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Nocturnal ranging behaviour of urban hedgehogs, *Erinaceus europaeus*, in relation to risk and reward

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Urban areas have both positive and negative influences on wildlife. For terrestrial mammals, one of the principal problems is the risk associated with moving through the environment while foraging. We examined nocturnal patterns of movement of urban-dwelling hedgehogs in relation to (1) the risks posed by predators and motor vehicles and (2) nightly weather patterns. Hedgehogs preferentially utilized the gardens of semidetached and terraced houses. However, females, but not males, avoided the larger back gardens of detached houses, which contain more of the habitat features selected by badgers. This difference in the avoidance of predation risk is probably associated with sex differences in breeding behaviour. Differences in nightly movement patterns were consistent with strategies associated with mating behaviour and the accumulation of fat reserves for hibernation. Hedgehogs also differed in behaviour associated with the risks posed by humans; they avoided actively foraging near roads and road verges, but did not avoid crossing roads per se. They were, however, significantly more active after midnight when there was a marked reduction in vehicle and foot traffic. In particular, responses to increased temperature, which is associated with increased abundance of invertebrate prey, were only observed after midnight. This variation in the timing of bouts of activity would reduce the risks associated with human activities. There were also profound differences in both area ranged and activity between years which warrant further investigation.

Urbanization is widely viewed as deleterious for wildlife (Paul & Meyer 2001; McKinney 2006; Grimm et al. 2008). Yet some species may be more abundant and/or have higher rates of survival and reproduction in urban areas because of, for example, the absence or low abundance of some types of predators (Cypher & Frost 1999), an increase in the availability of food or other resources supplied deliberately or accidentally by humans (Baker et al. 2000; Fuller et al. 2008; Jones & Reynolds 2008; Robb et al. 2008a, b; Davies et al. 2009) or a reduction in levels of human persecution (Harris & Smith 1987). Despite such potential advantages, however, one of the principal problems faced by terrestrial mammals is simply moving through the urban environment while minimizing the risks associated with natural and man-made mortality and disturbance.

The European hedgehog is a cursorial insectivore weighing less than 1.5 kg that is found throughout lowland Britain; it is active from April to September and hibernates from October to March (Morris & Reeve 2008). Hedgehogs are opportunistic feeders, primarily consuming invertebrate prey such as molluscs, beetles and earthworms (Morris & Reeve 2008). Counts of casualties on roads have declined markedly in several regions during the last decade (Anon 2008), potentially indicating a decline in populations in those areas. Possible factors for this decline include: predation by badgers, *Meles meles* (Young et al. 2006); an increase in road density and road traffic; increased use of agricultural chemicals, including insecticides, molluscicides and anticoagulant rodenticides (Dowding et al. 2010); and habitat changes associated with modern agricultural practices, such that hedgehogs in Britain now appear to be more common in areas of human habitation than agricultural habitats (e.g. Young et al. 2006).

Within urban areas, the nightly movements of hedgehogs are potentially affected by two principal hazards, badgers and various human activities, and by the effect of weather conditions on invertebrate prey availability. Badgers are present in some towns and cities within Britain (Harris 1984; Delahay et al. 2009). Since badgers are the only natural predator in Britain capable of killing

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healthy adult hedgehogs, we may expect hedgehogs to avoid areas frequented by badgers. Studies of the response of foraging hedgehogs to badger odours have, however, produced equivocal results (Doncaster 1993; Ward et al. 1997). In part, this may be because both species eat invertebrates (Delahay et al. 2008; Morris & Reeve 2008) and hence the movements of both hedgehogs and badgers are likely to be influenced by the effects of temperature and rainfall on invertebrate prey availability (Crawford-Sidebotham 1972; Edwards & Lofty 1977; Young et al. 1991, 1993; Ruppert & Barnes 1994; Raworth & Choi 2001; Burt 2002). Paradoxically, variation in weather conditions may therefore mean that good foraging conditions for hedgehogs are mirrored by increased badger activity and hence risk of predation; if suitable foraging areas are scarce, this predation risk could be particularly high. Vulnerable species may reduce the risk of predation by utilizing interstitial areas between the territories of the dominant species (Sargeant et al. 1987) or, where home ranges overlap, by utilizing different habitats (Nelson et al. 2007) or restricting movements to very localized areas (Moehrenschlager et al. 2007). It has been argued that the increased relative abundance of hedgehogs in human-occupied habitats may represent a shift in patterns of occupancy to minimize predation by badgers (Young et al. 2006).

Hedgehogs are also very vulnerable to a variety of human activities, particularly road traffic. They are frequently the most commonly recorded mammal in road casualty surveys (e.g. Huijser 1990; Huijser & Bergers 2000). Previous analyses of real versus simulated movement patterns have suggested that major roads carrying large volumes of traffic are a major obstacle to the movements of urban hedgehogs (Rondinini & Doncaster 2002) and that, for the most part, they tend to occupy the quieter suburbs where traffic volume is substantially lower: whether their foraging activity is impacted by roads and traffic in these quieter suburbs is unknown. For example, even in these ‘quiet suburbs’, there is a marked temporal difference in patterns of traffic flow associated with human activity before and after midnight. A recent analysis showed that red foxes, *Vulpes vulpes*, a much more agile and faster-moving species, crossed roads more frequently after midnight when levels of road and foot traffic had subsided (Baker et al. 2007). It is not known whether hedgehogs in urban areas also make such fine-scale adjustments in their movement patterns.

Predation by dogs is less of a threat to urban hedgehogs than road traffic, but is still a significant cause of mortality (Stocker 2005; Morris & Reeve 2008). A survey of fatalities among hedgehogs brought to three wildlife rescue centres showed that 2.3% had been injured by dogs and cats (Reeve & Huijser 1999).

In this study, we examined the nocturnal movement patterns of hedgehogs in Bristol, U.K., to determine how badgers, traffic and human activity, and weather influenced their ranging behaviour, and how hedgehogs have adapted their patterns of movements to living in urban environments. Specifically we addressed the following questions: (1) how do patterns of habitat utilization compare with those of badgers in the same locality; (2) do patterns of activity and habitat utilization suggest that hedgehogs are avoiding areas of increased risk from humans; (3) how do patterns of temperature and rainfall affect nightly patterns of movement before and after midnight; and (4) do hedgehogs exhibit any avoidance behaviour of minor roads?

METHODS

Study Area

The study was conducted in a residential area of approximately 1.5 km^2 in the Stoke Bishop/Westbury-on-Trym suburbs of northwest Bristol, U.K. between May and September 2004 and 2005. This site has been the location of studies on the behaviour and ecology of red foxes (e.g. Baker et al. 2001) and Eurasian badgers (e.g. Cresswell & Harris 1988a, b) and consists of a mixture of high- and low-density housing with associated private residential gardens (mean density 11.1 houses/ha: Newman et al. 2003), amenity grasslands, allotment gardens and a cemetery (Saunders et al. 1997). The area was bordered by A- and B-category roads, whereas the majority of the roads within these boundaries were C-category or unclassified (Department for Transport 2007) and carried low volumes of traffic, declining from about 150 vehicles/h at 2000 hours to less than 20 at 0000 hours, and less than 10 from 0000 to 0400 hours (Baker et al. 2007). A-roads are major thoroughfares throughout U.K. cities; B-roads principally connect A-roads; and C/unclassified roads are minor thoroughfares that permeate industrial and residential suburbs. All three types of road typically have two lanes of traffic, one in each direction. On the study site, the posted legal speed limit for all roads was 30 mph (48 km/h). Badger density was approximately 4.4–7.5 adults/km in the 1980s (Harris & Cresswell 1988; Cresswell & Harris 1988a); the appearance of new setts suggested that it was higher at the time of the study, but exact densities were unknown.

All animals were captured under licence from Natural England and all capture and handling procedures were approved by the University of Bristol’s ethical review group. Hedgehogs were found by systematically searching pavements, road verges, front gardens, footpaths and playing fields at night using a torch, captured by hand, placed in a cardboard box containing bedding, sexed, weighed and checked for parasites and injuries. In this paper, body mass refers to mass at initial capture in a given year, that is, where animals were tracked in both years, their mass at capture in each corresponding year has been used in the analyses. Individuals were marked with a unique combination of coloured heat-shrink tubing (RS Components, Corby, U.K.), with two ‘tags’ attached to each of the left front, right front, left rear and right rear quadrant of the dorsal spine surface using superglue. Hedgehogs weighing more than 550 g were fitted with a radiotransmitter (Biotrack, Dorset, U.K.: 7 g on acrylic mount) attached to a clipped area of the dorsal spines midway along the back using dental acrylic. Transmitters were positioned so that the antenna trailed behind the animal. Individuals were released either about 30 min after capture or the following night. Hedgehog density was 0.17 animals/ha (C. V. Dowding, unpublished data). Where possible, animals were recaptured at the end of the study and transmitters removed.

Individuals were radiotracked on foot continuously from 2100 to 0300 hours BST using a hand-held three-element Yagi antenna and CE12 receiver (Custom Electronics of Urbana Inc., Urbana, IL, U.S.A.). Locational positions (fixes) were recorded every 5 min, the animal assigned to a 25×25 m grid cell, classified as active or inactive based on fluctuations in signal strength and assigned to one of six habitat categories: (1) back and (2) front gardens of semidetached and terraced houses; (3) back and (4) front gardens of detached houses; (5) roads and road verges; and (6) other habitats (amenity grassland, scrub, allotment gardens). Hedgehogs were typically tracked from distances of 50 m or less. Although some habitat categories were smaller than the resolution of the radiotracking regime (e.g. front gardens, road verges), in these instances animals were directly observable; other habitats (e.g. back gardens, amenity grasslands) were present as relatively large tracts. Consequently, we are confident that we were able to assign animals to these habitats accurately. We discriminated between back and front gardens because front gardens are typically smaller, less enclosed, in closer proximity to pedestrians and pet dogs walking on pavements, and often contained significant areas of paved ground, for example for parking cars.

Individuals were radiotracked for 1–5 nights in a single year or across both years. Three movement parameters were derived for