Roads as barriers to movement for hedgehogs

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Summary

1. Movements of hedgehogs, Erinaceus europaeus L., were analysed in relation to roads by recording their nocturnal foraging trajectories in urban areas adjacent to major road systems. Four male and four female hedgehogs at each of two sites were each tracked over five replicate trajectories of more than 3 h, using radio-telemetry and direct observation.

2. Frequency of road crossings and use of habitat were compared to simulated random trajectories. For each observed trajectory, 100 trajectories were simulated with the same distribution of speeds as observed, but with random direction.

3. Observed trajectories had lower rates of crossing large but not small roads than simulated, indicating that hedgehogs treat large roads as barriers during nightly foraging activities. Most hedgehogs were never observed to cross roads, whereas almost all simulated trajectories did cross both large and small roads.

4. Crossing behaviour differed by site, but not by sex.

5. Roads and road verges had the lowest rank in a habitat preference analysis at both sites, while playing fields, gardens and urban areas were preferred habitats. These results are discussed in relation to the regional scale preference for urban areas, and the attraction to road verges while dispersing, shown by hedgehogs.

Key-words: Ecological barrier, Monte Carlo simulation, ranging behaviour, small mammal

Introduction

As conduits for human vehicular traffic, roads represent major barriers to the movements of many organisms and a source of mortality across taxonomic groups, from seeds and invertebrates through to birds and large mammals. Notwithstanding, many organisms cross roads and their verges are also corridors to some species (Forman 1998; Forman & Alexander 1998; Spellerberg 1998). Continuous stretches of grass verge can act as dispersal corridors for mammals that use habitat edges, including hedgehogs Erinaceus europaeus L. (Doncaster, Rondinini & Johnson 2001).

Hedgehogs are among the most commonly encountered victims of road traffic wherever their populations coincide with road networks. In the Netherlands it is estimated that between 113 000 and 340 000 are killed each year on roads (Huijser & Bergers 1998); in Belgium between 230 000 and 350 000 per year (Holsbeek, Rodts & Muyldermans 1999). Throughout Western Europe, road deaths occur at an overall annual rate of approximately 1–2 per kilometre of road (Huijser, de Vries & Bergers 1998). Hedgehog populations can reach high densities in urban areas, nevertheless, and the road mortalities may constitute a small fraction of population sizes (e.g. Huijser, de Vries & Bergers 1998; Reeve & Huijser 1999).

Do roads act as barriers to the foraging activities of hedgehogs? Do hedgehogs tend to avoid crossing roads while foraging? We have found no adequate test of these questions in the literature, although hedgehogs are recognized to be a good model for exploring the effects of habitat fragmentation caused by human infrastructure on the movement of individuals between populations (Becher & Griffiths 1998). The few studies that have directly tested individual-level hypotheses about barriers to movements have relied on capture–mark–recapture techniques (e.g. Joyce, Holland & Doncaster 1999 on carabid beetles; Mader 1984 on carabid beetles and forest-dwelling mice; Mader, Schell & Kornacker 1990 on carabid beetles and spiders; Richardson et al. 1997 on small mammals). For larger animals such as hedgehogs, individual trajectories can be monitored by continuous sampling with radio telemetry, and responses to roads can be measured from Monte Carlo simulations in association with GIS (geographical information systems).

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Here we report on the movement behaviours of hedgehogs tagged with transmitters, in replicate segments of undisturbed nightly foraging. These segments were observed according to a protocol that allowed us to test the null hypothesis that roads are traversed at the same frequency as random expectation. The technique we develop here can be extended straightforwardly to test such questions on other species and different landscape structures.

**Materials and methods**

**FIELD OBSERVATIONS OF FORAGING TRAJECTORIES**

This study was conducted after the end of the breeding season and before the start of winter hibernation. Two sites with abundant hedgehogs were located in Southampton city, Hampshire, separated by 11 km and both adjacent to motorways. The sites were Thornden (grid reference SU 449 217) and Redbridge (grid reference SU 377 136), with habitat configurations shown in Fig. 1. Both sites were composed of a large school playground and an abutting motorway, surrounded by houses. At each site, 4 adult males and 4 adult females were located by torchlight while they were foraging on short-grass fields (all ≥1-year-old, mean mass 973 ± 62 g SE). After capture by hand and weighing, each was tagged with a radio-transmitter (Biotrack, Wareham, Dorset: 7 g on acrylic mount) and released immediately. Hedgehogs at Thornden were tracked from 1 to 17 September 1999; those at Redbridge from 21 September to 15 October 1999. Each hedgehog was tracked on five replicate segments of its nightly foraging range within a period of 6–13 days (except for one female at Redbridge for which only a single trajectory was recorded). Each segment lasted an average of 3 h 12 min ± 5 min (mean ± SE, N = 76 trajectories on all animals), during which the individual was located on average 11·1 ± 0·2 times (N = 896 locations on all animals). The interval between radio-locations was 10–20 min, depending on the time needed to locate other hedgehogs (usually 2–4 hedgehogs were tracked simultaneously). Tracking was done without disturbing the subjects, and radio-locations were confirmed by direct observations where possible under ambient light.

All fieldwork was done under UK Home Office Licence PPL: 30/00043.

**ANALYSIS OF FORAGING TRAJECTORIES**

For each observed trajectory, 100 random walks from the same start point were simulated, each with the same number of locations and the same frequency distribution of distances between consecutive points as the observed trajectory, and each constrained to finish as close as or closer to the start point than the last observed location. The component of randomness was only in the direction taken from one location to the next and in the order of consecutive distances. Any simulated locations that fell in impossible places, such as inside buildings, were shifted to the nearest possible location. This design simulated the displacements a hedgehog could perform over a time span equal to each observation period, starting from the observed

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**Fig. 1.** Radio locations on hedgehogs at the two study sites, and minimum convex polygon surrounding all simulated locations. All of the barriers shown on the map could either be crossed (roads were unfenced, and garden fences were easily crossed by hedgehogs) or circumvented (all buildings were discrete units). The habitat category of Other included in the simulated MCP at Thornden contained only 2% of the simulated locations of two hedgehogs. For this reason Other was pooled with the abutting motorway in the habitat analysis for this site.
starting point and with the same site fidelity as the observed animal. As with observed trajectories, simulated trajectories were linear interpolations of paths and thus did not represent the actual route taken from one point to the next. 

Trajectories were analysed with respect to roads and other habitats after digitizing habitat structure at the two sites from maps produced by the Ordnance Survey (scale 1:25 000) with a GIS package (vector digitizing software CartaLinx, raster software IDRISI, Clark Laboratories, Worcester, MA).

**TYPES OF ROADS**

Asphalt roads were divided into categories of small (<4-m wide, mostly access roads), large (24-m wide, mostly through roads and trunk roads), and motorway (2–3 traffic lanes and recovery lane in each direction, central reservation and scrub verges). A further category, blind alley, was present in residential housing where short extensions of small road ended without connecting to other roads. Motorway traffic was typically 4–5 cars min⁻¹ during the middle portion of the night when hedgehogs were being followed; other roads had infrequent traffic at this time. We calculated the rate of crossing each road category per kilometre of trajectory for each observed trajectory, and for the 100 replicate simulations of that observed trajectory. Median observed and simulated rates were then calculated per individual. The difference between these observed and simulated medians then provided the dependent variable for two-factor analysis of variance on Site (random factor) and Sex. Residuals were tested for normality (Anderson–Darling test) and homogeneity of variances (Levene’s test), and were not found to depart significantly from these assumptions.

Significant deviations of observed trajectories from simulated random expectation were sought with a paired-sample permutation test (Siegel & Castellan 1988), rather than by parametric analysis of variance, because of the large number of zeros in observed crossing rates.

**HABITAT CLASSIFICATION**

Five habitat categories were considered: Road (including road verges), Urban (buildings and synthetic surfaces), Garden (house gardens only), Playing Field and Grass (including grass patches abutting roads in residential areas), and Woodland. Separate analyses were performed for the two study sites, since the Woodland category used by the Thornden hedgehogs was unavailable at Redbridge.

The proportions of observed locations in each habitat category were compared to a measure of habitat availability given by proportions of simulated locations in each habitat category. The compositional analysis of Aebischer, Robertson & Kenward (1993) was used to rank habitat categories according to preference, based on the difference between observed and simulated use of habitat. Overall habitat rankings were obtained for pooled individuals within sites, and for each individual.

**Results**

Hedgehogs each covered an area of 5·0 ± 0·7 ha (mean ± SE), measured by minimum convex polygon (MCP) from the sum of radio locations. Area did not vary significantly by Site, Sex or the interaction of Site and Sex. Hedgehogs moved a mean of 380 ± 30 m per trajectory (maximum 1240 m for male 3 at Thornden), at a mean speed of 111 ± 7 m h⁻¹ (maximum 340 m h⁻¹ for male 3 on the same night). Trajectory lengths tended to be longer at Thornden than Redbridge (\(F_{1,12} = 4.83, P < 0.05\)), principally because hedgehogs at Redbridge were tracked for slightly shorter segments of the night due to being more widely dispersed. Apart from this effect, movement parameters did not vary by Site or Sex.

**TYPES OF ROADS**

Eight of the 16 hedgehogs did not cross any category of road, although roads were crossed by the simulated trajectories of all 16 hedgehogs. Overall, hedgehogs were observed to cross roads in 18 of 76 trajectories (up to six times per trajectory). With more than 75% of observed trajectories never crossing roads of any type, the median (and interquartile range, IR) was 0·0 (0·0–0·0 IR) crossings per km of observed trajectories. This compares with 0·36 (0·08–0·77 IR) crossings per km of simulated trajectories. None of the observed trajectories crossed motorways or large roads, compared to an expected rate of 0·22 (0·08–0·49 IR) and 0·44 (0·09–0·56 IR) per km of simulated trajectory, respectively (Fig. 2). The medians of zero with large interquartile ranges for small roads and blind alleys at Thornden (Fig. 2) reflect the result that more than half of the individuals were never observed to cross these road types, whereas a few individuals crossed them frequently. The probabilities that the crossing rates did not differ between observed and simulated samples are given in Table 1, which shows a general trend of decreasing probability with size of road when sites are pooled. Except for a site effect on large roads (\(F_{1,12} = 5.09, P < 0.05\)), deviations of observed from simulated crossing rates did not vary by Site or Sex.

**HABITAT CLASSIFICATION**

At both sites, habitat use given by the distribution of observed locations departed significantly from availability given by the distribution of simulated locations (Thornden: \(\chi^2(4) = 22.71, P < 0.001\) for five habitat categories; Redbridge: \(\chi^2(3) = 10.14, P < 0.02\) for four habitat categories). Road was the least preferred habitat at both sites. Road was significantly avoided.
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In individual level analyses, Road was the lowest ranked habitat (rank 5) for 4 of the 8 hedgehogs at Thornden, while it ranked 1, 2, 3 and 4 for one each of the others. At Redbridge, Road was the lowest ranked habitat (rank 4) for 6 of the 8 hedgehogs, while it ranked 1 and 3 for the other two. Those individuals with a high preference for Road tended to make relatively heavy use of motorway verge habitat, where they had day rest sites.

Discussion

Our field test has shown an overall significant tendency for both sexes alike to avoid crossing roads, with avoidance increasing in proportion to road width. Most hedgehogs made little use of road verges compared with playing fields and gardens. The difference between sites in habitat preference (Table 2) probably reflects a general difference between the two sites in patterns of movement, with most hedgehogs at Thornden foraging in a large school playing field and resting during daytime in the surrounding gardens, and those at Redbridge moving less frequently from gardens to playing field. Seasonal effects could have contributed to these site differences, since Redbridge was studied after Thornden, and within a month of the onset of hibernation for some individuals (Reeve 1994).

The absence of motorway crossings and the low frequency of crossing large roads, among individuals having roads within their foraging ranges, suggests that hedgehogs experience fragmentation of the urban landscape by these linear features. These findings are consistent with observations by others on movements of insects (Joyce et al. 1999), amphibians (Fahrig et al. 1995) and voles (Swihart & Slade 1984; Merriam et al. 1989; Richardson et al. 1997). Forman & Alexander (1998) have reported that a road 6–15 m wide can cause a tenfold decrease in the probability of small mammals moving between two habitat patches. Many hypotheses have been proposed to explain road avoidance by wildlife, including traffic noise and vibration, and roadside lighting (review in Forman & Alexander 1998). We have observed two test hedgehogs crossing blind alleys under sodium street lights and no traffic, in separate instances between 0100 and 0300 h. They both ran with legs extended to raise the belly above the ground, in contrast to a lower posture when foraging (which can also involve running from one prey to the next). Similar road-crossing behaviour has been reported for hedgehogs by Reeve (1994) and Mulder (1999), suggesting that a reluctance to cross roads may reflect an aversion to the synthetic surface itself, perhaps compounded by the exposure and illumination.

Although roads are a cause of mortality for animals in general (e.g. amphibians and reptiles (Fahrig et al. 1995; Ashley & Robinson 1996), birds (van der Zande, ter Keurs & van der Weijiden 1980), and for hedgehogs in particular (Reeve & Hujsjer 1999), the very low overall number of road crossings we observed among the test hedgehogs supports the hypothesis that most of them were not at risk most of the time. By the same token, local populations do appear to be bounded by large roads and motorways, though not by smaller roads. Our observations are consistent with the population viability analysis of Bergers & Nieuwenhuizen (1999) on 30 hedgehog populations in the Netherlands.
predicting that road fencing would dramatically reduce the number of viable populations and the total area occupied by them. In fact our test hedgehogs did cross small roads, suggesting that the drawback of some of the actions aimed at reducing hedgehog mortality on roads could be an increased isolation of subpopulations.

Field experiments by Doncaster et al. (2001) have shown that some large roads do not present barriers to hedgehogs dispersing out of unfavourable areas (also inhabited by badgers which predate hedgehogs: Doncaster 1992, 1993). Indirect evidence from analysis of molecular microsatellites suggests that the genetic flow between subpopulations is large enough to avoid genetic differentiation (Becher & Griffiths 1992). Male hedgehogs show a greater ranging behaviour than females and are known to outnumber them in road casualties in the breeding season (Reeve & Huijser 1999). Although these results appear to conflict with the low number of road crossings performed by our test hedgehogs, they relate only to dispersals and movements in road casualties (Reeve & Huijser 1998). Male hedgehogs show a greater ranging behaviour than females and are known to outnumber them in road casualties in the breeding season (Reeve & Huijser 1999). Although these results appear to conflict with the low number of road crossings performed by our test hedgehogs, they relate only to dispersals and movements in road casualties (Reeve & Huijser 1998). Male hedgehogs show a greater ranging behaviour than females and are known to outnumber them in road casualties in the breeding season (Reeve & Huijser 1999).

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