When Corridors Collide: Road-Related Disturbance in Commuting Bats

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ABSTRACT As an increasingly dominant feature in the landscape, transportation corridors are becoming a major concern for bats. Although wildlife–vehicle collisions are considered to be a major source of mortality, other negative implications of roads on bat populations are just now being realized. Recent studies have revealed that bats, like many other wildlife species, will avoid roads rather than cross them. The consequence is that roads act as barriers or filters to movement, restricting bats from accessing critical resources. Our objective was to assess specific features along the commuting route, road, or surrounding landscape (alone or in combination) that exacerbated or alleviated the likelihood of a commuting bat exhibiting an avoidance behavior in response to an approaching vehicle. At 5 frequently used commuting routes bisected by roads, we collected data on vehicles travelling along the roads (such as visibility and audibility), commuting bats (such as height), and composition of the commuting route. We revealed that commuting route structure dictated the frequency at which bats turned back along their commuting routes and avoided the road. We found that gaps (>2 m) in commuting routes, such as the road itself, caused bats to turn away just before they reached the road. Furthermore, we found that turning frequencies of bats increased with vehicle noise levels and the locations at which bats responded to vehicles corresponded with areas where noise levels were greatest, including gaps <2 m. This suggested that bats had a disturbance threshold, and only reacted to vehicles when associated noise reached a certain level. We found that threshold levels for our study species were approximately 88 dB, but this value was likely to vary among species. Thus, our findings indicate that restoring (e.g., replanting native trees and shrubs in gaps) and establishing commuting routes (such as planting tree-lines and wooded hedgerows), as well as creating road-crossing opportunities (such as interlinking canopies) will improve the permeability of a road-dominated landscape to bats. Furthermore, our study highlights the influence of the soundscape. We recommend that effective management and mitigation strategies should take into account the ecological design of the acoustic environment.

KEY WORDS anthropogenic disturbance, commuting, landscape permeability, microchiroptera, road ecology, soundscape.

Wildlife–vehicle collisions have been documented for numerous bat species (Choquene 2006; Lesiński 2007, 2008) and such fatalities are considered an influential source of mortality for bats (Capo et al. 2006, Gaisler et al. 2009). Nevertheless, studies have only recently focused on the less apparent, indirect effects of transportation corridors on bats (Russell et al. 2009). As a barrier or filter to movement, roads can reduce access to suitable foraging or roosting sites (Schaub et al. 2008, Kerth and Melber 2009). This in turn has the potential to influence the abundance and distribution of individuals and populations at both local and regional scales (Eigenbrod et al. 2009).

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Roads are a dominant and ever-increasing feature in the landscape, thus managers must understand how road networks affect wildlife (Frair et al. 2008, Fahrig and Rytwinski 2009, Russell et al. 2009). With many bat populations in decline globally, wildlife managers, and developers alike are required to manage and mitigate for the anthropogenic disturbance caused by roads and road networks (Wray et al. 2005, King 2006). To effectively minimize the impacts of roads, we need to understand both the anthropogenic and ecological factors that influence how bats move across the landscape. We address this need by exploring the factors that potentially cause road-related avoidance behavior in commuting bats.

A preliminary study conducted by Zurcher et al. (2010) revealed that bats responded to vehicles on a rural road that intersected their commuting route. Bats within 40 m of a road were recorded turning back along their commuting routes as motor vehicles approached. Frid and Dill (2002) suggested that bats perceive vehicles as predators, conducting
evasive maneuvers when they become aware they are at risk. Although the study conducted by Zurcher et al. (2010) was one of the first research projects to identify road-related avoidance behavior in commuting bats, it did not explore the rationale behind the behavior (see also Berthinussen and Altringham 2011). Facilitating factors and circumstances, such as physical, audible, and visual characteristics, pertaining to the commuting route, road, and surrounding landscape likely influence the probability that bats will exhibit road-avoidance behaviors, as have been documented in other wildlife species (Bautista et al. 2004, Alexander et al. 2005, McGregor et al. 2008). By identifying these contributing factors, we can more effectively develop and implement management and mitigation strategies that minimize the barrier and filter effects of roads and increase landscape permeability (Fair et al. 2008).

Our objectives were to 1) determine if structurally different commuting routes varied the frequency at which commuting bats exhibited road-related avoidance behaviors, and 2) identify the circumstances (i.e., features in the commuting routes and surrounding landscape) and triggers (i.e., vehicles presence) that led to the type of road-related avoidance behavior observed by Zurcher et al. (2010).

STUDY AREA

We conducted our study in the area surrounding the Indianapolis International Airport in Marion County just west of Indianapolis, Indiana, USA. The area covered approximately 88 km² and was composed of a matrix of small remnant woodland habitat patches, riparian corridors, agricultural, industrial and residential areas, and an extensive transportation infrastructure (Sparks et al. 1998). Although the area was fragmented by encroaching urban development, it remained crucial summer roosting and foraging habitat for several North American bat species. Since 1994, long-term telemetry studies have revealed that the Indianapolis International Airport area has a diverse community of bats, including the federally endangered Indiana myotis (Myotis sodalis), the state endangered evening bat (Nycticeius humeralis), big brown bat (Eptesicus fuscus), eastern red bat (Lasiusurus borealis), hoary bat (Lasiusurus cinereus), little brown myotis (Myotis lucifugus), northern myotis (M. septentrionalis), and tri-colored bat (Perimyotis subflavus; Whitaker et al. 2004). As a result of this long-term study, roosting sites, foraging areas, and commuting routes have also been identified for these local species in the area surrounding the airport (Whitaker and Sparks 2008, Sparks et al. 2009). We used this information to locate sites where bat commuting routes were intersected by transportation corridors. We identified 10 potential study sites based on frequency of use by radio-tracked bats (we initially selected sites with more than 5 bat passes recorded). At each of the potential study sites, we conducted a preliminary observational survey when ambient temperatures exceeded 7°C and wind speeds were low (<5 m/s) between 4 May 2009 and 12 May 2009 (Scanlon and Petit 2008, Baerwald and Barclay 2011). In these surveys, we monitored bat activity along the commuting route between the hours of 2000 and 2400 to confirm that sites were actively and frequently used by bats prior to our main survey period and that bats using the commuting routes exhibited road-related avoidance behaviors as recorded in Zurcher et al. (2010). Among the sites that met the above criteria, we selected 5 sites with commuting routes that varied from each other in their structure and composition. At these 5 sites, the transportation corridors that biselected the commuting route comprised a standard 4.2-m 2-lane rural county road with a 1–2 m grass verge or gravel soft shoulder (specifications from Indiana Department of Transportation [INDOT]). All sites were over 10 km from each other and traffic volume between the hours of 2000 and 2400 ranged from 20 to 40 vehicles per hour (data from INDOT). Site 1 represented a major flyway for local bat species including the Indiana myotis and a known roost site for this species was >50 m from the road-commuting route intersection. The commuting route itself comprised a 2–3 m mown grass path bordered on the east with newly planted deciduous trees (<2 m in height) and shrubs, and to the west by mixed growth woodland with a thick understory. Site 1 was also used in the study conducted by Zurcher et al. (2010). By including it in our study, we were able to establish whether bat activity in 2009 was consistent with that recorded in 2008. Site 2 contained a commuting route parallel to a hedge and fence row adjacent to an open grass field, and was identified as a frequently used flyover for little brown bat, northern myotis, and Indiana myotis. Site 3 was located next to an old growth deciduous hedgerow and creek along the southern border, which was adjacent to an agricultural field of corn to the north. A known big brown bat roost was located within the wooded hedgerow approximately 50 m from the road-commuting route intersection. Similarly, the intersection at site 4 was approximately 50 m from a big brown bat roosting site. The commuting route represented a 3-m wide grass trail bordered on either side by old growth deciduous hedgerows with dense shrub undergrowth. Finally, site 5 represented a major flyway for Indiana myotis and little brown bat and had a water course and wooded riparian zone bordering both sides.

METHODS

Surveys

From 13 May 2009 to 13 July 2009, we conducted field surveys to determine if the responses of bats to approaching vehicles along roads that bisected their commuting routes were influenced by the structure and characteristics of the commuting route and surrounding landscape. At the 5 selected sites, we collected data on commuting route structure (hereafter referred to as habitat surveys), visibility, and audibility of vehicles along the commuting route (referred to as sensing surveys), and movement and behavior of commuting bats in the presence and absence of vehicles (known as crossing surveys).

To determine whether road-related avoidance behavior exhibited by commuting bats was influenced by their immediate surroundings, we conducted spatially specific habitat surveys along each commuting route. In these surveys, we
recorded the structural and compositional characteristics of each route within a 40-m length extending from the road. We based this 40-m extent on the field study conducted in 2008 by Zurcher et al. (2010) at site 1. We surveyed approximately 80 m of the commuting route and although we observed bats exhibiting disturbance-related responses to approaching vehicles from the road that bisected their commuting route, we did not record bats responding to vehicles >40 m from the road. We therefore concentrated our surveys within this 40-m stretch to maximize our chances of observing road-related avoidance behaviors. In addition, we conducted surveys during the primary foraging period (see crossing surveys below); therefore, the majority of our observations would be of bats leaving their roosts and moving along commuting routes in the direction of their foraging habits (Sparks et al. 2005a, Walters et al. 2007). Thus, we only surveyed the 40-m length of commuting route with the greatest numbers of bats moving in the direction of the road. To determine which stretch of commuting route we surveyed, we used the long-term telemetry data available and data collected in the preliminary observational surveys to identify directional frequency of use by bats at each site. In all instances, the direction the majority of bats flew corresponded with the location of the nearest roost site (i.e., bats commuted from roost to foraging sites).

Along each selected 40-m stretch, we recorded the following characteristics down each edge of our commuting corridors at 1-m intervals from the road: 1) the presence of a tree, shrub and/or herb layer; 2) the presence of other features, such as a fence; and 3) whether discernable features were absent (i.e., a gap). At each interval, we also recorded the width, length, and breadth of the tree canopy if present. In addition, we carried out all habitat surveys during the day, independent of both weather conditions and other surveys (described below).

We conducted a series of sensing surveys to determine whether road-related avoidance behavior exhibited by commuting bats was related to visibility and audibility of approaching vehicles within their immediate surroundings. For these surveys, we recorded noise levels and visibility of approaching vehicles at 1-m intervals along the 40-m length of each commuting route between 2000 hours and 0100 hours. At each 1-m interval, we used a digital sound pressure level meter (Nady Systems, Inc., Emeryville, CA) to record the peak noise levels generated by vehicles as they passed through the intersection of the road and commuting route. As each vehicle approached, we also recorded 1) the status of their headlights (low or high beams) and 2) whether the headlights were visible (yes or no) to bats as they moved along their commuting route. For the latter, we used an inspection mirror on an extendable pole, extended to the height bats predominantly flew along each commuting route as observed in the preliminary surveys (mode = 11 m). Over a minimum of 3 survey days (depending on traffic volume) conducted at intervals >1 week per site, we recorded 5 vehicles travelling from each direction along the road at each 1-m interval along the 40-m length of commuting route; totaling 400 passing vehicles recorded at each study site. Using average noise levels (dB) generated for each 1-m interval in each direction, we created a map delineating the spatially specific variation in noise levels and visibility of vehicle lights across the 40-m length of each commuting route surveyed (see Supplemental Fig. S1, available online at www.onlinelibrary.wiley.com).

We conducted sensing surveys on nights independent of all other surveys when wind speeds were low (<5 m/s), temperatures were above 7°C and only when bats were recorded actively using a site at the time of survey. This was to ensure that 1) all conditions were equivalent to those in which resident bats were generally active (Verboom and Spoelstra 1999, Erickson and West 2002, Burles et al. 2009), and 2) noise level recordings were not influenced by background noise generated by greater wind speeds.

To explore whether a correlation existed between road-related avoidance behaviors exhibited by commuting bats and their immediate surroundings, we conducted a series of crossing surveys in which we collected data specifically on the behavioral responses of bats to approaching vehicles. For these, we conducted 2 crossing surveys at each commuting route (approximately 1 month apart) during the primary foraging period of local bat species from dusk (approx. 2000 hr) to 0100 hours (Sparks et al. 2005a, b). We completed 10 crossing surveys, equating to 10 surveys days, over the survey period. We only conducted these surveys when temperatures exceeded 7°C, wind speeds were low (<5 m/s), and bats were active.

For each survey, 2 observers stood along the 40-m stretch of commuting route and detailed the interactions between commuting bats and approaching vehicles. One observer was positioned where the road intercepts the commuting route, and the other was located 20 m from the road. Both surveyors used night vision binoculars (NOBG1, Night Owl Optics, El Paso, TX) to observe bats as they moved along the commuting corridors. With a field of view of 60 m by 35 m, we were able to see approaching bats before they reached the 40-m length of commuting route. Once we observed a bat, we determined whether the individual was commuting or foraging. From the long-term telemetry and behavioral data collected in the area (see Sparks et al. 2005a, Whitaker and Sparks 2008), we established that the flight characteristics of resident foraging and commuting bats could easily be distinguished. From over 40 radio-tracked bats, we determined that local bat species forage at speeds of 0.08 km/min (SE = 0.01) on average and commute at an average of 0.25 km/min (SE = 0.03). These flight speeds are comparable to those recorded for similar bat species (Hayward and Davis 1964, Kennedy and Best 1972, Zhang et al. 2007). We also calculated the tortuosity (the mean vector length of successive turning angles) and determined that commuting and foraging bats had a mean tortuosity of 0.88 (SE = 1.6) and 0.25 (SE = 2.8), respectively (where 1 represents a straight line as described in Batschelet [1965]). We therefore only considered bats in our survey when they exhibited a direct straight line flight along the commuting route towards the road. We also defined turning, the road-related avoidance response identified by Zurcher et al. 2010, as a bat flying...
directly along the commuting route towards the road and then turning 180° and flying directly away from the road back along their commuting route. When we observed turning, we continued to monitor that individual until it was out of our visible range (approx. 80 m along the commuting route). If we observed a bat return to the road, we recorded the time it passed each observer (see acoustic detection below), but did not record whether it successfully or unsuccessfully crossed the road or turned again. This approach helped minimize multiple observations of the same individual.

For each individual commuting bat observed, we estimated the height (m) at which each bat flew using features along the commuting routes as a guide (e.g., trees, telephone poles). Alternatively, we used 12-m extendable poles positioned near each surveyor to gage bat flight height. We also recorded whether the bat crossed the road successfully and in instances where bats turned, we recorded the time and distance (m) of the bat from the road using glow-in-the-dark tent pegs placed at 5-m intervals along commuting routes. In addition, for each bat observed, we documented the presence or absence of a vehicle as the bat approached the road. When a vehicle was present, we recorded vehicle type: cars (non-commercial passenger vehicles), trucks (including pick-up trucks and sport utility vehicles), and large commercial transport vehicles. We also recorded (1) travel direction (N, S, E, or W), 2) peak noise level emitted (dB) by each passing vehicle at the intersection of road and commuting route using a decibel recorder, 3) headlight status (low or high beams), and 4) if applicable, distance (m) of the vehicle from the road-commuting route intersection when the bat turned. We used landmarks and telephone poles at known distances parallel to the road to estimate vehicle distance from this intersection.

To identify commuting bats to species, we positioned 2 ANABAT sd1 bat detectors (Titley Scientific, Lawnton, Australia), 1 with each observer (i.e., 1 at the road-commuting route intersection and 1 midway along the 40-m stretch of commuting route surveyed) to record the echolocation calls of commuting bats. We placed each detector within the center of the commuting route with the microphone pointing vertically up. As none of the local species were considered to have quiet echolocation calls (Humboldt State University 2011) and the commuting routes themselves were open and generally free of clutter, a 20-m vertical and 10-m horizontal detectable range was regarded an appropriate range for detecting local species. After completing crossing surveys, we used time-stamps to match up individual echolocation calls with each bat passing we observed. From ongoing mist-netting activities in the local area, we obtained recordings of calls from individual bats (including big brown, evening, hoary, Indiana myotis, little brown, northern, red, and tricolored bat), which we used to establish a local call library. We then compared calls from crossing surveys with the call library using AnaLookW (version 3.3q, Titley Scientific) to identify commuting bats to species.

**Analysis**

To determine if the overall structure of each commuting route influenced the frequency at which bats exhibited road-related avoidance behaviors, we used a \( \chi^2 \) analysis to separately compare 1) the turning frequencies of bats in the presence of vehicles, 2) bat turning frequencies with vehicles absent, 3) road crossing rates of bats in the presence of vehicles, and 4) bat road crossing rates when vehicles were absent, between our 5 survey sites. To establish if bat activity and road crossing rates varied temporally, we carried out a paired 2-tailed \( t \)-test to compare the results of surveys undertaken at site 1 in 2009 with those recorded in 2008 by Zurcher et al. (2010). To assess whether turning and road crossing frequencies of bats in the presence and absence of vehicles varied significantly at each commuting route, we conducted a series of \( \chi^2 \) tests, 1 for each site.

Finally, we used a Classification and Regression Tree (CART) procedure to evaluate if turning by commuting bats in the presence and absence of vehicles was correlated to the condition of the commuting route and/or the visual and audible stimuli imposed upon the bats at the specific location they turned. This was based on the assumption that in the instances disturbance thresholds were met, bats would immediately respond (Fernández-Juricic et al. 2004). More specifically, we used CART to identify those variables, alone and in combination, that significantly influenced the probability of a bat turning (the response variable).

We selected this recursive partitioning method, because it could 1) create more accurate models than an equivalent polynomial logistic regression, 2) deal with complex, context dependent multivariate data in an environment free of distributional assumptions, 3) handle missing data, and 4) visually and explicitly identify the relationships and patterns between predictor variables (Vayssieres et al. 2000, Swihart et al. 2007). As our response variable represented a categorical value (i.e., bat turned, yes, or no), we built 2 classification trees; 1 for those bats that turned in the presence of vehicles and the other for bats that turned in their absence. For the former classification tree, we identified 13 independent predictors and for the latter we applied 6 predictor variables (i.e., we excluded any vehicle-related variables). Categorical predictor variables included vehicle type and whether they used low or high beam headlights from our crossing surveys. We used data collected in the habitat surveys to describe the commuting route at the specific location each bat turned (e.g., if a bat turned 10 m from the road, we used data that described the commuting route characteristics specifically at 10 m from the road). Thus, we included presence of a tree layer, shrub layer, herb layer, or fence in our CART analysis. We also included as categorical variables the visibility of both low and high beamed vehicle headlights along the commuting route (yes or no) from sensing surveys and bat species as recorded in the crossing surveys.

Continuous variables from the crossing surveys, included distance of vehicle from bat, peak noise levels of passing vehicles, and height at which the bat flew. From habitat surveys, we used distance from nearest gap in the commuting route. Finally, we included vehicle noise levels at the location a bat turned into the CART analysis. For this latter variable, we used data collected in the sensing and crossing surveys to estimate the noise level produced by an approaching vehicle.
at the specific location each bat turned. To calculate these subjective noise levels, we multiplied the proportional difference between the average noise levels at the road-commuting route intersection and the average noise levels at the location a bat turned (both recorded in the sensing surveys), with the noise levels generated by the vehicle that caused each bat to turn, as recorded during the crossing surveys.

To establish an optimal tree size, we used the area under the receiver operating characteristic (ROC) curve and the relative error index. The area under the ROC curve (AUC) demonstrates the model’s predictive performance (i.e., its ability to differentiate significant patterns between the different predictor variables; Fielding and Bell 1997). This metric ranges between 0 and 1 with greater values indicating better performance. The relative error index provides another measure of accuracy by revealing the relationship between classification errors and the number of nodes (i.e., tree size). It ranges from 0 to 1.0, where 0 indicates a perfect fit and 1 emphasizes that the predictor variables cannot be discriminated beyond chance. Finally, we used a V-form cross validation to validate our model because it performs independent tree size tests without requiring a separate dataset or a sub-section of the dataset used to build the main classification tree (Breiman et al. 1983). Using 90% of our dataset, we built 10 test trees. We calculated the average of all the classification error rates generated for each of the test trees, known as the cross validation cost. We then repeated the process 10 times with replacement, building 10 separate test trees each time. In each case, we held back a different 10% subset of the dataset. We compared the resulting 10 cross validation costs to identify the minimum cross validation cost. During the main classification tree building procedure, we then restricted the maximum tree size based on this minimum (i.e., the relative cost of tree did not exceed the minimum cross validation cost).

RESULTS

During the 10 crossing surveys, we observed 266 bats approaching the roads on commuting routes. In the absence of vehicles, 70 out of 159 (44%) of the bats crossed the road, and 89 (56%) turned away before they reached the road. In the presence of vehicles, 34 out of 107 (32%) crossed the road and 73 (68%) did not. However, turning and crossing frequencies among sites varied (see Supplemental Table S1, available online at www.onlinelibrary.wiley.com). We recorded echolocation calls for 141 bats along the commuting routes. Using the call library, we identified 17 calls to species. The range of heights at which bats flew along the commuting routes at our sites varied (ranging from 2 m to 40 m). However, the mode height at all sites was 11 m, corresponding with the canopy height of trees found at the sites. We also noted that bats that crossed the roads flew higher on average than bats that turned. This height difference ranged from 0.2 m to 2.1 m between sites. Similarly, the distance of bats from vehicles when a bat turned varied between and within sites (ranging from 0 m to 250 m). Finally, we found no discernible differences between noise levels of vehicles, noise levels at the specific location a response occurred, or the visibility of headlights on the behavior of bats among our sites. However, our sites varied in their structure and audible and visual characteristics considerably (see Supplemental Fig. S1, available online at www.onlinelibrary.wiley.com).

We found that site significantly influenced the frequency at which commuting bats exhibited road-related avoidance behaviors. The \( \chi^2 \) analysis revealed significant variation among our 5 sites in the turning frequency of bats in the presence of vehicles (\( \chi^2 = 80.00, P < 0.001; \) ranging from 2 to 48), bat turning frequencies with vehicles absent (\( \chi^2 = 25.56, P < 0.001; \) ranging from 0 to 29), road crossing rates of bats in the presence of vehicles (\( \chi^2 = 23.33, P < 0.001; \) ranging from 1 to 64), and bat road crossing rates when vehicles were absent (\( \chi^2 = 74.12, P < 0.001; \) ranging from 5 to 103). In comparison, we found no significant difference in the turning frequency and crossing rates of bats at site 1 between 2008 and 2009 (\( \chi^2 = 1.0076, P = 0.3879; \) indicating no temporal variation. Finally, we were unable to identify a clear pattern of bat behavior in the presence or absence of vehicles among sites, because behavior rates varied greatly within the sites. For example, the majority of bats at site 1 turned in the presence of vehicles (45%; \( \chi^2 = 29.47, P < 0.001 \)). In comparison, bats at site 2 and 4 predominately crossed in the absence of vehicles (49% and 68% respectively; \( \chi^2 = 36.97, P < 0.001 \) and \( \chi^2 = 24.18, P < 0.001 \)) and at site 3 more bats were observed turning in the absence of vehicles (57%; \( \chi^2 = 12.71, P = 0.0053 \)).

In the CART analysis to determine which predictor variables (i.e., vehicle, commuting route, and/or bat characteristics) alone or in combination influenced the probability of a bat exhibiting turning behavior in the presence of a vehicle, the classification tree demonstrated a good performance with a reasonable fit (AUC = 0.89 with a relative error value of 0.36). Primarily, evasive maneuvers were influenced by the presence of trees, which was an influential variable in 100% of occasions. Vehicle noise represented the second most influential variable (73%), followed by distance of the bat from a gap in the commuting route (54%), location-specific noise levels (41%) and height at which the bat flew (30%). No other characteristics had a significant influence on the bats’ turning behavior in the presence of vehicles.

The first split in the vehicle presence CART analysis indicated that when trees were absent along the commuting route, bats were more likely to turn (Fig. 1A). In the absence of trees, turning responses were further increased with vehicle noise. Vehicles producing noise levels above 88 dB
resulted in 100% of bats turning. In contrast, when trees were present, the distance of the nearest gap from the bat influenced turning behavior. The closer to a gap, the more likely a bat would respond to an approaching vehicle. The analysis revealed that 88% of bats turned when less than 1 m from a gap in their commuting route. Turning frequency decreases by 5% between 1 m and 2.5 m. At distances of over 2.5 m from the nearest gap, bats were influenced by the audible level of noise at their location. When noise levels along the commuting route were below 66 dB, less bats exhibited turning behavior (22%). In instances where noise levels exceeded 66 dB, the height at which the bats flew strongly influenced the turning probability. At heights below 9 m, 43% of bats displayed turning behavior. Between 9 m and 13 m, only 27% of bats turned, and above 13 m, we recorded 10% of bats turning.

In comparison, the classification tree to determine which predictor variables influenced the probability of a bat exhibiting turning behavior in the absence of a vehicle demonstrated excellent performance with a good fit (AUC = 0.93 with a relative error value of 0.29). The selected model identified that the presence of a tree layer was an influential variable in 100% of occasions. Width of a gap in the commuting route represented the second most influential variable (64%), followed by height at which the bat flew (52%) and shrub layer (36%). No other characteristics had a significant influence on the bats' turning behavior in the absence of vehicles.

The first split in the vehicle absence CART analysis indicated that when trees were absent along the commuting route, bats were more likely to turn (Fig. 1B), however, the presence of a shrub also had a significant influence. When both trees and a shrub layer were absent, 89% of bats turned. In the presence of at least a shrub layer, turning behavior decreased by 10%. In contrast, when trees were present, turning behavior was dictated by the size of the gap in the commuting route. If the gap was over 4.5 m wide, 82% of bats turned. However, turning rate decreased as gap width decreased (e.g., 60% bats turned when a gap was between 2.5 m and 4.5 m). At gaps under 2.5 m in width, the probability of a bat turning then depended on the height at which the bat flew. At heights below 7.5 m, 63% of bats turned. Between 7.5 m and 14 m, 9% of bats turned, and above 14 m, no bats turned.

**DISCUSSION**

Our findings revealed that road-related avoidance behavior exhibited by commuting bats was primarily influenced by the structure of the commuting route. Among the commuting routes surveyed, selected for their structural differences, we found significant variation in the turning frequencies of bats at each site. Our CART analysis confirmed that commuting route structure significantly influenced turning frequency. In the absence of vehicles, bats readily turned when trees and shrubs were absent. For example, at site 3, bordered by an agricultural field, over 50% of bats observed turned in the absence of vehicles. Similarly, as bats approached gaps of 2.5 m or more within tree lined commuting routes, 84% readily turned before reaching the gap. This included the road itself, representing a gap of 10 m. We observed 41% of bats turn just before the road when vehicles were absent. These results are consistent with other studies that have

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**Figure 1.** Classification tree identifying the conditions that trigger the turning behavior exhibited by bats along commuting routes bisected by roads in Indiana in 2009 A) in the presence of approaching vehicles and B) in their absence. Each terminal node provides the percentage and number (in parenthesis) of turning and crossing events included.
shown that gaps in tree lines, hedgerows, and tree canopies can render commuting routes unsuitable for bats (Fenton et al. 1998, van der Ree et al. 2010).

The CART analysis also revealed that turning rates of bats increased along the more exposed commuting routes when vehicles were present. For example, we recorded no road-related avoidance behavior at site 4, a commuting route bordered on both sides by unbroken linear features. Similarly, bats turned more readily along commuting routes with gaps in tree lines when vehicles were approaching. For example, at site 1, among the 48 bats that responded to approaching vehicles, 72% turned when they reached a gap in the tree line. This increase in turning behavior was correlated with an increase in the audibility of vehicles. At gaps and along exposed commuting routes, noise levels were approximately 20 dB higher than along intact tree-lines. We can only speculate that the sound of an approaching vehicle is either 1) perceived as a predator or 2) reduces a bat's ability to detect whether potential threats are close by (Walters et al. 2007, Heffner et al. 2010). If bats did perceive vehicles as predators, we would expect bats to respond to any approaching vehicle. However, our findings show that bats turned more frequently when approaching vehicles emitted noise levels above 88 dB. This supports the latter hypothesis that the sound of approaching vehicles reduces the ability of bats to detect potential threats (Koay et al. 1998). These findings indicate that bats have a disturbance threshold (Fernández-Juricic et al. 2004, Bennett et al. 2009).

Furthermore, the height at which bats flew had a significant influence on their turning frequency. With vehicles absent, bats flying at heights equivalent to the tree canopy (8–13 m) exhibited less turning than those bats flying above or below the canopy. In contrast, with vehicles present, bats flying at both tree canopy level and heights above the tree canopy (>15 m) exhibited less turning behavior. One explanation might be that increasing height increases bat-to-vehicle distance, which in turn reduces noise levels. Again, this suggests that bats have a disturbance threshold.

The implications of this threshold are that any gaps in commuting routes (including roads) have the potential to act as barriers or filters to bat movement (McGregor et al. 2008, McCown et al. 2009). Repeated disturbance by approaching vehicles could inhibit bats from commuting through such areas (Bautista et al. 2004, Alexander et al. 2005). In turn, this could prevent bats from accessing critical foraging habitat, thereby restricting their resource availability and potentially affecting their breeding success, survival, and ultimately the persistence of roost sites (Henry and Kalko 2007, Hein et al. 2009, Matheson et al. 2010).

However, our study indicates that landscape features, such as a single tree-line, can greatly reduce vehicle noise. A tree line essentially acts as a sound barrier masking the noise generated by vehicles. Moreover, bats commuting along tree lines did so at heights equivalent to the tree canopy (Kalcounis et al. 1999). As an overlapping mass of leaves and branches, the tree canopy represents a more effective sound barrier compared to a line of intermittent tree trunks. Similarly, many studies have shown that a variety of bat species routinely commute along woodland edges, hedge-rows, and fence lines (Verboom and Spoelstra 1999, Fellers and Pierson 2002, Racey and Entwistle 2003). The structure and composition of such linear features indicate that they will also act as effective acoustic barriers (Matsinos et al. 2008, Brown 2010).

MANAGEMENT IMPLICATIONS

In areas with extensive road networks, landscape permeability by bats may be reduced enough to cause population consequences for bats locally and regionally (Duchamp et al. 2004, Berthinussen and Altringham 2011). Our study has therefore demonstrated the need for 2 distinct strategies. The first is to ensure that linear features bisected by roads are connected, where possible. This may involve interlinking tree canopies from 1 side of the road to the other. The second strategy would be to restore (including replanting scrubs and trees in gaps), enhance (encourage interlinking tree canopies through pruning, trimming, and coppicing activities) and establish linear features, such as tree lines, hedgerows, and fence lines. This should improve permeability of the landscape overall, but also keep noise levels, such as those produced by vehicles, below disturbance thresholds (Kalcounis et al. 1999, Oprea et al. 2009, Tremblay and St Clair 2009).

Efforts to manage bats should take into account the ecological design of the acoustic environment (Carles et al. 1999, Brown 2010). We encourage research that further evaluates the effect of anthropogenic modifications on the soundscape and we support the development of management strategies that will alleviate the implications of these modifications on wildlife (Zhang and Kang 2007, Jung and Kalko 2010).

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