NEW ZEALAND JOURNAL OF ECOLOGY

SHORT COMMUNICATION

Spatially explicit capture-recapture estimate of hedgehog population density in exotic grassland, New Zealand

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Published online: 29 November 2023

Abstract: European hedgehogs (*Erinaceus europaeus)* in New Zealand are considered a pest species due to their impacts on native species and are targeted in trapping programmes. A robust estimate of hedgehog population density using spatially explicit capture–recapture (SECR) is lacking and can provide the parameters σ (the spatial decay parameter for a half-normal home-range kernel to model the decline in encounter probability with distance between the home-range centre and trap) and g_0 (the nightly probability of capture by a trap placed at the animal's home-range centre) needed to model optimal trapping or detection arrays. We estimated the density of hedgehogs in pasture habitat on the Otago Peninsula, South Island, New Zealand, using SECR during late February/early March as 0.46 ha^{-1} (95% confidence interval 0.26–0.82 ha^{-1}; $g_0 = 0.02$; $\sigma = 85.7$). The mean body mass of captured hedgehogs (482 g, range: 180–890g, $n = 32$) indicated a mix of adults and juveniles. Future research should evaluate prey availability as well as hedgehog density to develop a better understanding of the relationship between hedgehog abundance, prey availability, habitat and climate.

Keywords: σ and g_0, insectivore, introduced predator, *Erinaceus europaeus*, spatially explicit capture-recapture

Introduction

European hedgehogs (*Erinaceus europaeus*) are native to Western and Northern Europe (Seddon et al. 2001) and were introduced into New Zealand in the 19th century (Jones 2021). They are a hardy species and a successful urban adaptor (Pettett et al. 2017) capable of exploiting a broad range of habitats (Dickman 1988). While predominantly insectivorous (Brockie 1959; Campbell 1973; Wroot 1984; Nottingham et al. 2019), in New Zealand their diet includes the eggs of ground-nesting birds (Moss 1999; Sanders & Maloney 2002), vulnerable reptiles (Jones et al. 2005; Spitzen-van der Sluijs et al. 2009), and endemic invertebrates (Jones et al. 2005; Jones & Norbury 2011). Furthermore, they compete for resources with indigenous insectivorous birds (Hamilton 1999; King 2005; Innes et al. 2010) and are disease reservoirs (Jahfari et al. 2017). With few predators and abundant food, they have expanded their distribution throughout most of New Zealand (Jones 2021) and are now, due to their impacts on native species, targeted in trapping programmes (Reardon et al. 2012; Norbury et al. 2013).

Despite the ubiquity and abundance of hedgehogs, their numbers have been established for only a limited number of sites and habitats (Moss & Sanders 2001) and these densities are either relative indices (capture rates) or based on minimum numbers of animals encountered over a period (summarised in Jones 2021). Capture-recapture methods provide a more robust estimate of population density by estimating the unsampled fraction of the population, while spatially explicit capture-recapture (SECR) models also account for variable detectability of animals associated with their movements relative to trap locations (Efford 2004; Efford & Fewster 2013). Spatially explicit capture-recapture estimates density and parameters that are needed to predict the detection or capture rates of potential surveillance and trapping regimes (Anderson et al. 2022). These spatial detection parameters are known as σ (the spatial decay parameter for a half-normal home-range kernel to model the decline in encounter probability with distance between the home-range centre and trap), and g_0 (the nightly probability of a hedgehog being captured in a trap at the centre of its home range).

Hedgehogs are abundant in intensively farmed lowland and coastal districts (Jones & Norbury 2006; Tempero et al. 2007; Haigh et al. 2013). The Otago Peninsula (9800 ha) is largely coastal farmland with small urban centres. The encroachment of urban habitats and extensive farmland make the peninsula prime habitat for hedgehogs (Hubert et al. 2011). This study aimed to produce a robust estimate of the density of hedgehogs in exotic pasture on the Otago Peninsula using SECR (Efford 2020), providing the first density estimate of its kind in New Zealand, as well as parameters required to optimise trapping regimes for hedgehog management in pasture habitat.

DOI: https://doi.org/10.20417/nzjecol.47.3555

Methods

The study site was the Harbour Cone Reserve on the Otago Peninsula, Dunedin, New Zealand (45°51′ S, 170°38′ E), which consists of exotic pasture grasses grazed by sheep (*Ovis aries*), stands of Monterey cypress (*Cupressus macrocarpa*) and Monterey pine (*Pinus radiata*), steep hills, sheltered valleys, farm buildings, tracks, and roads, typical of the predominant habitats on the peninsula. Eighty-nine live-capture traps (large Elliott Aluminium folding box traps; 15.0 × 15.5 × 46.0 cm) were spaced approximately 90 m apart to create a grid of c. 100 ha (Fig. 1). Each live trap was baited with approximately 15 g of wet fish cat food. A blaze of flour, icing sugar, and curry powder (ratio: 4 cups:1 cup:2–3 tsp respectively) extended 30 cm from the trap entrance. Traps contained water in a small dish and bedding of either old newspaper or grass and were covered by hessian sacking or tarpaulin to prevent overheating. The trapping period was initially planned to be 6 days during expected fine weather in late February and early March 2018 (late summer and early autumn), when hedgehogs are active. Due to two multi-day periods of wet weather during which traps were closed, and to low recapture rates, the trapping period instead started on 27 February and ended on 21 March. Traps were checked daily and were set for 15 days in total. Unoccupied traps were reset after 3 days, and water, bedding, and bait were changed. Captured hedgehogs were marked using coloured PVC electrical tubing cut into rings and attached by superglue (Selleys Araldite 5-minute Epoxy; Jones 2006). The tubes, attached high on the spines to avoid adhering to the skin, were grouped into four quadrants on the hedgehogs' backs with 2–3 tubes per quadrant in a predetermined left-right, top-bottom code including 'blank' quadrants. This created unique patterns for identifying individuals. The weight of captured hedgehogs was recorded and the individual sexed if possible: smaller animals were difficult to sex, and stressed animals were released quickly as they were unlikely to relax and uncurl, which is required for sexing.

Density was calculated with spatially explicit capture–recapture methods in the *secr* package v. 4.5.8 (Efford 2020) in R v. 4.2.1 (R Core Team, 2022). The population was assumed to be closed (no births, deaths, immigration, or emigration) during the short trapping period (Otis et al. 1978). Based on pre and post model-fitting checks that identify an appropriate buffer width to encompass the range of all individuals that could have been captured in the grid (*secr* functions RPSV, suggest.buffer, and esa.plot), we selected a buffer width of 300 m around the trapping area, leading to a total mask area of 244 ha.

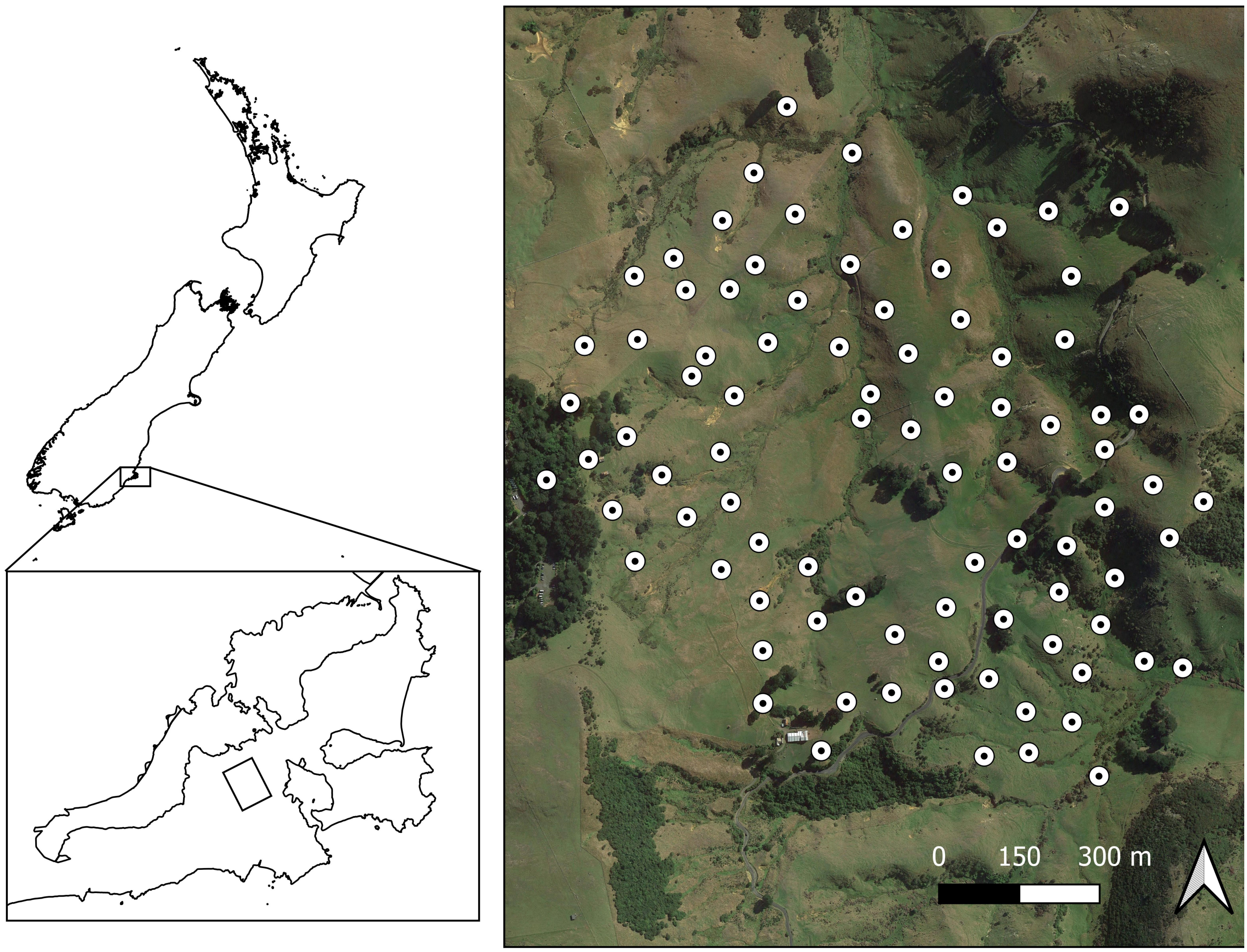

Figure 1. Locations of traps within a 100 ha grid used for spatially explicit capture–recapture of hedgehogs (*Erinaceus europaeus*) on the Otago Peninsula, New Zealand.

Model fitting

We chose a half-normal detection function to represent the decline in capture probability of an individual with increasing distance from the centre of its home range. This function is commonly used in *secr* (Efford 2004), and alternative detection functions (negative exponential, hazard rate) did not lead to substantial differences in parameter estimates (D, g_0 and σ). We chose five candidate models to represent plausible variability in the trapping process. The first was a null model (g_0 and σ constant). The next four models each had an additional parameter applied to g_0 as a representation of individual behavioural change in response to capture. These were: (1) model b, which depicts a change in capture probability in response to capture that remains throughout the trapping period (Otis et al. 1978; Borchers & Efford 2008); (2) model bk, a long-term behavioural response to capture that is specific to a trap location; (3) model B, a transient behavioural response that lasts only until the next trapping occasion, and (4) model Bk, a location-specific transient behavioural response. Models were fitted to the data with maximum likelihood methods using a multi-catch estimator (Efford et al. 2009). Model fits were compared using Akaike's Information Criterion corrected for small sample size (AICc) (Hurvich & Tsai 1989). The best-performing model (lowest AICc) was chosen, and we derived density from this model.

Results

We captured 32 individual hedgehogs in 89 traps that were open for 15 days; 18 recaptures were recorded of eight individuals, each recaptured up to five times. Nine hedgehogs were male, 12 female and 11 unknown, with a mean weight of 482 g (180–890 g; median 460 g) across all individuals (Table 1). Hedgehogs weighing between 400 and 600 g are thought to be juveniles (Parkes 1975; Gorton 1997): nineteen individuals (59%) weighed less than 500 g and 11 (34%) less than 400 g. The best-supported model according to AICc was model B, which depicts a behavioural response to capture lasting until the next trapping occasion (Table 2). The B model had an Akaike weight of 0.8, indicating high support; the next best model had ΔAICc = 3.34, well above the margin of c. 2 indicating substantial support (Burnham & Anderson 2002). Based on this model, the population density estimate at this site was 0.46 hedgehogs ha^{-1} (95% confidence interval 0.26–0.82 ha^{-1}). The g_0 parameter estimate for model B increased when parameter B was true, i.e. for the trapping occasion following when an individual was first captured. That is, individual hedgehogs were more likely to be recaptured the day following initial capture (a 'trap-happy' response).

Discussion

Here we present a robust estimate of population density and the first estimates of g_0 and σ for hedgehogs in New Zealand. The population density of hedgehogs estimated in exotic pasture in this study (0.46 ha^{-1}) is lower than densities calculated using less robust methods in other habitats in New Zealand. Parkes (1975) estimated that densities in dairy pasture and pine plantations in the Manawatu region (North Island) ranged between 1.1 ha^{-1} in winter and 2.5 ha^{-1} in summer and autumn, with the frequency of sightings varying seasonally and daily; more hedgehogs were seen in fine than in wet weather. Based on these results, our estimate should reflect maximum densities at our study

Table 1. Results summary of hedgehog (*Erinaceus europaeus*) live-trapping on the Otago Peninsula, New Zealand, in 89 traps set for 15 days in February–March. Some individuals could not be sexed.

Total number of individuals	Total number of recaptures	Sex distribution	Mean weight (g) (range)	Median weight (g)
32	18	9 Male; 12 Female; 11 Unknown	482 (180–890)	460

Table 2. Results of the AICc analysis of candidate models to estimate population density and associated parameters of hedgehogs (*Erinaceus europaeus*) on the Otago Peninsula, New Zealand. Models B, Bk, bk, and b depict alternative behavioural responses to capture (see Methods). ~1 indicates a constant. The most well supported model (shaded) was model B. No other models were considered well-supported, as ΔAICc > 2.00. Ď is estimated density per ha and its 95% confidence interval, $\hat{g}_0$ and $\hat{\sigma}$ jointly define the estimated detection function, and AICcwt is the model weight.

Model	Parameters	$\hat{D}(SE)$	95% CI	($\hat{g}_0$) (SE)	$\hat{\sigma}$ (SE)	Log likelihood	ΔAICc	AICcwt
B	g_0~B σ~1	0.46 (*0.14*)	0.26–0.82	0.015 (*0.006*)	85.67 (*11.74*)	−250.65	0.00	0.80
Bk	g_0~Bk σ~1	0.37 (*0.09*)	0.23–0.59	0.018 (*0.006*)	92.30 (*13.84*)	−252.32	3.34	0.15
null	g_0~1 σ~1	0.35 (*0.08*)	0.22–0.54	0.023 (*0.007*)	85.90 (*11.81*)	−255.59	7.24	0.02
bk	g_0~bk σ~1	0.37 (*0.10*)	0.23–0.62	0.016 (*0.007*)	94.82 (*15.55*)	−254.51	7.73	0.02
b	g_0~b σ~1	0.31 (*0.10*)	0.17–0.59	0.028 (*0.015*)	85.85 (*11.70*)	−255.52	9.75	0.01

site as it was made during summer/early autumn (February/March) and traps were open only during fine weather. Density of hedgehogs on dairy pasture in Canterbury (South Island), calculated using a capture–recapture model (Jolly 1965) from spotlight surveys of marked and unmarked animals over 2.5 years, varied between < 4 ha^{-1} in winter to 8 ha^{-1} in March (Campbell 1973). Gorton (1997) estimated hedgehog density using mark-recapture on farmland consisting of pasture and patches of native bush and pampas grass (*Cortaderia selloana*) at Lake Wairarapa (North Island) between October and May and reported a density of 0.88 ha^{-1}, closer to our estimate.

Hedgehog density estimates also vary in the UK and Europe: in Ireland, Haigh (2011) estimated 3.07 hedgehogs ha^{-1} in a lowland mixed agricultural landscape, whereas Hubert (2011) in north-eastern France used distance sampling to arrive at an estimate of 0.44 ha^{-1} in a rural, mostly agricultural landscape. Bethoud (1982, in Hubert 2011) reported 0.5 hedgehogs ha^{-1} in rural Switzerland and Parrott et al. (2014), using night-time lamped whole-site searches in west and south-west England, reported densities of 0.47 ha^{-1} on amenity grassland and 0.04 ha^{-1} on pasture. The different sampling methodologies make it difficult to draw any conclusions regarding patterns of density across habitats and climatic regions, and future insights will depend on the repeated application of robust methodology such as SECR, while accounting for variation in detectability related to breeding, hibernation, and trap type.

The availability of food, shelter and nesting sites, the presence of predators, and climate all influence hedgehog presence, habitat preferences, and therefore densities (Kristiansson 1984; Micol et al. 1994; Jensen 2004; Riber 2006). In the UK and Europe, open pasture appears to be favourable habitat only when badgers (*Meles meles*), which prey on hedgehogs, are absent (Doncaster 1994; Young et al. 2006; Haigh 2011; Williams et al. 2018), and sufficient macro-invertebrate prey are available (Haigh et al. 2012). Earthworm (*Lumbricus* spp.) abundance has been identified as an important regulator of hedgehog numbers on agricultural and urban land in France (Hubert 2011) and Oxfordshire in the UK (Doncaster 1994). The fact that pasture is a favourable rural habitat in Europe suggests that the hedgehog density we observed in this study likely reflects a healthy population, especially since there are no predators. Patches of shrubland and forest within our study area would have provided habitat for nest and shelter sites and hibernacula. Future studies in New Zealand should attempt to measure prey availability as well as hedgehog density to develop a better understanding of what drives the relationship between hedgehog abundance and habitat.

The mean body mass of hedgehogs in our study (482 g, $n = 31$) was lower than values reported for February by Parkes (1975; 628 g for females ($n = 9$) and 622 g for males ($n = 13$) and by Gorton (1997; 688.7 g; SE = 10.8). The body mass of hedgehogs in the Manawatu region ranged between 603 and 789 g across all months. Parkes considered individuals weighing under 400 g to be juveniles, and Gorton treated those weighing < 500 g as juveniles but acknowledged that it was difficult to distinguish between adult and juveniles when weights were between 400 and 600 g. In the UK, the mean weight of males was 846 g and of females 792 g (Dowding et al. 2010). The low weights of many of the hedgehogs in our study indicates the presence of juveniles, which may have been dispersing out of their natal territories. As young hedgehogs do not become fully independent until 6–7 weeks of age (Jones 2021) this result suggests some hedgehogs at our study site were born as late as January: births of litters in Wellington (North Island) have been recorded in November, December and as late as February and March (Brockie 1959).

Our study design was imperfect: there was a gap in the middle of the grid, and we combined data over the entire trapping period into one 'session' for analysis, despite two pauses in trapping when traps were closed due to wet weather. This decision was made because it is unlikely that either capture probabilities or density varied substantially across the short trapping period, and we could derive more robust estimates by combining all the data. It is possible that we have over-estimated density if there were movements into and out of the study area: adults are known to make movements over distances comparable to the study area size over 20 days (Doncaster et al. 2001), and dispersal by the high proportion of juveniles (34–59%) could also have reflected both immigration and emigration, resulting in an estimated population size that is larger than actually present (Efford & Schofield 2020).

The estimates we have obtained of g_0 and σ are important parameters used by tools such as TrapSim (Gormley & Warburton 2017) to investigate the trapping effort required in surveillance or eradication regimes, including proposed trap spacing and number of trap nights. Our parameters, which apply to hedgehog populations in landscapes consisting of sheep pasture with patches of trees, a very common landscape throughout much of New Zealand, should therefore be useful in guiding future management of hedgehogs in New Zealand.

Acknowledgements

We thank the Hereweka Harbour Cone Trust and Brendon Cross for giving us access to the land, all the volunteers who assisted in data collection, and Chris Jones who provided advice on field methods and study design. We are also grateful to the anonymous reviewers who contributed constructive comments on the manuscript.

Additional information and declarations

Funding: Funding and field support was provided by the Department of Zoology, University of Otago.

Authors' contributions: YvH, PJS, DJW & LS contributed to the concept, all authors contributed to data collection, CRP analysed the data and drew the figure, YvH wrote the first draft and all authors revised and edited the manuscript.

Conflicts of interest: The authors declare no conflicts of interest.

Data and code availability: Data and code are available via the Zenodo open-access repository https://doi.org/10.5281/zenodo.8327724.

Ethics: This work was approved by the University of Otago animal ethics committee under AUP101-17.

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Received: 18 April 2023; accepted: 16 August 2023
Editorial board member: Warwick Allen