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RESEARCH

European hedgehogs rear young and enter hibernation in New Zealand's alpine zones

Nicholas J. Foster[1]*, Richard F. Maloney[2], Mariano R. Recio[3,4], Philip J. Seddon[1] and Yolanda van Heezik[1]

[1]University of Otago, Department of Zoology, Dunedin, New Zealand
[2]Department of Conservation, Dunedin, New Zealand
[3]King Juan Carlos University, Móstoles, Spain
[4]Department of Ecology, Swedish University of Agricultural Sciences, Uppsala, Sweden
*Author for correspondence (Email: nicholasjordanfoster@gmail.com)

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Abstract: European hedgehogs (*Erinaceus europaeus*) occur in New Zealand's high alpine zones, but it is not known if populations persist in such areas year-round. We hypothesised that hedgehogs respond to the arrival of winter conditions (cold temperatures, snowfall, and lack of available food) by making short-distance altitudinal migrations to lower elevations. We tested this by capturing and fitting GPS/VHF backpacks to six adult female hedgehogs at elevations between 1500 and 1800 m, and by following their movements throughout the austral summer to winter period (January to June) 2020. We found no evidence to suggest that hedgehogs abandon their summer/autumn home ranges and move to lower elevations with the arrival of winter conditions, which indicates that at least a proportion of hedgehogs enter hibernation in New Zealand's alpine zones. Two females were found rearing young above 1600 m, further indicating that hedgehogs are resident species in these zones.

Keywords: altitudinal migration, *Erinaceus europaeus*, high elevation, persistence, winter

Introduction

European hedgehogs (*Erinaceus europaeus*) were introduced to New Zealand in 1869 and are now widely distributed across the North and South Islands (Brockie 1975). Of all of New Zealand's introduced mammals, hedgehogs are the only species that hibernate. Hibernation is a physiological and behavioural adaptation that allows hedgehogs to survive periods of unfavourable conditions and resource unavailability by storing energy as body fat and lowering their metabolic rate (Humphries et al. 2003). The period during which hedgehogs hibernate in New Zealand is strongly influenced by latitude, with hibernation taking place over several months in lowland areas of the South Island, compared to populations that hibernate only during short, cold periods in the north of the country (Jones 2019), where some may not hibernate at all (Wodzicki 1950).

Hedgehogs are found in New Zealand's alpine zones up to 2000 m above sea level (a.s.l.) and become less abundant with increasing elevation (Brockie 1975; Foster et al. 2021). This trend has been attributed to increased rates of overwinter starvation in increasingly cold areas of New Zealand, brought about by a presumably lower abundance of invertebrate prey and a lengthened hibernation period (Brockie 1975). Studies in Europe have reported only 35% of juvenile hedgehogs surviving beyond their first winter, with the majority of deaths occurring throughout the winter period (Morris 1969; Kristiansson 1990). Mortality rates of adult hedgehogs are also highest in winter with survival rates estimated at 66%, the likely cause being inadequate fat reserves (Kristiansson 1990). As winter conditions arrive, hedgehogs that are present in New Zealand's alpine zones could conceivably take advantage of longer foraging and breeding seasons by making short-distance altitudinal migrations to lower elevations that have comparably milder climatic conditions, thereby improving survivability. Hedgehogs are not a migratory species; however, they have demonstrated flexibility in their foraging strategy by changing their spatial utilisation of habitat and altering searching behaviour with the temporary availability of food (Parkes 1975; Cassini et al. 1994). Making short-distance movements when alpine terrain becomes unfavourable, in terms of food availability or climatic conditions, might afford individuals a greater opportunity to accumulate body fat stores and improve their chances of surviving a shorter hibernation period at lower elevations. The costs and benefits of doing so would be weighed against those of hibernating in-situ and conserving energy stores (Webb & Ellison 1998).

Determining whether hedgehogs persist in New Zealand's alpine zones is important, as landscape-scale management programmes that aim to remove hedgehogs from upland areas require a sound understanding of the ecology of hedgehogs in these zones. Such programmes could be spatially-refined by needing only to target contracted distributions of hedgehogs at times when high-elevation populations have moved downwards and are still actively foraging during the shoulder seasons. We hypothesised that hedgehogs move to lower elevations

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when winter conditions threaten. We tested this hypothesis by capturing and GPS/VHF tagging hedgehogs at high elevations and following their movements from late summer to early winter. Here, we present the first information on the response of hedgehogs to winter conditions in New Zealand's alpine zones.

Methods

The study area was located at the head of Camp and Bush Streams (1500–1950 m a.s.l.) in the Two Thumb Range, Canterbury, in New Zealand's South Island (-43.7242° S 170.6902° E). We captured hedgehogs between 20 January and 17 March 2020 (the height of the austral summer) using a combination of large metal box traps (Elliott Scientific Equipment, Upwey, Vic.) baited with cat food (Whiskas® Ocean Fish Loaf), and night spotlighting transects. Upon capture, we determined the sex and body mass of hedgehogs and fitted all individuals above a weight threshold of 485 g with a small GPS/VHF backpack made from a low-cost GPS unit (Allan et al. 2013) before releasing individuals where captured. Depending on battery size, GPS/VHF backpacks weighed 32–39 g and did not exceed 6.6% of a tagged hedgehog's body mass, a rule that Recio et al. (2011) deemed appropriate for hedgehogs. Static tests of these devices led us to expect mean location errors between 4.17 m and 5.28 m, which we considered to be acceptable for recording the movements of hedgehogs (NF, unpubl. data). We scheduled devices to record location fixes every 5 min each night, from one hour before sunset to one hour after sunrise. We recaptured tagged individuals every two to three weeks at which time they were weighed and reequipped with charged GPS units. Hedgehogs carried devices until late April/May, several weeks after hedgehogs commence hibernation in the lower elevation habitats of this region (Moss 1999). As we were unable to replace GPS tags during New Zealand's Level 4 COVID-19 lockdown (26 March–28 April 2020), GPS device batteries went flat and GPS data were not collected throughout the late autumn period.

We collated all data collected throughout multiple GPS deployments for each individual and separated data into either active or inactive categories, as indicated by hedgehog movements in relation to den sites which were identified as daily movement data were amassed. We combined the mean nightly elevation produced from hedgehogs' active data location fixes every three days with the elevation of capture locations recorded when deploying, retagging and recovering devices, to plot the elevations that individual hedgehogs used throughout the study period. Nights when hedgehogs did not leave their dens were considered separately to display trends of inactivity. A HOBO data logger (Onset Computer Corporation 2002) was positioned at 1750 m and set to record the ambient temperature at 1-hour intervals from 15 January to 30 April. To plot the elevation of snow coverage across time, we interpolated manual measurements of the lower limit of the snow line in the immediate study area using regularly-acquired 10 m resolution imagery provided by Sentinel 2A and 2B satellites (Copernicus Sentinel data 2020). We then used active GPS data to determine the summer/autumn home ranges of each hedgehog, which we define as the spatial use of each individual hedgehog based on its active data only, between 1 February and 28 March 2020. To do so, we used the heatmap function in QGIS (QGIS Development Team 2020) which uses Kernel Density Estimation (KDE) to produce a density raster from point data, and used the contour function to derive 50% and 95% isopleths. We located hedgehogs several weeks after winter conditions arrived (characterised by regular mean daily temperatures below 10°C and snowfall that persisted on the ground for extended periods) and after hibernation has been recorded to commence in lowland habitats of the region (mid-April; Moss 1999). We then overlaid the final known location of each individual hedgehog, which was assumed to have been recorded after the commencement of hibernation, against their summer/autumn home ranges to determine if they had moved out of such areas.

Results

We captured and GPS-tagged six adult female hedgehogs at elevations between 1550 and 1800 m. We found no evidence of five tagged individuals moving to lower elevations with the onset of colder temperatures and the presence of snow at the end of April (Fig. 1). The sixth hedgehog was found dead in its summer/autumn home range near the end of the study, likely caused by a large malignant melanoma that was revealed upon post-mortem examination (Dr Alyssa Calder, Animal Welfare Office – University of Otago, pers. comm.). This individual was not included in movement analyses. One individual, hedgehog #3, was left tagged for an additional month as it was found to be using a lower area within its home range and it was thought that a downward movement might yet occur. When located again on 31 May, this hedgehog was in a den at a higher elevation under snow cover within its summer home range.

Tagged individuals typically made nightly movements in the terrain surrounding active den sites, with some making occasional forays into higher elevation habitat before returning to den at lower elevations (hedgehog #2 & #3; Fig. 2). Individuals' elevation ranges varied between 64.6 m and 274.3 m (mean = 170.1 m, SD = 95.5 m). Two of the tagged individuals were found with young shortly after initial capture: hedgehog #1 was found on 21 January in an elaborate den at 1620 m a.s.l., with three hoglets, each weighing approximately 180 g; and on 6 February, hedgehog #2 was found in a den at 1660 m a.s.l. with one hoglet weighing 200 g (Fig. 2).

When each hedgehog was located a final time in late April/May, all were found within their summer/autumn home ranges (Fig. 2), and the VHF transmitters of all hedgehogs except for hedgehog #3 were operating in mortality mode (a specific pulse rate that is activated after 24 hours of zero motion), which indicated that no movement had occurred in the previous night. Several hedgehogs were found denning beneath undisturbed snow that had been present in the area for more than a week, as indicated by satellite imagery (Figs 2, 3). When handled, several hedgehogs exhibited signs of partial arousal from hibernation, described by Herter (1934) and Suomalainen and Saarikoski (1970) as a semi-dormant state of minimal motor movement and a lack of response to acoustic stimuli. The individuals we observed freely uncurled in-hand, slowly extended their limbs and exposed their underbelly, and were not responsive to touch or sound (Fig. 3). This behaviour was markedly different from their typical response of forming tight, defensive balls and tucking away their limbs and underbelly when handled. There was evidence of short periods of inactivity during cold weather in mid-March, with GPS data indicating that hedgehogs were inactive for periods of up to three days at a time, several weeks

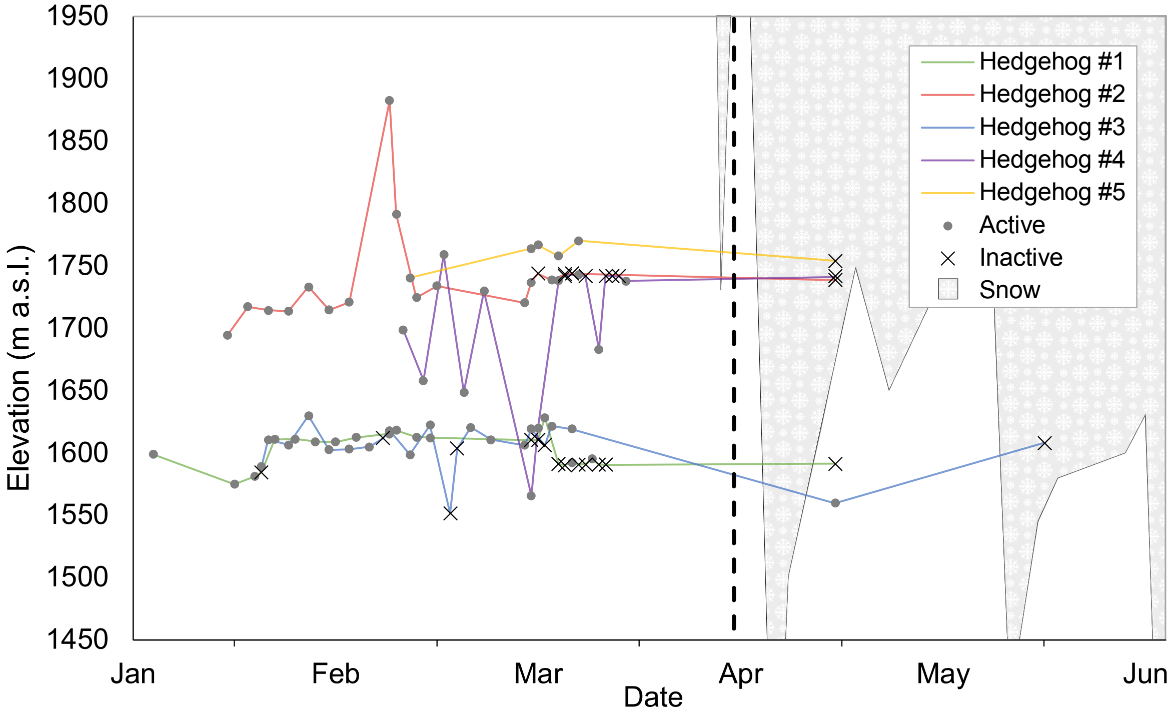

Figure 1. Elevation (m a.s.l.) of hedgehog locations across the study period, with the reported commencement of hibernation in mid-April at lower elevations marked with a vertical dashed line (Moss 1999), and the presence of snow on the ground indicated by the shaded areas. Each point represents either the mean elevation of the hedgehog across three nights (GPS data) or the elevation of a hedgehog located by VHF radio telemetry. Crosses indicate single nights of zero activity. Points are joined with a line to track the elevation records of individual hedgehogs over time and coloured to correspond with location fixes of the same individual in Fig. 2.

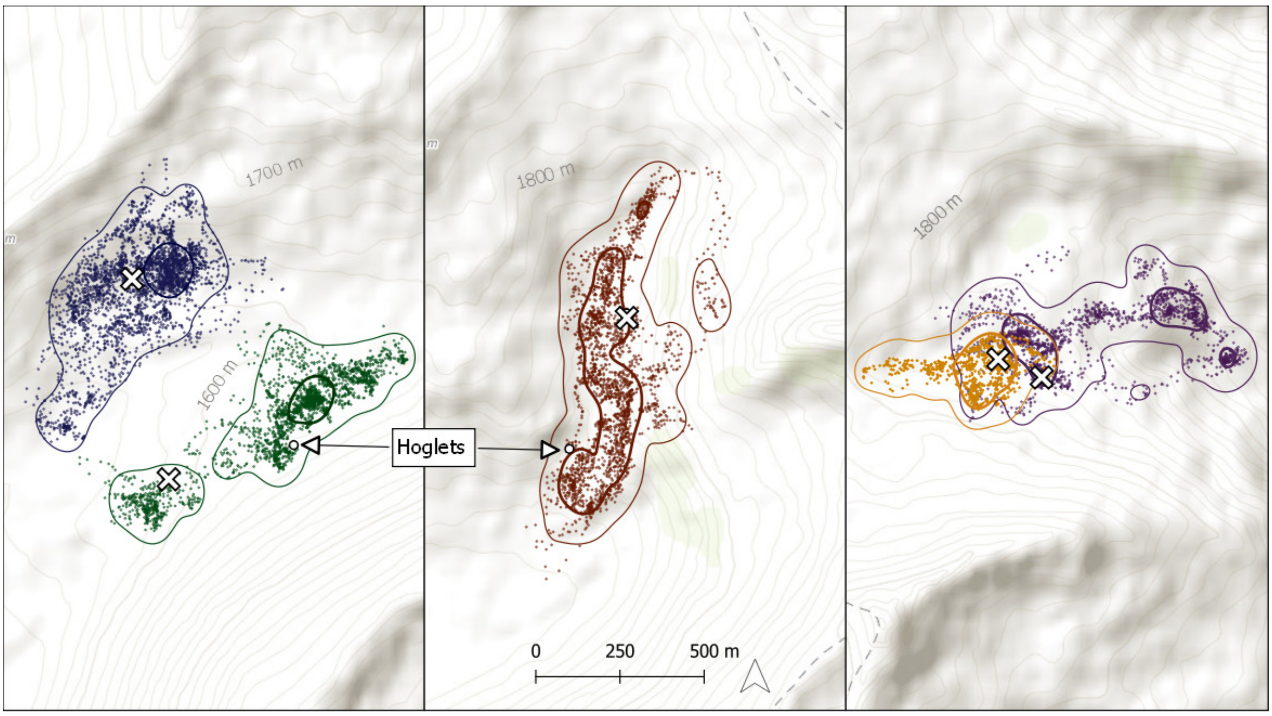

Figure 2. GPS locations of hedgehogs between 20 January and 28 March 2020, with 95% (outer lines) and 50% (bold lines) isopleths. Final locations, recorded in late autumn, are marked with an X. The den sites where young were found are marked for hedgehogs #1 (green) and #2 (red). Hedgehog home ranges from left to right correspond to IDs: #3, #1, #2, #5, #4.

Figure 3. Hedgehog #5 exhibiting signs of partial arousal from hibernation at 1750 m on 30 April 2020 (left), and hedgehog #3 found denning at 1608 m a.s.l. beneath undisturbed snow on 31 May 2020 (right).

before snow was present in the study area. At this time, body weights of the six tagged hedgehogs ranged from 528–816 g (mean = 663 g). Although mean 24 h temperatures dipped below 5°C on several occasions between 15 January and 15 March, they typically ranged from 10–17°C. The mean 24 hr temperature exceeded 10°C on only two occasions between 15 March and 30 April.

Discussion

We found no evidence of female hedgehogs responding to the arrival of winter conditions by moving out of the areas that they used in summer/autumn to lower elevations nearby. As data were collected for five female hedgehogs only, we cannot infer the same for all hedgehogs, especially due to observed differences in hibernation timing between males and females (Parkes & Brockie 1977). However, our observations do indicate that at least a proportion of hedgehogs enter hibernation in New Zealand's alpine zones. The time at which hedgehogs commence hibernation depends on the costs and benefits of doing so (Webb & Ellison 1998). In the case of the female hedgehogs that we studied, the energetic cost of shifting foraging ranges in times of resource scarcity may outweigh the benefits of a lengthened foraging season, whereas hibernating in-situ may enable hedgehogs to maximise energy reserves to take into hibernation. Webb & Ellison (1998) demonstrated the energetic advantage of entering hibernation in low temperatures (5°C) and estimated that body fat stores sufficient for > 100 days of hibernation would be depleted in less than a day by a hedgehog in a normothermic state. Hedgehogs that do enter hibernation in the alpine zone likely remain there for the duration of winter, as movements during this time would expose individuals to low temperatures, cause them to expend irrecoverable fat reserves, and the near-complete snow cover would prevent them from locating hibernacula. Hedgehogs are presumably capable of remaining in hibernation in this zone throughout winter, considering that this species hibernates for up to eight months in the extreme north of their distribution in Europe (Rautio et al. 2014) and that New Zealand's winters are comparably shorter.

Movement data that showed inactivity for periods lasting several days in mid-March suggest that intermittent hibernation at high elevations may commence earlier than Moss's (1999) estimate for lowland areas of mid-April. We noted that the mean 24hr temperature exceeded 10°C on only two occasions (mean = 5.7°C, SD = 3.4°C) between 15 March and 30 April, a threshold below which hedgehogs hibernate (Kristoffersson & Soivio 1964; Jones & Sanders 2005; Bexton 2016). The consistently low temperatures during this period suggest that the hedgehogs we studied responded to ambient temperature rather than a scarcity of food resources, though neither the specific food resources that are important to hedgehogs, nor their seasonal availability are known in the context of New Zealand's alpine zones. Between 30 April and 31 May, hedgehog #3 moved to a different den location, during which time the area cleared of snow. This behaviour may suggest that like hedgehogs in lower elevations, individuals at high elevations take advantage of foraging opportunities during periods of relatively warm weather when snow is not present (Reeve 1994), or that as Haigh et al. (2012) and Rasmussen et al. (2019) observed, hedgehogs in New Zealand's alpine zones may shift between several hibernacula throughout winter when it is possible to do so. Hedgehog #3's movement resulted in the individual denning at a higher elevation within her home range and gave no indication that she responded to a strong environmental cue of snowfall persisting on the ground for close to a week by moving to a lower elevation. The observation of two adult females rearing young in the alpine zone further supports the notion that hedgehogs present in the high elevations of New Zealand reside permanently in these zones. Interestingly, the other four adult females were not found with young at any point during the study. It is not known whether this was coincidental or a result of resource limitation.

These results offer a key piece of information to Brockie's (1975) attribution of overwinter starvation as a primary cause of decreasing hedgehog abundance with increasing elevation. Our finding of hedgehogs persisting in New Zealand's alpine zones infers that such individuals are indeed subject to the factors that Brockie (1975) suggested to cause higher rates of overwinter starvation at higher elevations, of (1) a potentially reduced abundance of food for hedgehogs, and (2) a lengthened hibernation period which would require greater energy reserves to see individuals through hibernation (South et al. 2020), leaving a narrower window of time for both juvenile and adult hedgehogs to breed and gain sufficient fat reserves to successfully hibernate. Additionally, exposure to colder ambient temperatures with increasing elevation would further increase the risk of overwinter mortality, as the metabolic rate of hibernating hedgehogs increases considerably at extremely low temperatures (−5°C) and would more rapidly deplete energy stores (Soivio et al. 1968). Such an increase in mortality rates of adult hedgehogs throughout periods of colder than normal winter temperatures was reported by Kristiansson (1990). Increasingly mild, shorter winters as a consequence of climate change could cause hedgehog populations to increase in these zones because of decreased mortality rates and an increased potential for hedgehogs to have more than one litter per year. Hedgehog population growth would in turn result in increased predation pressure on vulnerable native fauna in this environment.

The lack of altitudinal migration to lower elevations in winter among the female hedgehogs that we studied indicates that eradication-level control programmes targeting introduced hedgehogs in New Zealand will need to address all habitat zones where hedgehogs are found, and cannot be spatially refined by needing to target only a contracted distribution of the species. A potential management benefit of hedgehog populations residing permanently at high elevations is that once they are eradicated or controlled to low densities, it may take some time for new populations to establish via dispersal from lower elevation areas. Any such programmes should be based on a sound understanding of how hedgehog activity is influenced by temperature in these zones, as this will be important for differentiating between low hedgehog activity and low densities or trapping rates.

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Author contributions

NF, RM, MRR, PS and YvH conceptualised and designed the study. NF carried out all data collection and analyses. NF wrote the manuscript, to which all authors contributed revisions and refinements. All authors read and approved the final manuscript.

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