



Contents lists available at ScienceDirect

# Transportation Research Part D

journal homepage: [www.elsevier.com/locate/trd](http://www.elsevier.com/locate/trd)

## Effects of local roads and car traffic on the occurrence pattern and foraging behaviour of bats



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### ARTICLE INFO

#### Keywords:

Bat calls  
Roads  
Chiroptera  
Corridors  
Foraging  
Forest  
Poland

### ABSTRACT

The most negative impacts of roads on bats are increased mortality caused by collisions with vehicles, noise pollution reducing both communication and foraging, and barriers to movement. To test the effect of roads and traffic on the occurrence and foraging habits of bats in forested landscapes in western Poland we compared 53 sites located along local asphalt roads of low to medium traffic volume with paired reference sites on unsurfaced forest roads. Acoustical monitoring systems with Anabat detectors were used at night to detect bats at all sites. Overall, we found a strongly significant preference of bats for local asphalt roads; 640 bat passes were recorded at asphalt roads but only 271 at reference sites. Furthermore, significantly more bat taxa, longer activity and a greater frequency of feeding buzzes (calls used during foraging) were also recorded at asphalt roads. However, significant benefits were not shown for all species. This study clearly shows that local asphalt roads in forested landscapes are important foraging areas for several bat species.

### 1. Introduction

The intensive development of road systems has resulted in traffic affecting most animals, especially during migration or dispersal. Roads cause the loss, deterioration and fragmentation of adjacent habitats (Forman and Alexander, 1998). Hence they negatively affect the local populations of many animals, reducing the density and diversity of species (Benitez-Lopez et al., 2010; Summers et al., 2011). Obviously, roads have a more direct effect on individuals via mortality due to collisions with passing vehicles (e.g. Lesinski, 2007; Russell et al., 2009; Lesinski et al., 2011). Chemical and noise pollution may also directly reduce reproductive success and alter the behaviour of animals living in the vicinity of roads (Barber et al., 2011). Noise pollution can reduce hunting success, especially for bats that rely on prey-generated sounds to locate their victims (Siemers and Schaub, 2011).

Previous research has indicated negative impacts of roads on bat populations. Traffic increases bat mortality through collisions with vehicles (e.g. Lesinski, 2008; Gaisler et al., 2009; Russell et al., 2009; Lesinski et al., 2011). However, relatively few articles are based on data that would allow an evaluation of other interactions between bat populations and traffic. Noise pollution from roads has been shown to reduce the foraging efficiency of the greater mouse-eared bat (*Myotis myotis*) which primarily hunts for insects

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<http://dx.doi.org/10.1016/j.trd.2017.08.011>

moving on the ground and uses passive listening to locate prey (Schaub et al., 2008; Siemers and Schaub, 2011). Detrimental effects on other bat species have also been reported (Bunkley and Barber, 2015; Luo et al., 2015). Berthinussen and Altringham (2012) showed a negative impact of high volume traffic (30–40 thousand vehicles per day) and of wider roads, which caused bats to avoid foraging near the road. For some species, roads are a movement barrier (Kerth and Melber, 2009; Abbott et al., 2012). For example, Indiana bats (*Myotis sodalis*) were reported to avoid crossing roads, especially in the presence of vehicles (Zurcher et al., 2010). Moreover, light pollution can reduce foraging areas and result in negative behavioural changes in foraging bats (Stone et al., 2009, 2012; Polak et al., 2011). On the other hand, there are many examples of the regular use by bats of street lighting in order to forage (e.g. Rydell, 2006), and despite examples of the negative impact of road development on bat populations, some bat species regularly use human-transformed habitats. Some of these species may now be regarded as synanthropic and regularly use buildings for hibernation, daily rest, and reproduction (Hale et al., 2012). Moreover, vehicle lights may lure insects to roads and consequently affect bat foraging behavior, and the presence of some species is positively associated with road cover at a small scale (Bellamy et al., 2013). However, the impact of roads on bats is still not well understood. For example, some papers suggest that bats avoid cars, but this was tested only on larger roads (Bennett and Zurcher, 2013), and there is no single study on the importance of more common road types of low or medium traffic volume, especially in Eastern Europe. In consequence, this prevents the development of specific mitigation measures.

In this paper, we address the question of how local roads affect the number of bat passes, species richness and behaviour of foraging bats. If traffic on roads only has a negative effect on the foraging of bats then we would expect lower bat densities near roads than in reference areas. Moreover, we analyse how the movements of individual cars affected bat foraging patterns. If bats really avoided car traffic then bat activity will be lower when the car is passing, because of an avoidance behaviour in response to an approaching vehicle. However, if bats do not respond to passing cars then we expect that bat activity will be randomly distributed in time, independent of car movements.

## 2. Methods

### 2.1. Study area

The study area in the Wielkopolska region of western Poland included local roads of low to medium traffic volume (up to 250 cars/h at night; asphalt width 5.4–11.2 m) within forests and extended over 170 km in a north-south direction (51°29′–53°01′N) and 60 km east-west (16°49′–17°48′E). The landscape of the studied area is characterized by a high proportion of arable land with many large forest fragments. The average forest cover in this part of Poland is 25% and the human population density is 114 persons per km<sup>2</sup> (Łowicki, 2008).

### 2.2. Selection of study sites

In order to select research sites we used satellite images and site visits to assess suitability. We chose six large (> 30 km<sup>2</sup>) forest fragments in which to conduct the study, thus ensuring relatively large alternative foraging areas for bats. Road sites were located along low to medium traffic volume asphalt roads with one lane in each direction. Within a single forest fragment, sites were separated from one another by at least 1 km to avoid recording the same individual bats, and were also located at least 300 m within the forest to avoid the impact of non-forest environments (including street lights) on bat behaviour. We avoided sites with clearings and young trees that could markedly influence the flight paths of bats. Our control consisted of paired reference sites located 100 m from the asphalt road sites, also at least 300 m from forest edges, on unsurfaced forest roads (width 2.3–5.8 m) with no vehicle traffic at night. This separation distance ensured that noise and light pollution from the asphalt road was not important (Schaub et al., 2008; Siemers and Schaub, 2011; Berthinussen and Altringham, 2012). For both types of roads, there were no street lights within 300 m, and were typically much further away. The recording of bat activity was carried out at 53 pairs of sites (mean number of pairs of sites per forest patch was  $8.8 \pm 0.9$  SE; range: 6–11).

### 2.3. Acoustic monitoring of bats

We used two sets of Anabat detectors to record bat activity (Anabat II, Titley Electronics, Ballina, New South Wales, Australia). During a pilot study, we determined that level 5 was a suitable sensitivity value for the detector. At level 5, we were able to focus the recordings on bat activity on the road and in the immediate surroundings. To eliminate any slight differences in sensitivity between the detector sets, we selected them interchangeably for recording on asphalt road and reference sites. Detectors were equipped with standard directional ‘Low Energy’ microphones. During recording, detectors were set 20 cm above the ground on the roadside, at 45° to the direction of the gaps in the canopies. We recorded during peak bat activity on eight nights in August 2011. Recordings were carried out only in the absence of rain, and with winds below 5 m/s. We started collecting data no earlier than one hour after sunset and finished 4 h after sunset. Bat activity was recorded simultaneously for 10 min, once at each pair of sites. We also recorded air temperature at each site. In addition, on the asphalt roads, we noted all passing vehicles and their direction of movement. The exact time each car passed was noted manually to a one-second accuracy using a PDA clock. During analysis of the data we corrected the time the car passed by using the characteristic car generated noise recorded by the Anabat detector.

### 2.4. Acoustic analysis and species identification

We recorded activity in the memory of a HP PDA IPQ 214 connected to the Anabat detector via a zero-crossing interface (Z-CAIM, Titley Electronics). We analysed only the good quality recordings of bat passes, i.e. those with a clear visible line of frequency during particular pulses. We defined a single passage here as consisting of at least 3 or more pulses, separated from the next pass by a time gap of at least 1 s. The bat calls based on recordings were analysed in AnalookW version 3.7w sound analysis software (developed by C. Corben, Australia). Pass duration was measured for each bat pass. The activity time was calculated as the sum of all pass durations. Foraging calls (feeding buzzes) within bat passes were manually identified from normal search phase calls. Bat species were identified from the sonograms of their calls using call shape, call duration and call end frequency. Echolocation signal characteristics were compared to known parameters for each species from the literature (Parsons and Jones, 2000; Russo and Jones, 2002; Obrist et al., 2004) and from a database of reference calls recordings. Species of the *Myotis* genus (potentially *M. daubentonii*, *M. nattereri*, *M. myotis*, *M. brandtii*, *M. mystacinus*) were grouped together, given the high similarity of their sonograms (Russ, 1999; Parsons and Jones, 2000). *Eptesicus serotinus*, *E. nilssoni* and *Vespertilio murinus* were considered as an *Eptesicus* group and *Plecotus auritus* and *P. austriacus* as a *Plecotus* group in analyses, due to the difficulty in distinguishing them based on echolocation parameters alone (Obrist et al., 2004).

### 2.5. Statistical analysis

Data are presented as mean ± SE, and descriptive statistics and basic statistical analyses were carried out using the software SPSS v.20. All performed tests were two-tailed. To compare number of bat passes (proxy for bat abundance) and number of bat taxa (proxy for species richness since some bats could only be identified to the genus level) between asphalt road and reference sites, we used a generalized linear mixed model (GLMM) with a negative binomial error structure and log link function. Forest identity and pair of sites (nested within forest) were random factors. Temperature, number of passing cars, and road width were included as covariates. The interaction between road width and type of road (asphalt vs. reference forest road) was included in each model to account for road edge effects (Supporting Information 2). We created a GLMM with a Gaussian error structure and identity link function and a GLMM with a binomial error structure and logit link function to analyse mean activity durations and the proportion of activities including a feeding buzz, respectively. The independent variables were the same as for the GLMM for the number of bat passes. Similar GLMMs were built to analyse the number of passes and activity of each taxon. A correction for false discovery rate in multiple testing (Benjamini and Hochberg, 1995) was used and we performed response homogeneity tests to determine whether or not taxa were uniformly detected in intervals 15 s before/after or 30 s before/after cars passed. This is essentially a chi-square test of whether the number of bat detections was the same across time categories in each taxa. We included the recording site identity in the model as an additional category. Likelihood Ratio chi-square statistics were calculated. All chi-square statistics were calculated in the Categorical Response Analysis module of JMP 9 software.

## 3. Results

### 3.1. Number of bat passes and species richness of bats

A total of 640 bat passes were recorded at asphalt roads and 271 bat passes at reference sites. 44% of all recordings were of

**Table 1**

The mean number of bat passes detected at reference sites along forest roads and at paired sites on asphalt roads 100 m from the former. The comparison of number of bat passes was made using generalized linear mixed models with a negative binomial error structure and log link function. Statistically significant effects are shown in bold.

Taxa	Common name	Mean per hour ± SE		p <sup>†</sup>
		Reference	Road	
<i>Barbastella barbastellus</i>	Barbastelle	6.57 ± 1.95	2.83 ± 0.91	<b>0.030</b>
<i>Eptesicus</i> spp. <sup>a</sup>	<i>Eptesicus</i> group <sup>a</sup>	7.92 ± 3.65	15.74 ± 4.45	0.046
<i>Myotis</i> spp. <sup>b</sup>	<i>Myotis</i> group <sup>b</sup>	6.11 ± 1.70	3.28 ± 0.82	0.882
<i>Nyctalus noctula</i>	Common noctule	1.36 ± 0.55	44.38 ± 9.89	< <b>0.001</b>
<i>Plecotus</i> spp. <sup>c</sup>	<i>Plecotus</i> group <sup>c</sup>	1.93 ± 0.51	1.40 ± 0.44	0.197
<i>Pipistrellus nathusii</i>	Nathusius's pipistrelle	0.41 ± 0.15	1.76 ± 0.63	<b>0.012</b>
<i>Pipistrellus pipistrellus</i>	Common pipistrelle	2.38 ± 1.03	3.74 ± 1.12	<b>0.016</b>
<i>Pipistrellus pygmaeus</i>	Soprano pipistrelle	0.40 ± 0.15	2.00 ± 0.63	<b>0.004</b>
All bat passes		30.68 ± 5.77	72.45 ± 11.32	<b>0.001</b>
Number of species/taxons		1.52 ± 0.19	2.46 ± 0.16	<b>0.013</b>

<sup>a</sup> *Eptesicus serotinus*, *E. nilssoni* and *Vespertilio murinus*.

<sup>b</sup> *Myotis daubentonii*, *M. nattereri*, *M. Myotis*, *M. brandtii* and *M. mystacinus*.

<sup>c</sup> *Plecotus auritus* and *P. austriacus*.

<sup>†</sup> Critical threshold for significance after Benjamini and Hochberg (1995) correction was 0.031.

**Table 2**

Mean duration of bat activity and the proportion of encounters which included a feeding buzz at reference sites along forest roads (Ref) and at paired sites on asphalt roads 100 m from the former (Road). Comparisons were made using a generalized linear mixed model with Gaussian error structure and identity link function (activity times), or a binomial error structure and logit link function (% of encounters with feeding buzz). nt = not tested, due to low sample size. Statistically significant effects are in bold. The final columns indicate at how many sites the species/taxon was recorded (N = 53).

	Activity time (mins) mean ± SE			% of encounters with feeding buzz mean ± SE			Number of sites	
	Ref	Road	P <sup>†</sup>	Ref	Road	P <sup>‡</sup>	Ref	Road
<i>Barbastella barbastellus</i>	1.18 ± 0.09	1.91 ± 0.31	<b>0.008</b>	2.0 ± 2.0	14.6 ± 8.6	0.076	17	16
<i>Eptesicus</i> spp. <sup>a</sup>	3.23 ± 0.36	3.70 ± 0.20	0.095	20.8 ± 10.6	13.9 ± 4.6	0.959	9	27
<i>Myotis</i> spp. <sup>b</sup>	2.98 ± 0.24	2.86 ± 0.22	0.793	11.9 ± 6.3	27.4 ± 9.5	0.058	18	17
<i>Nyctalus noctula</i>	3.30 ± 0.50	4.73 ± 0.33	0.062	0.0 ± 0.0	25.2 ± 4.8	<b>0.015</b>	7	34
<i>Plecotus</i> spp. <sup>c</sup>	1.86 ± 0.25	1.84 ± 0.27	0.768	0.0 ± 0.0	0.0 ± 0.0	nt	19	5
<i>Pipistrellus nathusii</i>	2.10 ± 0.40	3.13 ± 0.13	nt	0.0 ± 0.0	37.5 ± 23.9	nt	2	4
<i>Pipistrellus pipistrellus</i>	2.94 ± 0.35	4.00 ± 0.37	<b>0.011</b>	0.0 ± 0.0	19.1 ± 5.6	0.031	7	13
<i>Pipistrellus pygmaeus</i>	2.25 ± 0.55	2.09 ± 0.42	nt	0.0 ± 0.0	16.7 ± 16.7	nt	2	4
All	2.29 ± 0.17	3.90 ± 0.23	<b>0.009</b>	5.5 ± 1.7	19.8 ± 2.7	< <b>0.001</b>	37	53

<sup>a</sup> *Eptesicus serotinus*, *E. nilssonii* and *Vespertilio murinus*.

<sup>b</sup> *Myotis daubentonii*, *M. nattereri*, *M. Myotis*, *M. brandtii* and *M. mystacinus*.

<sup>c</sup> *Plecotus auritus* and *P. austriacus*.

<sup>†</sup> Critical threshold for significance after Benjamini and Hochberg (1995) correction was 0.021.

<sup>‡</sup> Critical threshold for significance after Benjamini and Hochberg (1995) correction was 0.017.

*Nyctalus noctula* and a further 23% were of *Eptesicus* spp. (Table 1). Whilst no bats were recorded at 16 of the reference sites, at least one bat was recorded at every asphalt road site. More than twice as many bat passes occurred at asphalt roads compared to reference sites (Table 1) after controlling for car density, temperature, road width and interaction terms. There was no indication that these effects were driven by an edge effect (Supporting Information 2). *Nyctalus noctula*, *Eptesicus* spp. (including *Vespertilio murinus*), *Pipistrellus nathusii*, *Pipistrellus pipistrellus* and *Pipistrellus pygmaeus* each had significantly higher number of bat passes at asphalt roads than at reference sites, while only *Barbastella barbastellus* had a significantly higher number of bat passes at reference sites (Table 1). The number of taxa was also significantly higher at asphalt roads (Table 1).

### 3.2. Bat activity and behaviour

Overall, bat activity was significantly greater (by more than 50% on average) and a significantly higher proportion of activity involved feeding behaviour (more than three times as common) on asphalt roads compared to reference sites (Table 2). For individual species, mean activity time was significantly greater on asphalt roads for *Barbastella barbastellus* and *Pipistrellus pipistrellus*. The proportion of activity involving feeding buzzes was only significantly higher on asphalt roads than at reference sites for *Nyctalus noctula* (Table 2).

### 3.3. The effects of car movements on bat activity

There was no significant effect of traffic volume on number of bat passes (slope = -0.006 ± 0.012, GLMM F<sub>1,100</sub> = 0.286, P = 0.594) (see Fig. 1) or number of species/taxons (slope = 0.007 ± 0.008, GLMM F<sub>1,41</sub> = 0.721, P = 0.401). Similarly there was no significant relationship between the number of bat passes of individual taxa and car density (all P > 0.202).

The response homogeneity tests indicated that all taxa had a similar response to passing cars, both when 15 s (Likelihood ratio  $\chi^2$  = 185.2, P = 0.891; Fig. 2) and 30 s (Likelihood ratio  $\chi^2$  = 140.6, P = 0.673) intervals were analysed.

There was no statistical evidence that bat activity varied between time categories associated with passing cars when data from 15 s and 30 s intervals were analysed (Fig. 2; all P > 0.2; data pooled across species because the homogeneity test was non-significant).

## 4. Discussion

### 4.1. Local asphalt road-bat interactions

Our findings indicate a strong preference of half of the surveyed bat species towards asphalt roads. However, the studied road system comprised mainly of local roads of low to medium traffic volume, especially at night when bats forage. No bat activity was recorded at 16 of 53 reference sites located on unsurfaced forest roads. In contrast, bat activity was recorded at all asphalt road sites. A greater number of both bat passes and taxa were recorded at asphalt roads. The novel findings in our study include longer activity and a greater frequency of feeding buzzes at asphalt roads.

All species in the *Pipistrellus* group appeared to prefer asphalt roads. Common noctule (*Nyctalus noctula*) was the species most significantly associated with foraging over asphalt roads. It is a fast flying bat that prefers foraging at a higher altitude than other species detected during our study (Bogdanowicz et al., 1999). Such a strategy probably allows it to remain reasonably safe over roads.

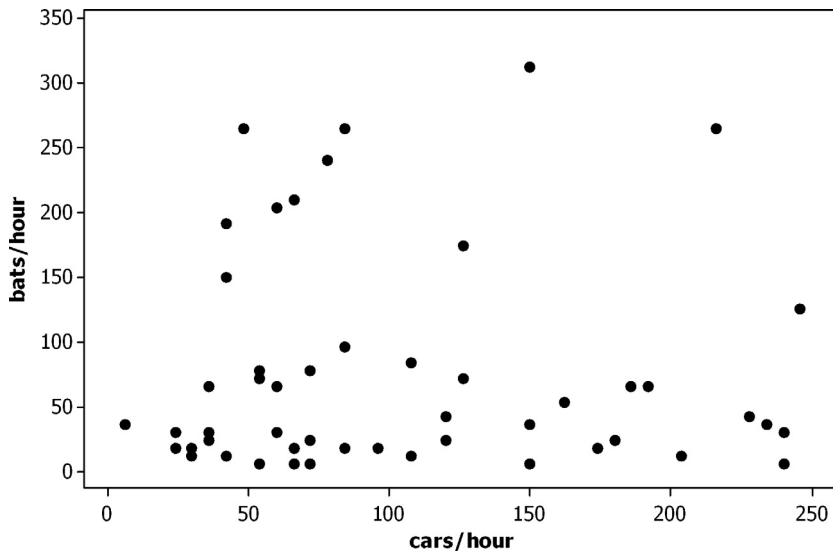


Fig. 1. The relationship between car density and number of bat passes on 53 asphalt roads in the study area, both scales converted to hourly values.

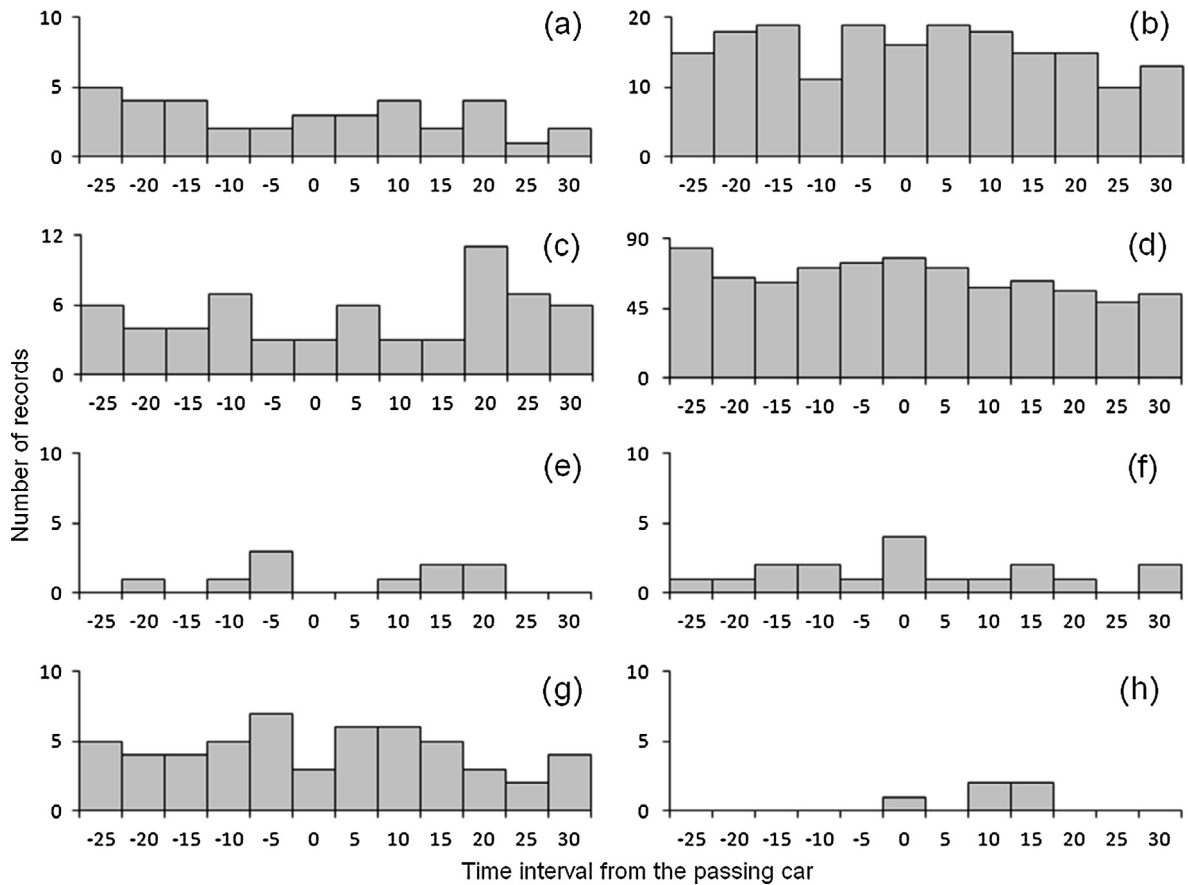


Fig. 2. The response of behavioural activity of *Barbastella barbastellus* (a), *Eptesicus* spp. (b), *Myotis* spp. (c), *Nyctalus noctula* (d), *Plecotus* spp. (e), *Pipistrellus nathusii* (f), *Pipistrellus pipistrellus* (g), *Pipistrellus pygmaeus* (h) to passing cars. Time was divided into categories and negative values indicate that bats were active before the car reached the recording site and positive values indicate that bats were recorded after the car had passed.

The level of bat casualties of common noctule on roads is generally low (Kieffer et al., 1995; Lesinski, 2007; Gaisler et al., 2009). Gaisler et al. (2009) showed that even though this was the most common species detected in the vicinity of a road its mortality was marginal. However, Lesinski et al. (2011) showed that in some locations this species may be one of the most frequently killed as a

result of collision with cars. This suggests a change in the typical foraging behaviour of some local populations of common noctule to regularly fly closer to the road surface.

A significant avoidance of asphalt roads and traffic was detected only for barbastelle (*Barbastella barbastellus*). This suggests a similar strategy to that of Indiana bat (Bennett et al., 2013). Although *Barbastella barbastellus* used asphalt roads less frequently, their activity on asphalt roads was of significantly longer duration. We can speculate that the longer pass duration of *Barbastella barbastellus* on asphalt roads reflects increased usage for foraging by some individuals. The lack of a significant preference by *Myotis* spp. is probably due to the fact that it is a group of taxonomically similar species, but with considerable differences in ecological demands (as habitat preferences) and foraging strategies (from gleaning to aerial hawking; Bogdanowicz et al., 1999). Moreover, a further possible reason may be that the greater mouse-eared bat (*Myotis myotis*) is known for its reliance on passive listening for the sounds of its prey during hunting and will thus avoid noise pollution (Schaub et al., 2008; Siemers and Schaub, 2011). On the other hand the *Myotis* taxon also includes species that use echolocation during hunting (Jones and Rayner, 1988; Bogdanowicz et al., 1999). For such species, moderate intensity noise pollution is not likely to be a limiting factor, however Luo et al. (2015) showed significant influence of noise on Daubenton's bats (*Myotis daubentoni*) which find prey by echolocation.

The attractiveness of asphalt roads for bats is probably influenced by a number of factors. The road, as well as the gap in the forest stand, is a linear landscape feature, preferred as foraging sites by bats (Rachwald, 1992; Berthinussen and Altringham, 2012). However, the spatial structure of the foraging area was probably not the deciding factor. Bat activity was significantly lower at unsurfaced reference sites, also located along linear gaps in the forest stand. Therefore, the differences in activity were most probably caused by the presence of traffic and its influence on prey species.

Asphalt surfaces absorb heat through the day and release it slowly, and both this and car lights may attract insects, especially at night (Saarinen et al., 2005; Horváth et al., 2010; van Langevelde et al., 2011). This in turn increases the effectiveness of bat foraging in such areas. In addition, a passing car involves a whole chain of reactions between the car and insects. First of all, remarkable changes in illumination/lighting and even heat may occur, which attracts and disorients potential bat prey (our pers. observations, but see also: Kriska et al., 1998). Secondly, the noise emitted by vehicles likely brings about a masking effect of noise, which makes it possible for bats to get closer to their prey without the latter expressing antipredator behaviour. A similar situation was found in the case of Caribbean hermit crabs (*Coenobita clypeatus*) where the masking effect was brought about by noise and lighting from motorboats (Chan et al., 2010). The third type of reaction is the presence of insects in the vicinity of a passing vehicle due to strong air movements caused by differences in air pressure between the car and the air around it. The air movements may also damage insects which impairs or prevents further flight. Additionally, some insects collide with vehicles (Skórka et al., 2013). However, no data have been collected that would allow an assessment of whether bats forage on damaged or dead insects. Another possible benefit of traffic to foraging bats is the substantial simplification of the environment's spatial structure caused by the presence of a flat asphalt surface, as opposed to the typically rutted and vegetated, uneven surface of forest roads. Such a simplified structure mimics natural rivers, the preferred foraging areas of the common noctule (Rachwald, 1992). Similarly, birds also show a preference for foraging in the simplified spatial structure provided by roads (Morelli et al., 2014).

We do not exclude the possibility that the observed higher number of bat passes at asphalt roads results from the edge effect since asphalt roads and reference sites differed in width because we were not able to find a reasonable sample of forest roads as wide as asphalt roads. However, our complex analysis (see Supporting Information 2) indicates that there is no evidence that either the increased taxon richness of bats or their number of passes at asphalt roads are the results of an edge effect. The edge effect itself may be shaped by many factors, e.g. resource abundance (Leslie and Sisk, 2004). This should be addressed in future studies.

#### 4.2. Vehicle-bat interactions

It has been shown that considerable numbers of bat deaths are caused by collisions with vehicles (Lesinski, 2007; Gaisler et al., 2009; Russell et al., 2009; Lesinski et al., 2011). Our data show that local asphalt roads within forests are intensively used by bats. No correlation between the numbers of car passes and bat passes was found. This suggests that relatively low traffic volume does not have a negative influence on foraging. However, the traffic volume of our busiest studied road was only about one-tenth of that of the M6 motorway in the UK, where Berthinussen and Altringham (2012) showed the negative influence of that road on bat activity. If bats express antipredator behaviour towards cars at the low traffic volumes in our study, then the number of bat passes would be lower when cars were passing. However, the analysis of our data does not indicate any substantial differences in bat activity just before, during or just after the passage of cars. This also indicates that the passage of cars does not encourage bats to forage more intensively.

#### 4.3. Conclusions

Despite reports of the adverse effects of roads on bats via increased bat mortality due to car collisions, our analyses present a counter argument. Local asphalt roads seem to be important foraging areas for several bat taxa in forested landscapes. Such roads may positively affect populations of bats unless road mortality is high.

#### Acknowledgments

This study was partially financed by the National Science Centre in Poland under project number N N304 030139.

## Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.trd.2017.08.011>.

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