999. The dot in the center of the figure represents the point where the bats were released, while the dots around the periphery of the circle represent the last observed heading for an individual bat. North is at the top of the figure. This group is not significantly oriented in any direction (Rayleigh Test, mean vector = 0.233, $n = 9$, $P > 0.1$).

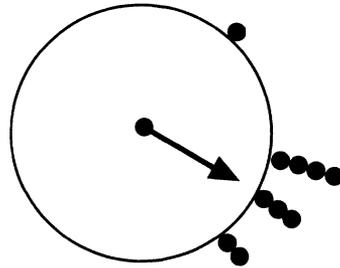
a roost site. Thus, for the final two groups in this experiment, the direction the bats fled was statistically compared to the direction in which the bats were released.

Because the first experiment indicated bats were responding as individuals instead of as groups, later experiments focused on the behaviors of individual bats. The 1999 releases were directed at testing the flight-to-cover hypothesis. A prediction of this hypothesis is that bats released at night are freed from potential predation by diurnal birds and thus would not be oriented in any particular direction. To test this prediction, bats were released within a woodlot at night. In addition to the wing bands described above, each of these bats was tagged with a small chemoluminescent tag (Büchler 1976).

Finally, to determine if the bats perceived woodland as escape cover (Zollner & Lima 1997, 1999), two releases of bats into fields adjacent to woodlots were conducted. The first of these was conducted in a corn (*Zea mays*) field that had just started to sprout 15 m north of the woodlot where the bats were captured. The largest stems were approximately 6 cm tall. The second release was conducted in an oldfield 25 m east of the woodlot where that group of



8



9



Figure 8.—Eleven bats released into a cornfield 15 m south of a woodlot at the Indianapolis International Airport in 1999 were significantly oriented toward the woodlot (V-test, $\mu = 4.12$, $P < 0.0001$).

Figure 9.—Ten bats released into an oldfield 25 m west of a woodlot at the Indianapolis International Airport in 1999 were significantly oriented toward the woodlot (V-test, $\mu = 4.13$, $P < 0.001$).

bats had been captured. The oldfield had been planted with seedling hardwoods in 1993 and contained many sapling trees. Both releases into fields were conducted diurnally in order to ascertain that bats could distinguish woodland cover at a distance (Zollner & Lima 1999). The resulting azimuths were tested to determine if they were oriented toward the woodlot and if the direction of release was related to the direction of flight.

Circular statistics (Batschelet 1981) were used to examine the direction in which bats fled. Rayleigh tests were used to determine if the bats in these experiments were oriented in any direction. V-tests, conversely, were used to determine if bats were oriented toward a pre-specified direction (in the direction of release or toward woodlots). All statistics were calculated by hand and a rejection level of $\alpha = 0.05$ was used for all tests.

RESULTS

Consistent with the common-target hypothesis, four of the five groups released into woodlots during the day had vanishing directions that differed significantly from random (Figs. 1–4), and were unimodally oriented. The fifth (Fig. 5) did have a significant overall orientation, but the bats flew in opposite directions. One of the two groups examined

for bias in the direction of release (Fig. 6.) showed such a bias, while the other did not. Finally, ten bats from four of the groups were observed entering a total of eight different roosts following diurnal release (Table 1). The rest of the bats from these groups entered at least one other roost that could not be observed. Although the common-target hypothesis predicted that bats would move toward a single alternate roost site, these observations demonstrate that group members fled to multiple roosts in the same direction(s).

In all of these cases, those bats that were not observed entering roosts were observed entering areas of dense cover. In addition, bats in one of the experiments described above were significantly biased toward the direction of release (Fig. 6) (V-Test, $n = 13$, $\mu = 1.80$, $P < 0.05$). The final group tested contained only five bats, and no relationship between the angle of release and the angle of escape was detected (V-Test, $n = 5$, $\mu = 0.07$, $P > 0.1$). One alternate explanation is that bats were fleeing to areas of dense cover to avoid predation by diurnal birds.

Experiments conducted in 1999 were aimed at testing this flight-to-cover hypothesis. Bats released at night (when diurnal raptors are absent), showed no significant overall orientation (Fig. 7) (Rayleigh Test, $n = 9$, $r = 0.233$, $P > 0.1$).

Bats released into fields during the day were significantly oriented toward the woods (Figs. 8, 9). All but one of the bats flew immediately into the woods. A bat from the group released into the oldfield made one loop over the observers and then flew directly into the woods. Bats released into fields showed no orientation relative to the direction of initial release.

DISCUSSION

It was hypothesized that northern long-eared bats in Indiana would demonstrate the same escape behavior as several species of Neotropical bats that flee *en masse* to new roosts when disturbed (Allen 1939; Bradbury & Vehrencamp 1976); but, instead, northern long-eared bats appear to simply flee to areas of dense cover and then select a roost independent of the decisions made by other roost mates. The common-target hypothesis, which predicts that all the bats from a group flee to the same roost, was not supported, based on the results of the first experiment (Figs. 1–5, Table 1). Although the bats released during the 1998 field season all showed significant orientation, three lines of evidence suggest this was not indicative of them entering a single roost. First, bats from each group were observed entering at least one roost, which was not used by the other bats (Table 1). Thus, each group fled to a minimum of two roosts. Second, one of the groups was released into a woodlot with thickets on both ends of the woodlot, and bats from this group flew into both thickets (Fig. 5). Third, at least one group (Fig. 6) was significantly oriented in the direction of release. The common-target hypothesis was not supported by these results, but the flight-to-cover was. This hypothesis was based on the orientation of the groups toward cover, and the bias in the direction of release shown by one of two groups tested (Fig. 6), while the second included only five bats and thus may have lacked sufficient power to detect an effect.

Such a behavioral mechanism makes intuitive sense for bats forced to flee their roosts during the daylight. As noted above, bats that fly during the day are particularly vulnerable to attacks by birds (Mueller 1968; Sparks et al. 2000; Speakman 1990, 1991a, b, 1995; Speakman et al. 1994; Twente 1954). Therefore, bats may flee towards dense cover to escape potential predators. This orientation could be attributed to the fact that the woods contain many potential roosts. Additionally, such dense vegetation may

offer protection to fleeing bats by both shielding them from view and slowing pursuing predators. In order to determine whether the observed significant unimodal orientations could be attributed to bats fleeing to areas of heaviest cover, two additional groups were used in 1999 for daylight releases next to woodlands.

Results from this second year of experiments provided additional support for the flight-to-cover hypothesis. As predicted, there was no significant orientation for bats released at night (Fig. 7). Bats released into open fields during the day were significantly oriented toward the woods (Figs. 8, 9). This suggests that the significant orientations observed in all eight diurnal releases (Figs. 1–5, 8, 9) were a response to a risk of predation. Mueller (1964) made similar observations about the orientation of bats during his studies on homing. He released bats at a variety of distances from their home roost and under a variety of conditions. While bats released during the day were oriented toward home, bats released at night were random in orientation.

Release sites during the current study were located adjacent to the roosts where bats were captured. Because no bat returned to the initial roost; these bats were not simply returning to their initial roosts. Perhaps, bats perceiving and flying towards cover confounded Mueller's (1964) observations of homing. His nocturnal results, however, are consistent with the predictions of the flight-to-cover hypothesis.

Although little is known about how bats respond to disturbance, assumptions about these behaviors form a major subset of hypotheses advanced to explain roost switching behaviors of many species of bats (reviewed by Lewis 1995). Lewis found that bats occupying long-standing roosts such as buildings, caves, and hollow trees rarely switched roosts, whereas species that occupied ephemeral roosts such as leaves and exfoliating bark frequently did so. Bats may switch roosts to avoid disturbance by people, to avoid predation, to minimize commuting distance to foraging areas, to limit parasitism, or to avoid unfavorable thermal conditions within the roost. Another potential benefit of roost switching is that this behavior might familiarize bats with other potential roosts in case their primary roost is disturbed or destroyed (Lewis 1995; Whitaker 1998; Sparks 2003). Sudden abandonment of roosts probably only occurs rarely in nature. Given

that flying during the day is hundreds of times more risky than flying at night (Speakman 1991a, b; Speakman et al. 1994), the few times that a bat does have to suddenly abandon its roost could be an important source of mortality.

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