Fine-scale movement of the European hedgehog: an application of spool-and-thread tracking

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Abstract: The European hedgehog is a significant predator species of rare and endangered ground-nesting birds in the riverbeds of the Waitaki Basin, South Island, New Zealand. Studies focusing on the movements and habits of this species have generally been limited to broad-scale radio-tracking studies or incidental trap-catch data. Within our study, we aimed to investigate the finer scale movement patterns of the hedgehog in relation to vegetation structure by using spool-and-thread tracking. We captured 30 hedgehogs (15 female, 15 male) within the study area, and spool-and-thread-tracked the movements of each over a single night. Only two of the 30 animals moved onto the gravel areas of the riverbeds where birds nest – hedgehogs may therefore not target birds' nests as a primary prey source, but rather as a secondary prey item. The movement paths were all non-random, and males demonstrated particular linearity in their tracks. This straighter and more directed movement may be due to more intensive mate search at this time of the year. We also assessed habitat use using a very high resolution habitat map (derived from Ikonos 4-m-resolution satellite image). Dense grassland was the most selected habitat type, perhaps because insect prey are at a higher density in this vegetation type. Hedgehogs (particularly males) also used boundaries of all habitat types significantly more than the centre of habitat patches. We found the spool-and-thread tracking technique does have limitations: (1) it could be inappropriate for animals exhibiting a significant escape response; (2) the data do not include a temporal dimension. However, these problems were not considered relevant for this study. Fine-scale studies such as this can provide increased power when investigating the ecology of species at a scale relevant to trap placement.

Keywords: animal movement; *Erinaceus europaeus occidentalis*; Ikonos; introduced predators; Waitaki Basin

Introduction

Introduced mammalian predators have been implicated in the decline or extinction of many of New Zealand's endemic species (King 1984; McLennan et al. 1996; Murphy et al. 2004). The European hedgehog (*Erinaceus europaeus occidentalis)* preys upon many ground-nesting bird species. One such species is the critically endangered black stilt or kaki (*Himanotopus novaezelandiae*), which nests on the braided riverbeds of the Waitaki Basin, South Island, New Zealand (BirdLife International 2003). Despite extensive control operations targeting introduced mammals in the Waitaki Basin, hedgehogs continue to have an adverse effect on the nesting success of ground-nesting river birds (Keedwell et al. 2002). Feral cats (*Felis catus*), hedgehogs and ferrets (*Mustela furo*) have been held responsible for 43, 20 and 18%, respectively, of nest losses of kaki and other birds in the riverbeds (Sanders & Maloney 2002). Further information on the fine-scale movement behaviour of species such as the hedgehog may enable us to improve our understanding of the ecology of the species with reference to the risk to ground-nesting birds. This information has been identified as essential for determining optimum placement of traps and poison bait stations; but such knowledge may also support alternative management strategies (such as habitat manipulations) that may discourage predators from important conservation areas (Norbury et al. 1998; Ragg & Moller 2000).

Few studies have investigated movement behaviour of hedgehogs in relation to landscape and vegetation structure and composition; those that have, have generally used broad-scale techniques such as radio tracking (e.g. Morris 1986; Baker 1989; Moss 1999), or incidental trap-catch data analysed *post hoc* (Cameron et al. 2005). Such studies have provided information that can aid predator management at a broad scale (e.g. Berry 1999; Ragg &

Moller 2000). However, there is some indication from these broad-scale studies that fine-scale habitat structure may play an important role in determining the areas individuals will move through. For example, Doncaster et al. (2001) used radio-telemetry to demonstrate that displaced hedgehogs showed an attraction to habitat edges, which were believed to act as corridors to better locations. Also, in an incidental-trap-catch study Cameron et al. (2005) found that hedgehogs were most often caught in traps within 2.5 m of low vegetative cover, and along predator pathways. These studies raise questions as to whether these structures are used continuously during foraging trips, or whether there are other areas or landscape structures that trapping efforts should focus on more to improve trap efficacy. This is the basis for the current research.

Refining the scale at which animal movement studies are carried out presents technical and logistical problems. Highly accurate animal movement data in combination with extremely high resolution habitat information are required. Options for gathering the appropriate animal location data include Global Positioning System (GPS) collars, as used for medium- to large-sized mammals such as ungulates and wolves (Merrill 2000; Johnson et al. 2002). Commercially available GPS devices are, however, not yet light-weight enough for use on many of New Zealand's introduced predators, and are often too costly for wildlife research projects. Spool-and-thread tracking has been developed as an inexpensive yet effective method of tracking fine-scale movements of small mammals (Miles et al. 1981; Woolley 1989). In an environment such as the Waitaki Basin, the thread progressively unravels and snags on boulders or vegetation as the animal moves, recording every turning point. In combination with GPS technology, spool-and-thread tracking can yield accurate movement data in a form compatible with GIS software. High-resolution satellite imagery (up to 1 m) is now available commercially (e.g. Ikonos, Quickbird), and this provides a user-friendly option for developing precise habitat maps.

This study aims to begin to develop and test possible research techniques for investigating the fine-scale habitat use of small mammals in New Zealand braided river systems, while building on knowledge of hedgehog habitat use. We employ spool-and-thread tracking to obtain high-accuracy movement data, and combine these with habitat maps generated from high-resolution satellite imagery. In doing so we also aim to address three main questions in relation to hedgehog movement patterns:
(1) Is a very fine-scale movement study meaningful? i.e. at a very fine scale, do hedgehogs move in a random fashion or are there obvious patterns in this movement?
(2) Which habitat or vegetation types appear to be important for foraging hedgehogs? How often do hedgehogs frequent the gravel/rocky areas where river birds nest?
(3) Do hedgehogs exhibit expected use of landscape

structure, including vegetation edges and linear vegetation strips?

Methods

Study area
The study was carried out in the Ohau and Tekapo braided riverbeds, Waitaki Basin, South Island, New Zealand (44°16–20′ S; 170°5–13′ E; Fig. 1). The river areas used in this study comprise long stretches of rocky and gravel areas interspersed with low-flow waterways. The water flow is heavily controlled by hydro dams located at the head of each river, and hence flooding events are rare. Both rivers have heavy invasive-weed infestations, particularly sweet briar (*Rosa rubiginosa*) and willow (*Salix* spp.). Nine species of native bird use the area as breeding habitat (Byrom 2002), several of which require open areas of gravels or rocks to nest singly or in colonies.

Habitat map
The habitat map used in this study was derived from a classified Ikonos satellite image, with 4-m resolution. The final habitat map was composed of six vegetation classes, considered to represent the major structural elements of the vegetation in the braided riverbeds. This number of classes also provided a very high level of classification accuracy. The Ikonos image was captured on 1 December 2002. The vegetation structure was unlikely to have changed significantly in the period between the image capture and the tracking element of this study (spring and summer 2003), as no flood events were experienced in the riverbeds in the years between and, as mentioned, water flow is heavily controlled. The final classes of the
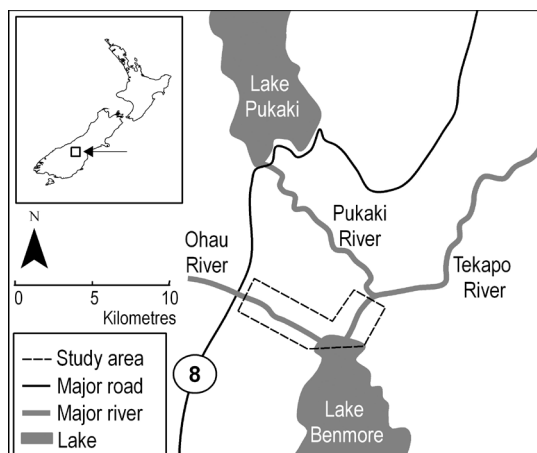

Figure 1. Location of the study site – Waitaki Basin, South Canterbury, South Island, New Zealand.

habitat map were: water; rocks and gravels; low-density vegetation on bare soil; dense grassland; medium- to high-density shrubs; high dense willow trees.

Animal trapping and tracking

Thirty hedgehogs (15 males, 15 females) were live-trapped using 20 Holden live-capture box traps (Mike Holden; www.traps.co.nz) and 50 Grieves cage traps (Grieves Wrought Iron and Wirework, 302 Travis Road, Christchurch, New Zealand). A total of 1500 ha was trapped between September 2003 and January 2004 (spring/summer). Blocks of approximately 300 ha were trapped for 10-day periods, with traps spaced 150–250 m apart. Traps were baited with fresh rabbit (*Oryctolagus cuniculus*), and checked within 3 h of sunrise. Trapped hedgehogs were provided with dry grass and water, and left in situ until dusk. Non-target species were immediately released.

Spool-and-thread tracking devices were attached, and the animals were released at dusk. A spool-and-thread backpack (weight 12.4 g, average 1.9% of hedgehog body weights) was glued to the spines on the rear of each hedgehog (Fig. 2). Backpacks were made by placing two spools side by side and enclosing them within heat-shrink plastic. Each spool (manufactured by Danfield (UK), distributed in New Zealand by Texspec NZ, Auckland) contained approximately 450 m of thread. It is unknown what proportion of the animal's entire nightly movement this length encompasses, but no hedgehogs were ever found still attached to the string. The total available thread length was approximately 900 m, which is close to estimates of home-range length for hedgehogs in the region (Moss 1999). The end of the thread was tied off to a fixed object and the animal was released at dusk. The resulting trail was followed and mapped the next morning using a GeoExplorer 3 GPS unit (Trimble). Location fixes were recorded every five seconds. Tracks were then downloaded and differentially corrected within Trimble

Figure 2. European hedgehog with a spool-and-thread backpack attached.

GPS Pathfinder Office 2.90, using the base station from the School of Surveying, University of Otago, Dunedin, New Zealand (190 km from the study site). The maximum horizontal error of the tracks was 3 m.

Analysis of animal movement paths

Three aspects of hedgehog movement pattern and habitat selection were investigated to address the three questions posed in the introduction: (1) test for random movement; (2) preferred habitat types; and (3) use of habitat edges.

Test for random movement

This analysis was carried out to determine whether hedgehogs move through their landscape at random at this fine scale, or whether the animals make directional choices due to other, potentially measurable fine-scale factors (e.g. habitat structure). The linearity of all tracks was compared with that of random walk tracks. One thousand random tracks were generated for each real track using Animal Movement Analysis 1.1 (Hooge & Eichenlaub 1997), an extension to ArcView 3.2® (ESRI): each distance travelled between turning points was equal to that observed in the true animal tracks, and random turning angles were substituted for the actual angles taken. This process provided data that enabled us to compare random movement patterns directly with real patterns. The statistics compared between real and random tracks were (a) R^2: the average straight-line distance each consecutive turning point moved away from the geometric centre (start point of the track); and (b) LI: the total linear distance between the start and end points of an animal's path, divided by the total length of the path (linear paths yield LI = 1; and LI < 1 is non-linear).

For each individual, observed R^2 and LI values were compared with the range of values given by the random tracks. Observed values that fell in the range of the top 5% of values for the random walk tracks indicated the movement path was significantly more linear than would be expected if turning angles were made at random. Alternately, if the R^2 and LI of an observed animal track was in the lower 5% of the range of values for the random walk tracks, then the observed track was considered significantly more constrained than would be expected from a random track (i.e. it exhibits higher site fidelity) (Hooge & Eichenlaub 1997).

Preferred habitat types

Compositional analysis (Aebischer et al. 1993) was applied to the data to determine if the hedgehogs preferred moving within certain habitat types. This statistical technique compares the proportion of each habitat available to an animal with the proportion actually used. In this study the habitat 'used' was considered that within a buffer of 15 m either side of the track. As recommended by Erickson et al. (2001), this buffer size accounts for all the effort associated

with the habitat map and animal tracks. This includes maximum error in the geo-referencing of the Ikonos image ($\pm$ 6 m); horizontal precision of the animal tracks recorded on the GPS ($\pm$ 3 m after differential correction); and a pixel size of 4 m (satellite image resolution). The habitat 'available' to an animal was considered the circular area around the start point, with a radius of the start-to-end point length of the real animal track (i.e. the total area that the spool-and-thread track could have recorded). Raw data on the total area of habitat types both 'used' and 'available' to each animal were converted into a percentage of the area covered. Compositional analysis requires that every habitat is used, so zero values were substituted with a small positive value, smaller than the smallest proportion of used habitats (Aebischer et al. 1993); this substitute value was 0.001.

Use of habitat edges

This section of the analysis aims to provide quantifiable evidence for fine-scale preferential boundary use as described by broad-scale habitat-use studies (Baker 1989; Pascoe 1995; Ragg & Moller 2000; Doncaster et al. 2001). A landscape index (edge-density index; edge length (km) per hectare; Haines-Young & Chopping 1996) was used to quantify the amount of each habitat boundary within the 15-m buffer zone of each animal track. This measurement was generated within Patch Analyst 1.0, an extension to the ArcView® GIS system (Elkie et al. 1999). An edge-density value was generated for each habitat type in the buffer zone of each observed animal track, and to create paired data, the index was also generated in the same way for 10 random walk tracks (i.e. 10 for every real track). Ten tracks were used because the asymptote of the mean was reached by this point in multiple simulations of edge-density measures for each real track, indicating that this number provided acceptable representation of edge use expected from random movement.

The mean index values for the real tracks were compared with the mean values from the random tracks, using paired *t*-tests, one *t*-test for each habitat type. Though repeated *t*-tests can increase the Type I error, other analyses were considered inappropriate for this type of data. As the length of the edge of one habitat type is not independent of the length of other habitat types (i.e. edges between two side-by-side habitat types are measure twice: once for each habitat type), the measurements cannot be considered independent. We attempted to carry out a Repeated Measures ANOVA to deal with this non-independence; however, as the degrees of freedom within this test are reduced, the sample sizes in this study were not large enough. The *t*-tests were thus appropriate for detecting overall differences between the real and the random data for each habitat type, and differences between the habitat types was not investigated. Summary statistics detailing the distance of each turning point within the tracks from the nearest habitat edge were also generated.

Results

General observations

Hedgehogs often did not follow existing animal runs; rather tracks would often amble through dense grass (Fig. 3). Short-term nests (where the animal had obviously remained for a portion of the night – string was balled up and a flat hollow had been made in the vegetation) were commonly found within dense long grass, and more permanent nests (twice found with young) were generally located in longer grass right at the base of sweet briar or other shrubs.

Test for random movement

The R^2 values for 12 females (80% of females) and 13 males (87.5% males) were significantly higher than for the corresponding random tracks. The LI values for 7 females (46.7% females) and 14 males (93.7% males) were significantly higher than the corresponding random values. Therefore, there is evidence that generally the movements of both male and female hedgehogs are more dispersed (non-random) than would be expected had they been moving randomly.

Preferred habitat types

Only two male hedgehogs were recorded as moving out onto the rocky/gravelly areas where river birds nest. The water was never entered by animals, and is only recorded in the habitat rankings below as it appears as a habitat type in the buffer zone when animals walk alongside rivers or lakes.

Male hedgehogs showed non-random habitat selection (Wilks Λ = 0.2353, χ^2_5 = 21.70, P < 0.001). A ranking matrix ordered the habitat types in the sequence: dense grassland > medium- to high-density shrubs > high dense willow trees > low- to medium-density plants on bare soil >>> rocks/gravels >>> water (Table 1; >>> denotes a significant difference between two consecutively ranked habitat types). Rocks/gravels and water were used significantly less than all other habitat types.

For female hedgehogs, comparison of habitat-use with habitat availability gave Wilks Λ = 0.5022 (χ^2_5 = 10.33, P = 0.066). A ranking matrix ordered the habitat types in the sequence: dense grassland > medium- to high-density shrubs > high dense willow trees > low- to medium-density plants on bare soil > water > rocks/gravels (Table 1).

Use of habitat edges

The mean edge-density values for male hedgehogs were significantly higher (*t*-tests, P < 0.001; Fig. 4b) than the values for the random tracks for five habitat types. All habitat types produced a *P*-value at this level of significance. The habitat edges used more than randomly were: rocks/gravels, high dense willow trees, medium- to high-density shrubs, dense grassland, and low-density
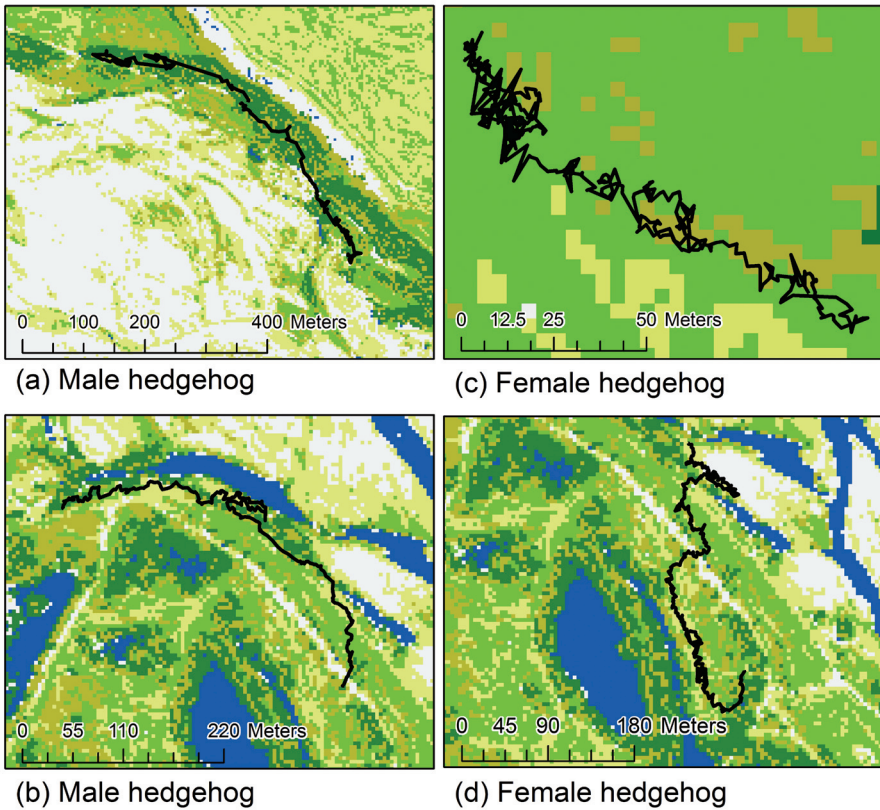
Figure 3. Examples of female and male hedgehog spool-and-thread tracks mapped with the six-class habitat map derived from an Ikonos satellite image of 4-m resolution.

Table 1. Results from the compositional analysis of hedgehog spool-and-thread tracks from September 2003 to January 2004. Habitat types are ranked in order of relative preference (1, highest; 6, lowest) with significant differences between consecutively ranked habitat types marked * ($P < 0.05$, from randomisation tests).

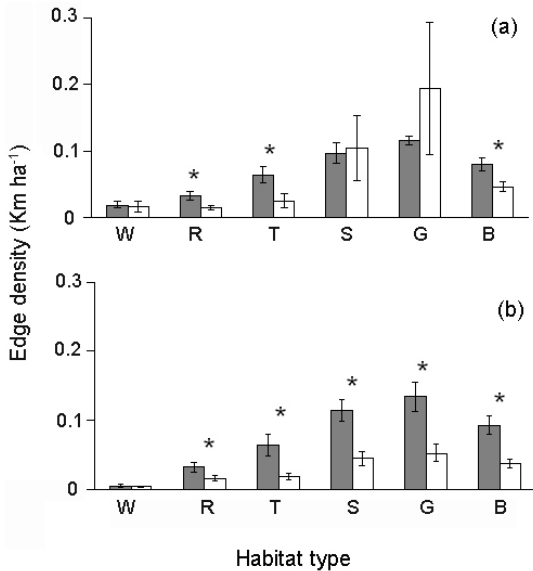|	Ranking of habitat types for each group	
	Female hedgehogs	Male hedgehogs
Habitat type	$n = 15$	$n = 15$
Water	5	6*
Rocks/gravels	6	5*
Low-density vegetation on bare soil	4	4
Dense grassland	1	1
Medium- to high-density shrubs	2	2
High dense willow trees	3	3

Figure 4. Bar graphs of edge use of different habitat types (W = water, R = rocks/gravels, T = high dense willow trees, S = medium- to high-density shrubs, G = dense grassland, B = low-density vegetation on bare soil) for (a) female hedgehog (dark grey) and corresponding random walk tracks (white), and (b) male hedgehog (dark grey) and corresponding random walk tracks (white). Edge use is represented by edge-density values of each habitat type in a 15-m buffer zone around each track. *n* = 15 for all groups. * denotes a significant difference between the means at $P < 0.05$. Error bars are standard errors.

plants on bare soil. This indicates that male hedgehogs use habitat edges, or ecotonal boundaries, more than expected had their movements been random.

The mean edge-density values for female hedgehogs were significantly higher (*t*-tests, $P < 0.01$; Fig. 4a) than the values for the random tracks for three habitat types. These habitat edges were: high dense willow trees, low- to medium-density plants on bare soil, and rocks/gravels. This indicates that female hedgehogs use the boundaries of only some habitat types for movement.

Discussion

Spool-and-thread tracking

This study successfully used fine-scale movement data from spool-and-thread tracking and high-resolution satellite imagery to quantify habitat and landscape use by hedgehogs. This methodology provided quantifiable evidence for hedgehog movement patterns that previously could only be inferred from broad-scale movement studies. These results must be interpreted alongside the limitations of these techniques, and in this sense this study also provides essential lessons on the interpretation and methodology of future fine-scale movement studies.

The interpretation of the movement data is potentially confounded by escape behaviour exhibited by the animal. After handling, the hedgehogs used in this study generally burrowed into nearby grassy areas and remained there at least until the researcher left. Tracks did not tend to exhibit long linear movements as we would expect to observe if animals were attempting to escape, thus we considered the effect of the escape response to be negligible. This study also originally attempted to use the spool-and-thread technique on ferrets (*Mustela furo*), a more mobile species. When released these animals tended to run directly into the undergrowth away from the researcher. Long straight movements were initially observed in the tracks. As the length of the escape behaviour was very difficult to quantify, the tracks were considered non-representative of normal ferret movement. These were therefore discarded from the study. This experience does provide a valuable lesson in understanding the limitation of the spool-and-thread technique. The suitability of the technique for the species under study should be considered carefully.

The lack of a temporal dimension to the animal movement paths in this study could also place limitations on the interpretation of this data, though the power and fine-scale information gained can be considered a beneficial compromise. The spool-and-thread tracks give no indication as to the amount of time an animal spent in each habitat patch, so the implicit assumption in this study is that presence in a habitat type is an adequate measure of relative intensity of use for active purposes (such as foraging or mate search). Recording only the movement path of an animal may however avoid a major bias that can exist in conventional methods where resting habitat types may become over-represented. This may be of particular problem when using, for example, radio-tracking in a hedgehog study. The capture response of a hedgehog is to remain in one position until the threat has been removed, and the animals are nocturnal, commonly resting in one place for the length of a day. Radio-tracking studies commonly obtain only a single-position fix over the course of a 24-hour period, potentially only obtaining location data for nesting or resting habitat types.

The spool and thread technique did provide very fine-scale data for this study, and was inexpensive and accurate. There are currently no modern tracking techniques that can provide the researcher with more accurate information. The spool-and-thread technique also has the potential to allow the researcher to answer further specific questions on how the animal physically moves through the vegetation, and what tracking marks (e.g. characteristic burrowing through vegetation) may identify the presence of the animal in an area.

Hedgehog movement patterns

Our study provides evidence that investigating movement at the scale of this study is appropriate, as patterns and non-random movement were observed across the length of the tracks. This analysis also revealed other interesting information relevant to hedgehog ecology. Male hedgehog tracks tended to be more linear than female tracks. Previous observational (non-quantitative) studies on hedgehog movement patterns have also shown a difference between the sexes. Wroot (1984), found that over 70% of female hedgehog movements were short, with few rapid movements. However males tended to move in a more rapid and linear style than females, allowing them to cover more ground. The hedgehogs in this study were tracked between September and January, much of which is the hedgehog-breeding season in New Zealand (November to January in the Waitaki Basin; Moss & Sanders 2001). This may explain the differences in movement patterns between the sexes. Campbell (1973) suggested that during the breeding season male hedgehogs are likely to search actively for mates, and are therefore more wide-ranging than females. Female hedgehogs also often have litters in a nest at this time of year (two females in this study were tracked back to nests containing litters), and may be less likely to travel long distances away from their offspring. This could reduce the mean squared displacement and linearity measurements, resulting in values closer to those of the random tracks. This tendency to stay within a more confined area than males is supported by the smaller home-range size of female hedgehogs observed in many studies (Moss & Sanders 2001).

The hedgehogs in this study tended to remain preferentially in dense grassland. Cameron et al. (2005) also found that hedgehogs were best trapped in low vegetation rather than bare substrate, supporting our finding. The most obvious potential explanation for the preference for grassland is a possible higher relative abundance of insect prey species in this habitat type. Previous studies in Europe have found strong links between hedgehog distribution and the density of invertebrate prey species (Micol et al. 1994; Cassini & Föger 1995). Further studies on invertebrate distribution within the study area would be required to test this. The presence of suitable nest sites has also been linked with hedgehog distribution (Parkes 1975), and Moss (1999) found that shrubs and tussock or grassland was the preferred nesting habitat. The selection of dense grassland by hedgehogs in our study therefore supports this.

Finally, this study provided support for the hypothesis that fine-scale landscape structure is important to hedgehogs. In this case habitat boundaries were used preferentially over more central areas, though this pattern was much stronger in males than in females. We suggest that the use of edge habitat is linked with directional movement or search behaviour at a higher level (e.g. in the search for mates rather than for insect prey) in which animals may be required to move greater distances at greater speeds. The overall higher linearity of the male hedgehog tracks supports this. Doncaster et al. (2001) and Morris (1986) also documented hedgehog use of habitat boundaries, suggesting that the edges of dense habitat types allow less encumbered movement.

Interestingly, in this study only two male hedgehogs were recorded to move out into the rocky or gravel areas where ground-nesting river birds have been known to nest. As the proportion of nests taken by hedgehogs is high (20%; Sanders & Maloney 2002), our result is unexpected. This would suggest hedgehogs rarely seek birds' eggs as prey. A study of the diet of hedgehogs in the area also demonstrated that only 4% of the guts studied contained the remains of birds' eggs (Jones et al. 2005). This result and the low frequency of animals travelling onto the gravel riverbeds support the hypothesis proposed by Jones et al. (2005) that a large hedgehog population could be supported primarily by invertebrate biomass, and small populations of native birds and lizards may suffer as a secondary prey source.

Conclusion

The combination of the very high resolution habitat-map and the accurate spool-and-thread tracking data enabled quantification of fine-scale habitat-use by hedgehogs. This research generally supported habitat-use findings from other radio-tracking and incidental-trap-catch data. This, in itself, adds to the body of information on habitat preferences of the European hedgehog that could be used to enhance trapping procedures. We demonstrated that it is worth following hedgehogs at this fine scale, and this may also be important for other species. Radio-tracking data can leave the researcher with a number of 'unknowns' resulting from inaccuracies and errors within the technique. Spool-and-thread tracking has enabled us to follow moment by moment each decision the animal has made with regards to its habitat and environment. This power alone allows us to support observations made using other techniques, but also enhances our understanding of the ecology and behaviour of the species at a much more intimate scale.

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