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The effect of a major road on bat activity and diversity

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Summary

1. It is well known that roads can have a significant impact, usually negative, on species and ecosystems. However, despite their protected status in many countries, little research has been done into the effects of roads on bats. With a view to making more informed management recommendations, we address the simple question: are bat activity and diversity (as measured with ultrasonic detectors) correlated with distance from a major road?

2. Broadband acoustic surveys were conducted on 20 walked transects perpendicular to the M6, a major road in Cumbria (UK), with bat activity recorded at eight spot checks per transect at different distances from the road. Climatic and habitat variables were also recorded, and the relationships between bat activity and these variables were investigated using generalised estimated equations (GEE) and ordinal logistic regression.

3. Total bat activity, the number of species and the activity of *Pipistrellus pipistrellus* (the most abundant species) were all positively correlated with distance from the road. Total activity increased more than threefold between 0 and 1600 m from the road. These effects were found to be consistent over 2 years.

4. *Synthesis and applications*. This study is one of the first to show that roads have a major negative impact on bat foraging activity and diversity and is broadly applicable to insectivorous bat communities worldwide. Mitigation requires that roads are made more permeable to bats through the use of effective crossings, such as underpasses and overpasses, and that habitat is improved within 1 km of major roads. Because the effectiveness of current mitigation measures is unknown, well-designed monitoring of mitigation is essential.

Key-words: barrier effects, bats, foraging activity, habitat degradation, *Myotis*, *Nyctalus*, *Pipistrellus*, roads

Introduction

Roads destroy and degrade habitat and dissect the natural landscape (Forman *et al*. 2003); yet as recently as 1998, Forman and Alexander described 'road ecology' as 'the sleeping giant', drawing attention to the potentially devastating, but largely unstudied, effects of roads on the natural world. Road ecology is now increasingly well studied (e.g. Frair *et al*. 2008; McGregor, Bender & Fahrig 2008; Halfwerk *et al*. 2011; Summers, Cunnington & Fahrig 2011), but there are relatively few studies of bats.

The density and diversity of a range of vertebrates, including birds (e.g. Canaday 1996; Summers, Cunnington & Fahrig 2011), are negatively correlated with road density and positively correlated with distance from the road (early work is reviewed by Trombulak & Frissell 2000; Coffin 2007). Roads may have a positive effect on some species. For example, densities of white-footed mice *Peromyscus leucopus* increase in proximity to roads because of the creation of favourable habitats along road verges and a reduction in predators (Rytwinski & Fahrig 2007), but the same species is reluctant to cross roads (McGregor, Bender & Fahrig 2008). However, it is likely that these positive effects are limited to relatively few species. Fahrig & Rytwinski (2009) reviewed 79 studies that between them investigated 131 species and found that negative effects were far more prevalent than positive effects.

Possible effects of roads on wildlife include mortality from vehicle collisions, habitat destruction, habitat fragmentation, barrier effects, edge effects and habitat degradation or disturbance from light, noise and chemical pollution. The magnitude of road effects is likely to vary over time and multiple effects will usually be cumulative in the long term (Balkenhol & Waits 2009). There may also be far reaching effects, such as the cascading consequences that can occur in ecological

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communities when the abundances of key species are altered (Francis, Ortega & Cruz 2009).

Most of the literature on road effects has focused on terrestrial mammals, amphibians and birds, with little research into the effects on bats. There are 17 resident species of bat in the UK and all are protected by both UK (The Wildlife and Countryside Act 1981; The Countryside and Rights Of Way Act 2000) and EU legislation [The Conservation (Natural Habitats &c.) Regulations 1994; The Conservation (Natural Habitats &c.) (Amendment) Regulations 2007]. All bat species are an important consideration in national and local recovery plans, and a licence must be obtained if it is necessary to disturb any species of bat in the UK. Furthermore, developers must demonstrate that they will put in place mitigation measures to minimise the impact and compensate for any loss to bat foraging or roosting habitat (Mitchell-Jones 2004). Similar laws apply in many other countries.

It is likely that bats are particularly vulnerable to road developments and will be slow to recover from disturbance because of their life history strategy of low fecundity, their longevity and their use of large areas of the landscape (Altringham 2008). Roads may affect bats in three principle ways: (i) kill by collision with vehicles, (ii) damage or degrade roosts and foraging areas and (iii) sever critical flight routes used for commuting and migration. Several recent studies show that bats of many species are killed by collision with vehicles (Lesinski 2007; Gaisler, Rehak & Bartonicka 2009; Russell *et al*. 2009; Lesinski, Sikora & Olszewski 2010). Mortality in many of these studies is probably severely underestimated because of the difficulty of finding corpses and their removal by scavengers (Slater 2002). Kerth & Melber (2009) found that a major road in Germany restricted habitat accessibility in female Bechstein's bats *Myotis bechsteinii* resulting in smaller foraging areas and reduced reproductive success. Noise pollution from traffic reduced foraging efficiency of *M. myotis*, a species that forages by passive listening (Schaub, Ostwald & Siemers 2008; Siemers & Schaub 2011), and Stone, Jones & Harris (2009) have shown that street lighting is a major deterrent to foraging and commuting lesser horseshoe bats *Rhinolophus hipposideros*. Other slow flying and/or gleaning species are also likely to be deterred by lights, but some faster flying species forage beneath street lamps that attract insect prey (e.g. Blake *et al*. 1994). Lights may also alter local bat population dynamics by attracting insects out of woodland, leading to diffuse exploitative competition (Arlettaz, Godat & Meyer 2000). Zurcher, Sparks & Bennett (2010) found evidence for road avoidance behaviour: bats approaching a road bisecting a commuting route were found to reverse their course more frequently in the presence of traffic.

These studies, and inference from studies of bats described later, suggest that roads are likely to have significant negative impacts on bats, leading to a reduction in population sizes. Bat populations have declined dramatically in the last century in the UK (Harris *et al*. 1995) and in many other countries, leading to increasingly strong legal protection. To satisfy legal requirements, costly mitigation measures are employed on road developments throughout Europe to reduce their impact on bats. However, there is little satisfactory evidence to support their effectiveness (e.g. Altringham 2008), and we have little knowledge of just how much roads do affect bats. This study is a step towards a more evidence-based approach to the bat–road issue. We ask the simple question: are bat activity and diversity (as measured with ultrasonic detectors) correlated with distance from a major road? We show that roads do affect bat activity, suggest what mechanisms underlie the effect and discuss appropriate mitigation and monitoring strategies.

Materials and methods

Acoustic surveys were conducted on walked transects approximately perpendicular to the M6, a major road in Cumbria, UK (Fig. 1) between June and September in 2009 and 2010. Ten unreplicated transects were walked in 2009, and in 2010 (with the addition of ten new transect routes), 20 transects were completed, each walked twice. The section studied consists of an 80 km stretch of road. The M6 (which runs from the middle of England to the Scottish border) is a well-established road, completed in 1971. It is a six-lane highway with a central reservation and a total width of 35 m or more. The maximum speed limit is 110 km h^{-1}, and the traffic volume on rural sections in Cumbria is 30–40 000 vehicles per day (Average Annual Daily Traffic, Cumbria County Council 2010). The M6 is predominantly unlit in Cumbria with the exception of interchanges, junctions and urbanised areas, and all transects were conducted along unlit sections. Bat activity was recorded for 10 min at each of eight spot checks along each transect at 0, 50, 100, 200, 400, 800, 1200 and 1600 m perpendicular to the road. This sampling regime was designed to detect even an effect restricted to the immediate vicinity of the road. Transects were selected using Ordnance Survey maps and site visits to assess their suitability. They were located either side of the road along minor roads or footpaths, through relatively homogenous habitat (avoiding large areas of woodland, water and human habitation) consisting of rural, undulating lowland used predominately for agricultural grazing. Spot check locations were measured and marked using online mapping tools (EDINA, http://edina.ac.uk, Edinburgh, UK) and (in the absence of suitable landmarks) a handheld GPS device (Garmin GPS 60Cx, http://www.garmin.com, Southampton, UK) to an accuracy of ± 10 m or better. Bat echolocation calls were automatically (high gain) detected using a Pettersson D240x broadband bat detector (http://www.batsound.com, Uppsala, Sweden), with 100 ms time expanded (to 1 s) calls recorded directly to a solid state recorder (Edirol R-09HR, http://www.roland.co.uk, Swansea, Wales, UK) in mp3 (320 kbps) format to reduce file size for storage. One to three calls were captured in each 100 ms recorded segment, sufficient for identification. Each transect commenced 30 min after sunset to allow for varying emergence times of different species and was completed two hours after sunset. To account for variation in activity patterns with time, in 2009, five transects were walked towards the road and five away from the road. In 2010, all transects were walked in each direction (away from and towards the road) on separate nights. Transects were only completed in favourable weather conditions, avoiding wet, windy or cold nights.

Temperature, wind speed, percentage cloud cover and altitude were also recorded at each spot check using a digital anemometer/thermometer (Techno line EA-3010, http://www.technoline.eu, Berlin, Germany) and GPS. Although transect routes were selected for their habitat homogeneity, the rich mosaic of habitats in the area meant that variation was still present. Habitat types were therefore recorded and classified into 5 categories (Table 1).

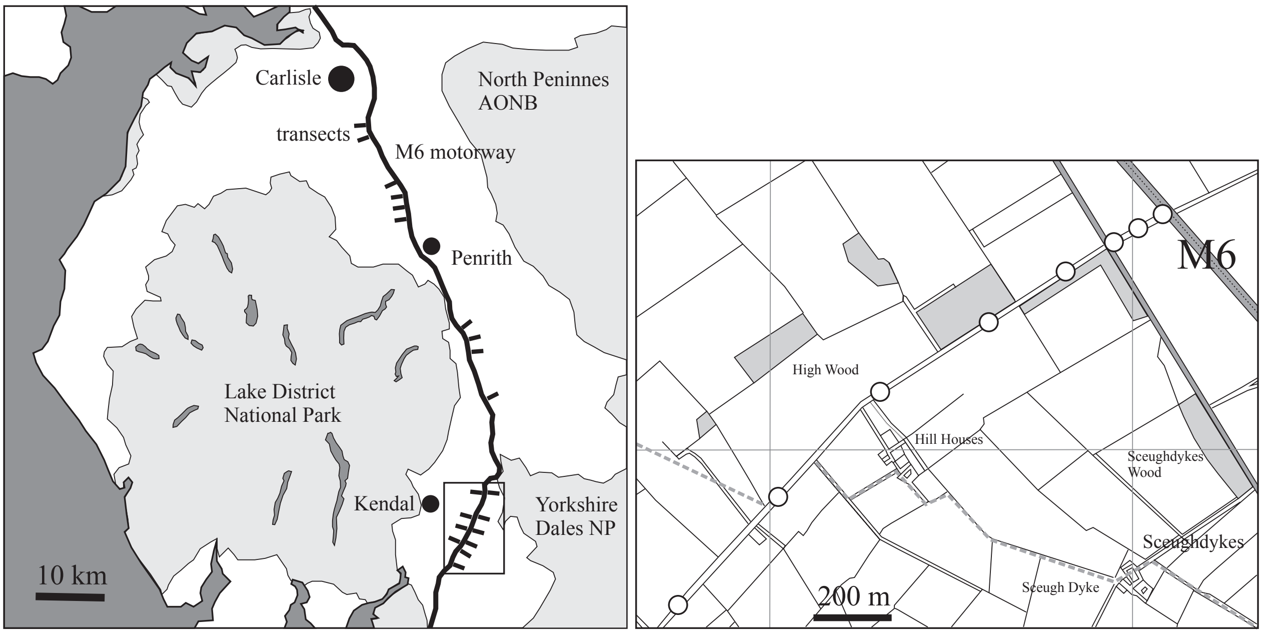

Fig. 1. Map of Cumbria, UK, (left) showing section of the M6 with transect routes (black markers). Boxed markers indicate transects used in 2009, all transects were used in 2010 (dark grey = Irish Sea, light grey = protected areas: NP (National Park)/AONB (Area of Outstanding Natural Beauty). An example of a transect route (right) with spot checks marked (white areas = open fields, light grey areas = woodland). Crown Copyright/database right 2010, an Ordnance Survey/EDINA supplied service.

Table 1. The criteria used to classify spot check habitat types

Grade	Habitat type
1	Fence or wall lining road/path and open fields beyond
2	Hedges/shrubby verges lining road/path and open fields beyond
3	Intermittent medium trees/bushes lining road/path and open fields beyond
4	Intermittent tall trees lining road/path and open fields beyond
5	Continuous tall tree cover lining road/path with woodland and/or open fields beyond

Traffic noise was measured at each spot check by recording for one minute directly onto an Edirol recorder with a sample rate of 48 kHz. Siemers & Schaub (2011) have shown that autobahn traffic noise > 25 kHz is negligible > 25 m from the road. Noise recordings were later analysed using GOLDWAVE digital audio editing software (http://www.goldwave.com) to produce a root mean square level for each recording. This was then converted into decibels and the relative loudness of recordings was compared.

Analysis of echolocation calls was carried out using Batsound Pro software (http://www.batsound.com). The mp3 files were converted to WAV format using GOLDWAVE. Bat species were identified from the sonograms of their calls using call shape, end frequency and the maximum energy frequency or 'F_{maxe}'(Parsons & Jones 2000). In most cases, bats of the genera *Myotis* and *Nyctalus* could not be identified to the species level because of similarity in call structure (Parsons & Jones 2000) and were therefore recorded to the genus level only. We know from capture data of our own and other researchers that *Myotis nattereri*, *M. mystacinus* and *M. brandtii* are widespread in the area and likely to be in our *Myotis* group. *M. daubentonii* is also present in the area, but unlikely to have been recorded on our transects because it is confined almost exclusively to water courses. *Nyctalus noctula* is widespread but *Nyctalus leisleri* is rare, so most recordings were probably *N. noctula*. A small number of *Pipistrellus* calls were classified only to genus level, because of the overlap of call parameters of *Pipistrellus pipistrellus* and *Pipistrellus pygmaeus*. *Plecotus auritus* is also known to be present in the area, but will be under-recorded because of its low intensity echolocation call (Parsons & Jones 2000), and too few recordings were made for meaningful analysis for this species. The number of 'bat passes' was used as a measure of bat activity. A single bat pass was defined as one or more clearly recognisable echolocation calls from a single species, separated from the next pass by a gap of at least 1s. Measuring bat activity provides a good surrogate for bat density in the study area because of the fidelity of bat colonies to roosting and foraging sites (e.g. Senior, Butlin & Altringham 2005).

A multiple regression model was built to investigate the relationship between bat activity and distance from the road and, at the same time, examine the effects of other variables (time, habitat and climate) that could influence bat activity and hence the relationship. This was performed by fitting appropriate generalised estimating equations (GEE) using the *geeglm* function from the library *geepack* (Halekoh, Højsgaard & Yan 2006) in the R program, version 2·12·1 (R Development Core Team 2006). This approach was used to account for within cluster correlation that violates the independence assumption in conventional regression analyses and leads to type 1 errors. GEE's adjust regression coefficients and variance to account for spatially and temporally correlated data, common in ecological research. In this study, a first-order autoregressive model AR(1) was used to account for auto-correlation between spot checks conducted along the same route and on the same night. Transect routes were assumed to be independent. The jackknife estimation principle was used to avoid bias because of small number of clusters (< 30). The number of total bat passes was transformed to a log(count + 1) to account for the presence of zero counts and large variations in activity observed between transect routes that resulted in heterogeneity. A Gaussian distribution with an identity link was used which gave the best fit to the data.

Explanatory variables used in the model were distance from the road, time after sunset and habitat type. All two-way interactions were not significant and were excluded in the model selection process. Climatic variables were excluded from the analysis as variation was found to be significantly greater between nights and across the season than within nights so were accounted for by modelling the nightly variation in the dependence structure. Noise measurements were also excluded as these were considered irrelevant because of their short operating range. Backward selection and Wald χ^2 tests were used to assess the overall significance of variables and produce the minimum adequate model. Plots of residuals were examined to check for normality and assess the appropriateness of the fitted model. The low abundance of most individual species or genera in this study did not allow for species-specific analysis, except for that of *P. pipistrellus*, for which the above model was repeated.

For the number of bat species/genera groups, a proportional odds ordinal logistic regression was performed using the *lrm* function from the library *Design* in the R program (Harrell 2009). The four identifiable groups of species/genera were treated as ordinal categorical variables defined as 1 (0 species/genera), 2 (1 species/genus), 3 (2 species/genera) and 4 (3 or 4 species/genera). A robust Huber-White 'sandwich' covariance estimator (Huber 1967) was applied using the R function *robcov* to correct for auto-correlation because of clustered samples (Harrell 2006), with clusters defined as in the GEE above. Explanatory variables were input as above and Wald χ^2 tests used for model selection. Appropriate graphical methods and statistical tests (χ^2 Test of Parallel Lines) were used to ensure model assumptions were met (Harrell 2006).

The results for the 2010 study are presented below and are supplemented by those from 2009 where appropriate to show the consistency observed over the 2 years of study. The less intensive study in 2009 was carried out to determine whether a more rigorous investigation in 2010 was justified.

Results

OVERALL EFFECTS

A total of 3407 bat passes were recorded during the study. The significant variables in the GEE minimum adequate model for the transformed number of all bat passes were distance from the road, time after sunset and habitat type (Table 2). The independent effects of each variable predicted by the model are shown in Fig. S1 in Supporting Information. Distance from the road was found to have a significant positive effect on the number of bat passes ($\chi^2 = 19{\cdot}26$, d.f. = 1, $P < 0{\cdot}0001$), as was habitat type, ($\chi^2 = 22{\cdot}5$, d.f. = 4, $P < 0{\cdot}001$). The results of the model show that there was a significant difference in bat passes between habitat type 1 and types 4 and 5 (Table 2). Time after sunset was found to have a significant negative effect on the number of bat passes ($\chi^2 = 5{\cdot}4$, d.f. = 1, $P < 0{\cdot}05$). Similar results were obtained in 2009 with almost identical coefficient estimates (Table 2), although habitat type was not found to be significant during the model selection process.

Although habitat type varied with distance from the road there was not a simple relationship of increasing habitat 'quality' with distance (See Table S1 Supporting Information). The preferred habitat, grade 5, was actually found to be more frequent in proximity to the road, whereas the least favourable habitats, grades 1 and 2, were found to be more frequent at spot checks away from the road, showing that variation in habitat, as assessed, did not bias the results.

Table 2. Results from the GEE analysis modelling log (1 + number of bat passes) as a function of distance from the road (m), time after sunset (min) and habitat type. All habitat analyses are in comparison with the habitat grade 1 as a reference point

	2010 Bat passes (all species)		2009 Bat passes (all species)	
Coefficients	Estimate	SE	Estimate	SE
Intercept	1·3526***	0·26689	2·4812	0·27911
Distance (m)	0·0008***	0·00017	0·0008***	0·00019
Time (min)	−0·0070*	0·00286	−0·0128***	0·00315
Habitat 2	0·4438	0·34835	–	–
Habitat 3	0·4215	0·21509	–	–
Habitat 4	0·8739***	0·22473	–	–
Habitat 5	1·2909***	0·33072	–	–
Correlation parameter	0·238	0·0857	0·0109	0·0704
Scale parameter	1·63	0·140	1·08	0·054

*$P < 0{\cdot}05$, ***$P < 0{\cdot}001$. GEE, generalised estimating equations.

Although bat activity was negatively correlated with time after sunset and positively correlated with habitat type, the effect of distance from the road was constant throughout the night and across different habitat types, with an approximate 3·5-fold increase in the number of bat passes between 0 and 1600 m from the road, when other significant variables were held constant (Fig. 2).

SPECIES-SPECIFIC EFFECTS

The species/genera detected during the study were *P. pipistrellus*, *P. pygmaeus*, *Nyctalus* and *Myotis*. The results for *P. pipistrellus* are consistent with those above and are given in Appendix S1. Although statistical analyses were not possible for the other individual species or genera, the trend appears to be for an increased number of bat passes with distance from the road (Fig. 3).

EFFECT ON THE NUMBER OF SPECIES

The final ordinal logistic regression model was found to be significantly better than the null model ($\chi^2 = 24{\cdot}9$, d.f. = 2, $P < 0{\cdot}0001$), and model assumptions of parallelism were met ($\chi^2 = 8{\cdot}88$, d.f. = 6, $P > 0{\cdot}05$). The results showed that the number of species/genera increased with distance from the road ($\chi^2 = 5{\cdot}59$, d.f. = 1, $P < 0{\cdot}05$) and habitat type ($\chi^2 = 21{\cdot}42$, d.f. = 1, $P < 0{\cdot}0001$). The log odds of observing a greater number of species at 1600 m from the road were found to be 2·5 times higher than at 0 m, and the log odds of observing a greater number of species in habitat types of grade 5 were found to be 6·2 times higher than in those of grade 1. The model also predicts a differential effect of distance from the road on the probability of observing a greater number of species/genera for each habitat type (Fig. 4). Lower habitat grades show a greater increase in probability for more species/genera with distance from the road.

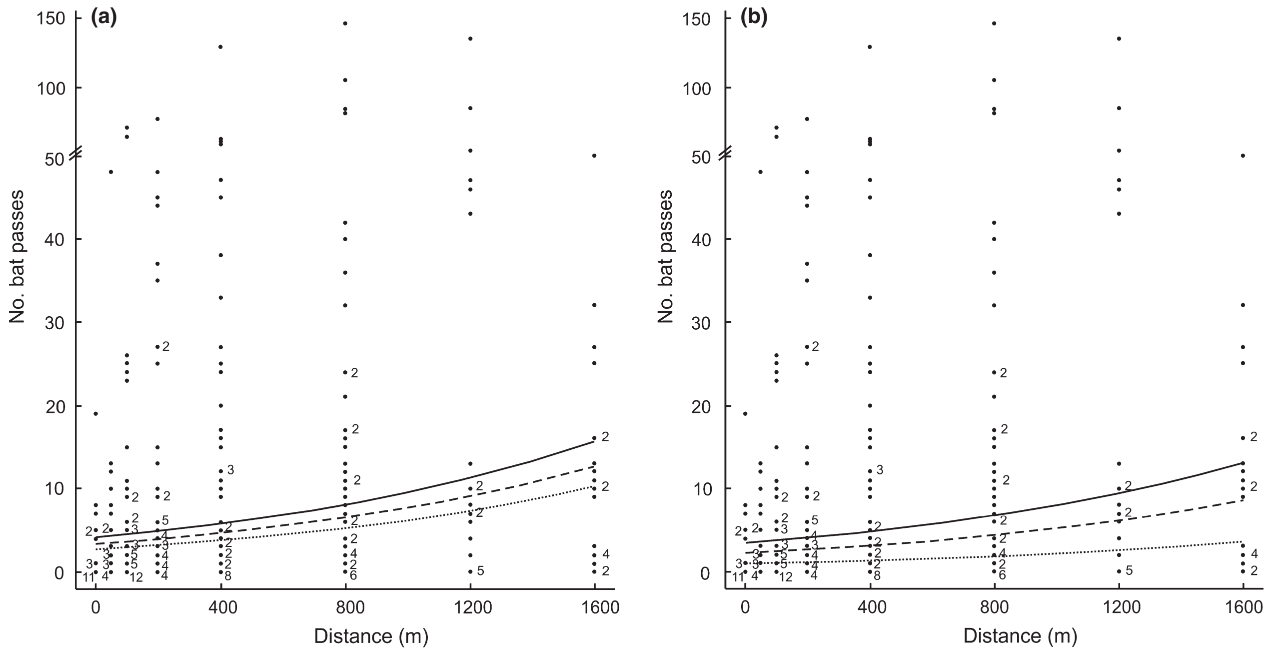

Fig. 2. Model predictions (a) The effect of distance on the number of bat passes at varying times after sunset, with habitat type held constant at grade 5, (solid line = 30 min, dashed line = 60 min, dotted line = 90 min). (b) The effect of distance on the number of bat passes for different habitat types, with time held constant at 55 min after sunset, (solid line = habitat grade 5, dashed line = habitat grade 4, dotted line = habitat grade 1). Note the change in y axis scale at 50. Numbers indicate number of replicate points.

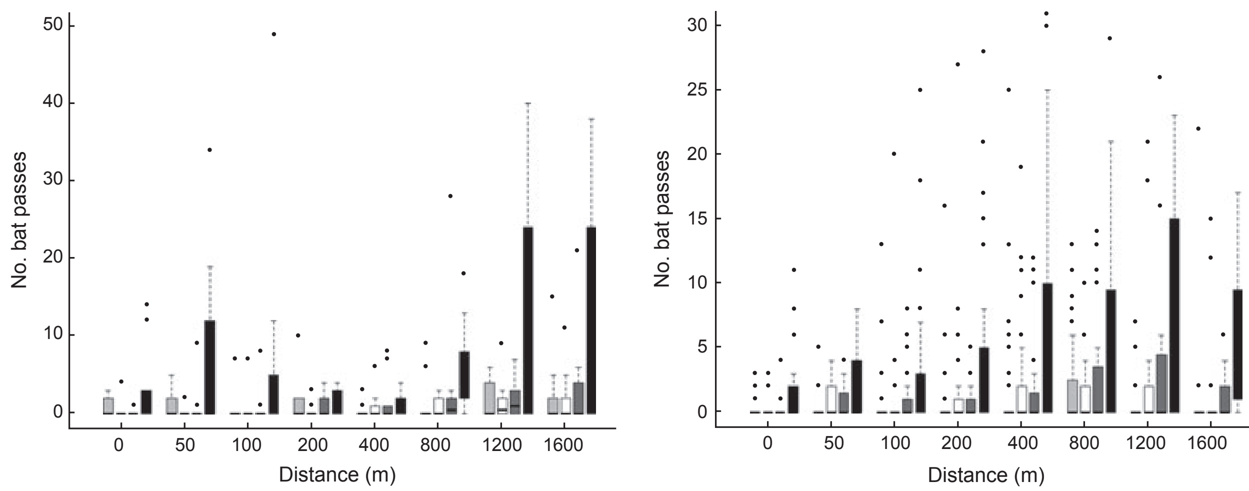

Fig. 3. Box plot of bat passes for each species at each distance from the road, showing median with lower and upper quartiles, for 2009 data (left) and 2010 data (right) (Black = *Pipistrellus pipistrellus*, dark grey = *Pipistrellus pygmaeus*, light grey = *Nyctalus* spp., white = *Myotis* spp.) (2010 data have been cropped for clarity; see Fig. 2 for full range of data points).

NOISE EFFECTS

Traffic noise levels were not included in the GEE models as they were considered to be irrelevant to the scale of this study because of the short operating ranges observed. Noise levels decreased significantly with distance from the road (Kruskal–Wallis, $\chi^2 = 93{\cdot}96$, d.f. = 44, $P < 0{\cdot}0001$), but 89% of the change occurred in the first 50 m and no significant variation was found beyond 100 m.

Discussion

THE EFFECTS OF TIME AND HABITAT

Despite the short duration of the transects, time after sunset was found to have a significant effect on bat activity. This may reflect greater mobility following emergence, before bats settle to forage at their regular sites. Potential bias was accounted for by performing transects in opposite directions, and the effect

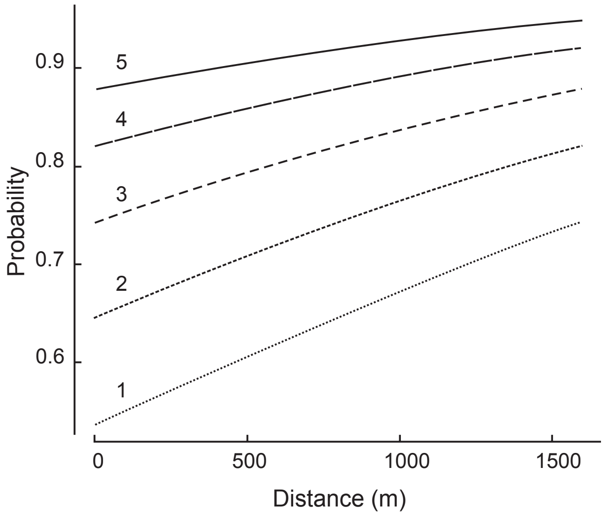

Fig. 4. Probability of observing an increase in one bat species/genus at varying distances from the road, and in different habitat types (grades labelled 1–5), based on the predictions from the ordinal logistic regression model.

of proximity to the road was consistent at all times. Our aim was to minimise habitat heterogeneity to minimise bias caused by habitat preference. However, although large areas of woodland and water bodies were avoided, some variation in habitat was inevitable, as reflected in the habitat grading system used. As expected, bat activity and diversity increased with the increase in the height and continuity of tree and hedgerow cover along transects. This is supported by many other studies (Walsh & Harris 1996a,b; Russ & Montgomery 2003). Also, the probability of observing more species groups away from the road increased most dramatically with distance for low habitat grades, suggesting that there are some subtle interactions between road effect, habitat and species that are worth further investigation.

ROAD EFFECTS

Despite a significant dependence on time and habitat type, we detected a marked independent decrease in bat activity and diversity in proximity to the road. This decline, to a distance of at least 1·6 km either side of the road, which for activity was consistent over 2 years, shows that major roads have a very significant impact on bat activity.

Possible reasons for lower activity and diversity closer to the road include habitat degradation because of light, noise and chemical pollution, a barrier effect or increased mortality because of road kill. Although habitat quality will affect bat activity, habitat type as we assessed it (in terms of the height and continuity of tree and hedge cover) is not responsible for the lower bat activity found close to the road in this study. Noise pollution also cannot explain the result, because noise levels were low and unchanging beyond 100 m. Studies on the gleaning greater mouse-eared bat *Myotis myotis* (Schaub, Ostwald & Siemers 2008; Siemers & Schaub 2011) show that even species that hunt by listening for prey-generated noise are not likely to be affected by roads more than 100 m away. Light pollution was not addressed in this study as the road sections studied were unlit. However, any effect of light pollution from road and vehicle lights is also likely to operate over short distances, because of the inverse square relationship between distance and light intensity. Road developments can disrupt local hydrology, and polluted run-off may degrade wetland foraging habitats (Hellawell 1988; Highways Agency 2001). Automobile exhaust gases close to a road have been shown to be associated with a decline in arthropod diversity and abundance (Przybylski 1979). However, this effect is also unlikely to be important over long distances: the effects on invertebrates of lead and other metals from cars are limited to 30 m from road sides (Motto *et al.* 1970; Muskett & Jones 1980). The many processes that may be degrading roadside habitats need further study, but none of those discussed are likely to explain changes in bat activity over 1·6 km.

However, reduced activity over large distances can be explained by the combination of a barrier effect and increased mortality because of roadkill. The home ranges of temperate insectivorous bat species typically extend 0·5–5 km from their roost (e.g. Bontadina, Schofield & Naef-Daenzer 2002; Senior, Butlin & Altringham 2005; Davidson-Watts, Walls & Jones 2006; Smith & Racey 2008), with most species showing high fidelity to roosts, foraging sites and commuting routes between them (e.g. Racey & Swift 1985; Entwistle, Racey & Speakman 2000; Senior, Butlin & Altringham 2005). A major road built close to a nursery roost, and acting as a barrier to bats, will cause the colony home range to be reduced through both destruction of habitat and severance of commuting routes. Bats will be forced to forage in smaller areas or commute greater distances, either away from the road to find new foraging sites or to find 'safe' crossing points along the road to commute to their original foraging sites. Mortality from roadkill is likely to be high because most species cross at heights that put them in the paths of vehicles (Verboom & Spoelstra 1999; Altringham 2008; Gaisler, Rehak & Bartonicka 2009; Russell *et al.* 2009). These effects will reduce the reproductive output of nursery colonies (e.g. Tuttle 1976; Kerth & Melber 2009) and may force colonies to relocate, both leading to a fall in bat density near to the road, as observed in this study. In long-lived animals like bats, both reduced reproductive success and increased mortality will have a profound effect on local colony size and overall population size (Sendor & Simon 2003; Papadatou *et al.* 2011).

There is considerable evidence to suggest that roads act as barriers. Throughout our study only three bats were observed flying over the road, all *Nyctalus* species at heights above 20 m. *Nyctalus* species are known to fly high and to forage in open spaces (Kronwitter 1988), which is likely to make them less susceptible to the barrier effects of roads and collision mortality. The absence of other species of bat flying over the road suggests that the severance of linear elements by the road may have caused the abandonment of previous flight lines. Indiana bats *Myotis sodalis* reverse their flight paths and exhibit anti-predator avoidance behaviour in response to approaching vehicles (Zurcher, Sparks & Bennett 2010). A recent study in Germany provides evidence for a strong barrier effect of a 4–5 lane road on Bechstein's bat, *M. bechsteinii*, a gleaning species (Kerth & Melber 2009). Female Bechstein's bats foraging close to the road had smaller foraging areas and lower reproductive success. Given the scale of the effects on bat activity in this study, it is highly likely that barrier and edge effects are negatively affecting the demographics and distribution of local bat populations in proximity to major roads. Similar effects have been found in other vertebrates. Reijnen & Foppen (1994) and Foppen & Reijnen (1994) showed that a decreased density of willow warblers *Phylloscopus trochilus* up to 200 m from a major highway was because of the negative influence of the road on population sizes, with reduced breeding success and increased emigration of territorial males. Studies on breeding grassland birds revealed a decrease in density of seven out of 12 species, with disturbance distances up to 3530 m from the busiest roads (50 000 vehicles per day), with collision mortality being a major contributor (Reijnen, Foppen & Meeuwsen 1996).

SPECIES EFFECTS

The number of species recorded was found to decline in proximity to the road, which suggests that some species may be more affected by roads than others. Kerth & Melber (2009) found stronger effects of a major road on habitat use for the gleaning bat species *M. bechsteinii* than for *Barbastella barbastellus*, which forages in more open spaces. It is therefore possible that the foraging ecology of gleaning and woodland species in this study (e.g. *Myotis*) makes them more susceptible, whereas high fliers that are known to feed in open spaces (e.g. *Nyctalus*) may be less affected. A correlation between the strength of a barrier effect of a road and the foraging ecology of rainforest birds has also been found (Laurance, Stouffer & Laurance 2004). Although species-specific analyses were not possible, the significant positive effect of distance from the road observed for *P. pipistrellus* was accentuated by the addition of the other species groups to the analysis. Given that *P. pipistrellus* is a generalist species (Vaughan, Jones & Harris 1997; Nicholls & Racey 2006), likely to be more adaptable to habitat change and degradation, these effects are likely to be even greater for specialists such as *Myotis* and *Plecotus* species, explaining the increased species richness away from the road.

CONCLUSIONS AND RECOMMENDATIONS

This study reveals low bat activity and diversity on either side of a well-established major road, showing that roads have a long-term negative impact on bat populations. The scale of this impact indicates a barrier effect. Mitigation can remove the barrier and/or remove its impact. To remove the barrier, we must make roads permeable and safe. Crossing points must connect effectively with known commuting routes to reduce the risk of abandonment and take bats safely under or over roads. Appropriate structures will be site specific and determined by local geography. Crossing structures have been installed throughout Europe in recent years, but because of inadequate and unfocused monitoring, there are no data to assess their effectiveness at either individual or population level (Altringham 2008). We must assess the effectiveness of current structures and build only those shown to work. To reduce the effect of the barrier, we should improve foraging habitat for bats within 1 km of the road. Demographic effects will be slow to reveal themselves, and monitoring over 10 years may be necessary to provide an insight into the full effects of road developments and mitigation on bat populations.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. The independent effects of significant variables on bat activity.

Table S1. The frequency of habitat types with distance.

Appendix S1. Results for *Pipistrellus pipistrellus*.

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