# NEW ZEALAND JOURNAL OF ECOLOGY

## RESEARCH

# Spatial ecology meets eradication of feral cats on Auckland Island

Mariano Rodríguez-Recio[1,2]* (iD), Rachael L. Sagar[3] (iD), Lindsay Chan[4], Finlay S. Cox[3] and Paul M. Jacques[3]

[1]Department of Biology and Geology, Physics and Inorganic Chemistry, Unit of Biodiversity and Conservation, Rey Juan Carlos University, C/Tulipán s/n, Móstoles 28933, Madrid, Spain
[2]Department of Ecology, Swedish University of Agricultural Sciences, Uppsala, Sweden
[3]Department of Conservation, PO Box 743, Invercargill 9840, New Zealand
[4]Department of Conservation, Private Bag 4715, Christchurch 8140, New Zealand
*Author for correspondence (Email: mariano.recio@gmail.com)

**Abstract:** Restoration initiatives of ecosystems transformed by human actions require optimisation of eradication measures of introduced species, particularly in fragile insular ecosystems. We studied aspects of the spatial ecology of introduced feral cats (*Felis catus*) on subantarctic Auckland Island of New Zealand to assist eradication efforts of pests from this remote, biologically rich island. Firstly, we estimated home range sizes and identified core areas of activity based on movement-rooted dynamic Brownly bridge models. Second, we used resource selection functions with generalised linear mixed models to identify seasonal patterns of space use associated to topographic, vegetation and other landscape predictors. Lastly, we quantified cats daily movement rates within home ranges. Average home range size was larger than on other offshore islands and mainland New Zealand, which might relate to lower cat densities and the abundance and predictability of food resources on the island. Cats mostly selected mosaic areas of forest, shrubs and tall tussocks near the coast, and in predominantly flat areas or nearby steep cliffs, which are all typical habitats of seabirds and terrestrial birds. Cats also selected alpine short tussocks during the cold season, likely related to the upsurge of mice (*Mus musculus*) due to tussock mast seeding and to transiting to steep cliffy areas. Male cats had home ranges that were larger, contained more core areas, and covered longer daily distances in the warm season than females, which might be associated with different breeding and reproductive behaviour. Eradication tools will need to target all habitats on Auckland Island with increased efforts in areas of identified higher use by cats. Understanding aspects of pest species' spatial ecology on offshore islands worldwide can assist decision-makers in optimising eradication programs such as Predator Free 2050 in New Zealand.

**Keywords:** animal movement, Auckland Island, eradication, feral cats, introduced mammals, islands, New Zealand, resource selection, subantarctic islands

## Introduction

Humans have caused longstanding impacts in ecosystems through habitat destruction, biological invasions, and polluting, which are major global threats to biodiversity. Currently, environmental restoration projects are taking a prominent role in national and transboundary initiatives worldwide, including in the context of the broadly divulged concept of rewilding, which involves the recovery of natural processes and ecological functionality in ecosystems modified from their original conditions (Navarro & Pereira 2015; Fernández et al. 2017). One challenge for these initiatives is the control of alien invasive species and the implementation of corrective measures against the dramatic direct and indirect impacts they cause in recipient ecosystems (Derham et al. 2018). The impacts of invasive species are exacerbated in island systems due to the ecological particularities and fragilities of these

isolated environments, which globally contain more than 20% of terrestrial plant and vertebrate species (Courchamp et al. 2003; Blackburn 2004; McGlone 2006) and where restoration projects are urgently needed (Holmes et al. 2019).

New Zealand is an insular nation where unique flora and fauna evolved in the absence of terrestrial mammalian predators (Parkes & Murphy 2003). The recent introduction of animals and plants to New Zealand, with 31 established mammal species (25 considered as pests), is a stark example of the severe threat and impact invasive species pose to native biodiversity, the environment, and the economy (McGlone 2006). Introduced mammals have caused the decline and extinction of many native species as well as significant transformations in the New Zealand environment (Clout & Russell 2006). Mammalian pest predators to New Zealand biota include brush-tailed possums (*Trichosurus vulpecula*), ferrets (*Mustela furo*), stoats (*Mustela erminea*), weasels

(*Mustela putorious*), pigs (*Sus scrofa*), mice (*Mus musculus*), rats (*Rattus exulans*, *R. rattus*, *R. norvegicus*) and feral cats (*Felis catus*). These species are well distributed across New Zealand, including many offshore islands (Parkes & Murphy 2003). To relieve the pressure caused by introduced mammalian predators, New Zealand authorities have implemented recurrent control to suppress pests in an effort to reduce environmental and economic harm, in addition to undertaking numerous pest eradications from islands (Clout & Russell 2006). In this vein, the New Zealand government announced the Predator Free 2050 (PF2050) goal; an ambitious action plan to restore ecosystems and the economy by eradicating brush-tailed possums, rats, and mustelids from all of New Zealand by 2050 (Russell et al. 2015). An interim goal of PF2050 is to eradicate all introduced mammalian predators from uninhabited offshore islands by 2025 (Department of Conservation 2020).

New Zealand offshore islands include the subantarctic islands – a UNESCO World Heritage Site (1998) – home to diverse endemic invertebrates, birds, and megaherb flora (typical large herbaceous perennial wildflowers of these islands). Following the successful eradication of rabbits (*Oryctolagus cuniculus*), mice and cattle (*Bos taurus*) from Enderby Island (Torr 2002), rats from Campbell Island (McClelland 2011), and mice from Antipodes Island (Horn et al. 2019), the proposed Maukahuka Pest Free Auckland Island project aims to contribute to PF2050 to transform subantarctic Auckland Island into New Zealand's largest pest-free landmass. Auckland Island is the only subantarctic island where invasive mammalian pests remain (Russell et al. 2020). However, the isolation, size, harsh climate and terrain of Auckland Island pose significant operational challenges for the eradication of these species.

The feral cat, one of the target species of the Maukahuka project, is included in the International Union for Conservation of Nature (IUCN) list of 100 of the world's worst invasive species (Lowe et al. 2004). Globally, feral cats have caused the extinction of at least 14% of bird, reptile and mammal species on islands (Medina et al. 2011), including on New Zealand offshore islands (Clout & Russell 2006). Europeans introduced cats into New Zealand, where they spread with minimal competition and established as a top predator (Gillies & Fitzgerald 2005). Feral cats are broadly targeted in control and eradication campaigns of predators all over New Zealand, and efforts have been assisted by scientific data on the ecology and behaviour of the species, including by the recent use of emerging technologies like light-weight GPS-collars (Recio et al. 2010, 2015; Recio & Seddon 2013; Cruz et al. 2014). Furthering knowledge on the spatial behaviour of feral cats is of great value to optimise monitoring and control methods (Fisher et al. 2015). To date, research has primarily focused on mainland New Zealand and information on the spatial ecology of feral cats on offshore islands is scarce (see Dowding (1998) on Motuihe Island and Strang (2018) on Ponui Island). However, the particularities of each island ecosystem, including the availability and distribution of resources to feral cats, make it necessary to further research these environments. A better understanding of space-use behaviour of feral cats can assist operational decision-making by providing predictions of the areas of increased space-use, allowing prioritisation and focused eradication efforts (Recio et al. 2017).

This research aims to assist the Maukahuka project in eradicating feral cats from Auckland Island by contributing the first information on the spatial ecology of the species in this remote location. Using lightweight GPS-tracking devices,

we relied on analyses of individual cat movement patterns to identify the spatial and seasonal use of resources that ultimately shape the space use of individuals and the distribution of the species on Auckland Island. Thus, we firstly analysed home ranges considering this estimator, conceptually, as the spatial representation of a cognitive map that animals keep-up-to-date (Powell & Mitchell 2012) and that ultimately defines different areas of the probability of animal occurrence during a specified period (Kernohan et al. 2001). We estimated home ranges and core areas of activity using dynamic Brownian bridge movement models (dBBMM; Kranstauber et al. 2012) based on underlying shifts of animal behaviour. Second, we modelled the resources underlying the disproportionate selection of home-range areas per season using resource selection analyses. We produced predictive maps on the relative probability of cat presence based on landscape variables of importance for feral cats that can be identifiable on-site by trappers during field operations and where removal efforts can be targeted. Lastly, we provided summary statistics on the trends of daily male and female cat movement rates within home ranges during the entire cat tracking campaign for a picture on the roaming capacity of male and female cats by season, which can provide further insights to managers on seasonal trap deployment and spacing. Our research approach aims to assist further research on similar eradication projects in oceanic islands worldwide.

## Methods

### Study area

Auckland Island is the largest island in the Auckland Islands archipelago (Motu Maha; 50.69°S, 166.08°E, 56 816 ha) located in the Southern Ocean 465 km south of mainland New Zealand (Fig. 1). It is the fifth largest island in New Zealand (45 891 ha, 43 km long, 27 km wide, 374 km of coastal perimeter). The terrain is typically mountainous with peaks up to 631 m. The western side is an almost unbroken c. 63 km extension of cliffs up to 400 m high. The eastern side is a more sheltered series of cirques and fjords. The climate is typically wet, cool, and windy. The daily weather is characterised by long periods of wind (mean daily run of ~700 km each month), frequent rainfall (311 days per year; 80–100 mm of precipitations per month) and annual averaged mean monthly temperatures of 8.1ºC (annual averaged high and low of 11.2 and 5.1ºC, respectively) (Lisle 1965).

Vegetation consists of a band of southern rātā (*Metrosideros umbellata*) forest around the eastern, southern and northern coasts. In most places, the rātā forest merges into a thick band of low, tight shrubland dominated by inaka (*Dracophyllum longifolium*), *Ozothamnus vauvilliersii* and *Myrsine divaricata*. Poorly drained low-altitude terraces comprise swamped terrain clad in cushion herbfields interspersed with patches of tussock grassland and shrubland bands. Above c. 300 m, low stature shrubland gives way to alpine tussock grassland (*Chionochloa antarctica*) and alpine fellfield.

The Auckland Islands are designated an Important Bird Area by Birdlife International and World Centre of Floristic Diversity by the IUCN. They host 25 seabird species, such as white capped albatross (*Thalassarche cauta steadi*), and 13 native terrestrial birds, with six endemic (Miskelly et al. 2020). Large-bodied and flightless invertebrates are included in a list of about 90 endemic invertebrate species. No herpetofauna is present. The New Zealand fur seal (*Arctocephalus forsteri*) and the New Zealand sea lion (*Phocarctos hookeri*) breed around the coast.

**Figure 1.** Auckland Islands archipelago.

## Cat data

Cats were captured on Auckland Island (n = 17; males = 12, females = 5) during November to December 2018, February and August 2019. Cats were captured using leg hold traps (cubby or walk-through sets) that were for the most part baited with fish or rabbit meat (un-baited sets on animal trails were occasionally used). Set traps were checked within 12 h of sunrise each day. Upon capture, cats were sedated and equipped with SIRTRACK/LOTEK™ GPS-collars model Iridium Lite Track 130 (130 g) (n = 13) or SIRTRACK/LOTEK™ LITETRACK GPS-collars of 60 g (n = 4). These collars weighed <5% of the body mass of an adult feral cat (Cochran 1969; Recio et al. 2010). The first collar model provided location data via the Iridium satellite system. For the second model, data were downloaded using radio-frequency transmission. Collars acquired locations every 2 or 4 h between October 2018

and September 2019, which varied between individuals. We divided this period into warm season (from the beginning of the sampling period up to 21 March 2019) and cold season (from 22 March 2019 to 21 September 2019). The full-raw dataset included 9101 locations reduced to 7061 after pre-processing based on animal movement properties previously applied on feral cats (Recio et al. 2014) to ensure only reliable locations were included in the analyses. Cat number 10 died early and due to the limited number of locations, we removed this individual from the dataset.

## Home range analyses

We identified the gradient of space use intensities within home ranges that emerged from underlying spatio-temporal patterns of individual cat movements using dynamic Brownian bridge movement models (dBBMM). These models account for

the location error of GPS devices while providing accurate estimations on the spatio-temporal aggregations of animal locations that identify the intensity of use of different areas of a home range (i.e. utilisation distributions, UD; Worton 1989). Home range estimation using dBBMM relies on bursts of movements depicting different behaviours of a tracked animal computed from underlying behavioural change point analyses (BCPA) (Gurarie et al. 2009; Kranstauber et al. 2012). The dBBMM overcomes previous methods, such as kernels (KDE; Worton 1989), Brownian bridge movement models (BBMM; Horne et al. 2007) or time local convex hulls (T-LoCoH; Lyons et al. 2013), because it models animal movement paths instead of points, accounts for temporal autocorrelation, large datasets and irregularly sampled data, and incorporates underlying shifts of animal behaviour by varying the Brownian motion variance.

We estimated dBBMM using the *amt* package (Signer et al. 2019) in R software (R Core Team 2020). We assumed a GPS-location error of c. 30 m (Recio et al. 2011), and specified a moving window size of 15 locations with a margin of 5 locations, which we identified as suitable to account for full cycles of diurnal and nocturnal activity. Finally, we identified 99%, 95%, and 50% UD (hereafter UD99, UD95 and UD50; Fig. 2); the latter indicates core areas of concentrated cat activity and presence within each home range. We calculated the effective home range by discarding the overlaid areas of dBBMM and minimum convex polygons (MCPs) overlapping the sea (fjords, gulfs) for realistic availability of home-range areas.

### Resource selection analyses

We modelled the disproportionate use of resources by feral cats in relation to their availability using resource selection functions (Boyce & McDonald 1999); this method is suitable for used vs available designs such as datasets obtained from telemetry methods. Used locations are known (GPS locations) and availability is defined as random points laid over an area of interest to characterise the environment where the animal could have been but we do not know if it was there (Boyce & McDonald 1999). Used/available designs are modelled as logistic regressions with a binomial dependent variable (used = 1, available = 0) and environmental predictors. We assumed availability within the UD99 defined in the home-range analyses because we discarded unrealistic outliers after our preliminary filtering based on animal movement properties. We drew two random locations per one used location (GPS location) in each individual UD99 and quantified how cats selected resources within their individual home ranges. This approach corresponds to a Scale 3, or Design III, resource selection function (Johnson 1980; Manly et al. 2004). Feral cats are present across the entire Auckland Island and we identified all the used and random locations within home ranges covering the whole range of values for each predictor considered for the entire island. Therefore, we considered Scale 3 sufficient to model resource selection and extrapolate predictions on selection patterns over the whole island.

We selected topographic, landcover (vegetation), and other predictors of assumed relevance for feral cat movement, shelter, and food resources. These predictors also accounted for accessibility by operators to conduct eradication work all over the island. All predictors were obtained from Department of Conservation resources or Land Information New Zealand (LINZ). We converted these predictors in 30 m resolution rasters using *st* (Pebesma 2018) and *raster* (Hijmans & van Etten 2012) spatial R packages, and ArcGIS 10.4 (ESRI, Redlands, USA). Topographic predictors were computed and extracted from a digital elevation model (DEM). They included elevation (m) at each used/available location, and the variables slope (degrees), aspect (degrees, −1 for flat
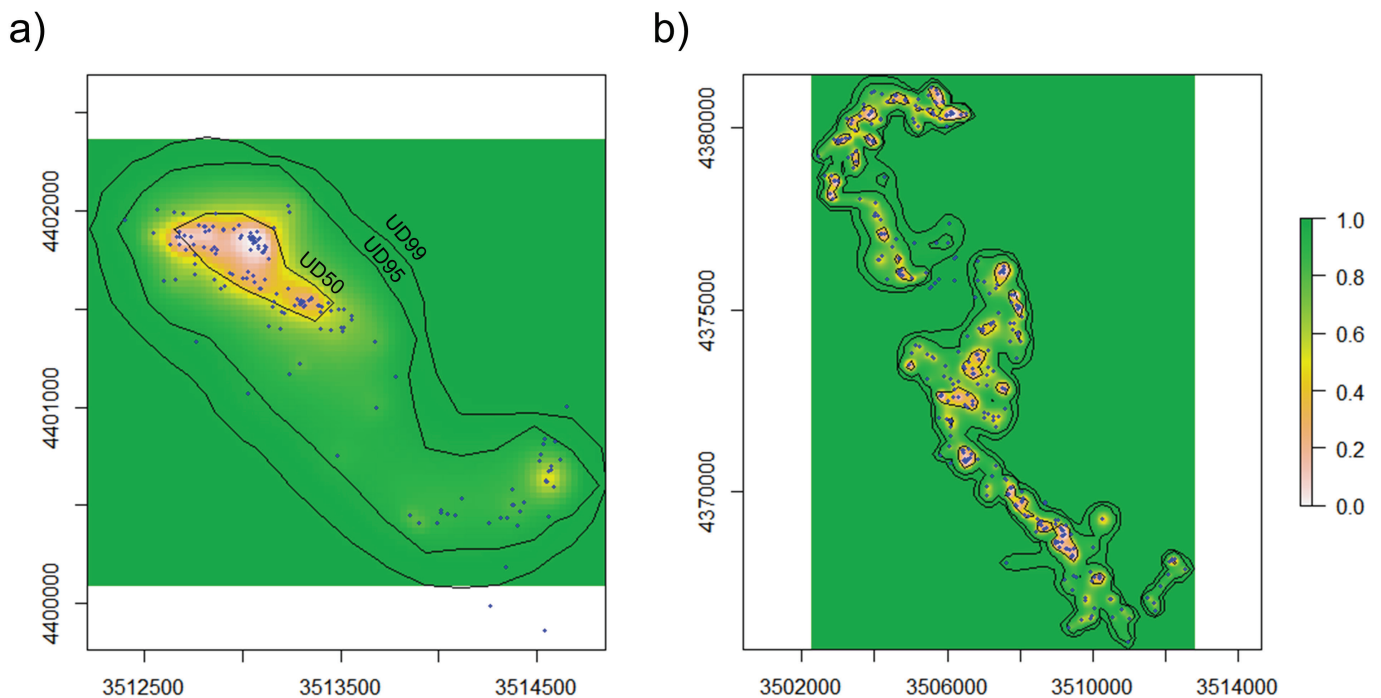


**Figure 2.** Examples of feral cat home ranges on Auckland Island estimated using dynamic Brownian bridge models (dBBMM). Illustrations show 99%, 95% and 50% utilization distributions (UD99, UD95, UD50, respectively). Illustration (a) represents a home range with a single core area (UD50) and belonged to female 17. Illustration (b) represents the home range of male 2, which is a more complex home range with multiple core areas.

areas) and roughness (the difference between maximum and minimum elevation value between surrounding cells) computed from the eight surrounding cells to each cell associated to the locations. We also quantified a response of cats to the density of cliffs within buffers of radii ranging between 90 to 2175 m (DeCesare et al. 2012). The latter distance corresponded to the maximum identified distance from a cat location to the home range boundary (UD99). The density within each buffer was determined as the number of cells classified as cliffs per the total number of cells in the buffer (discarding those depicting the sea). We finally used the percentage of cliffs within a 90 m buffer (hereafter cliffs90) because this was the distance with the smallest AIC (Akaike's Information Criterion) when modelled against the dependent variable.

Landcover predictors included dummy variables on the vegetation type in each used and random location. We considered the vegetation classes: open areas, shrubs, forests, tall tussocks, and alpine short tussocks (hereafter alpine tussocks). We also identified the presence of swamps as a dummy variable. We computed the distance to the coast as the decay function $e^{-\alpha d}$, wherein $d$ was the distance to the shore and $\alpha$ set to 0.008 (Nielsen et al. 2009). This function ensured local effects of the coast eroded precipitously as the distance increased and were irrelevant over 500 m from the shore. For consistency with model coefficients, we subtracted decay values from 1 to obtain values of 0 at the site and 1 at large distances. Lastly, we computed the density of human tracks within a 90 m buffer all over the island (hereafter tracks90). This distance best indicated the relative use of these features by cats and where operators can more easily intensify eradication efforts.

Preliminary correlation testing (r < 0.7; Hosmer & Lemeshow 2000) and variance inflation factor (VIF < 4; Zuur et al. 2010) ensured no predictor showing multicollinearity was included in the same model. Thus, we avoided elevation

and distance to the coast within the same models, as well as roughness and slope. We modelled scaled predictors vs use/availability using generalised linear mixed models (GLMM) with a binomial family and individual cat as a random effect in lme4 R package (Bates et al. 2015). Resource selection functions using GLMM accommodates autocorrelation among locations, unbalanced samples, and hierarchically structured data (Gillies et al. 2006). We proposed eight models (including the null and global models) as mathematical expressions of different hypotheses on resource selection by cats and ranked models using AIC. We applied these models in two additional multi-model inferences on subsets of the dataset for locations collected, respectively, during the warm and cold season. Lastly, the models' predictive ability was tested using a k-fold (here 5-fold) cross validation (Boyce et al. 2002).

### Movement behaviour
We conducted descriptive analyses on the daily distance travelled per day by male and female cats within individual home ranges by warm and cold seasons.

## Results

### Home-range analyses
The mean size of the effective (i.e. excluding overlap with the sea) UD99 of the 16 feral cat home ranges estimated using dBBMM was 10.17 ±2.04 km$^2$ (mean ± SE), with larger areas for males (12.75 ±2.63 km$^2$) than females (4.49 ±0.72 km$^2$) (Fig. 3). The mean number of core areas (UD50) within individual home ranges was 4.87 ±0.28 with a mean size of 1.23 ±0.21 km$^2$ (Fig. 3). Core areas were also larger (1.45 ±0.28 km$^2$) and more abundant (6.27 ±2.01) in male home ranges than
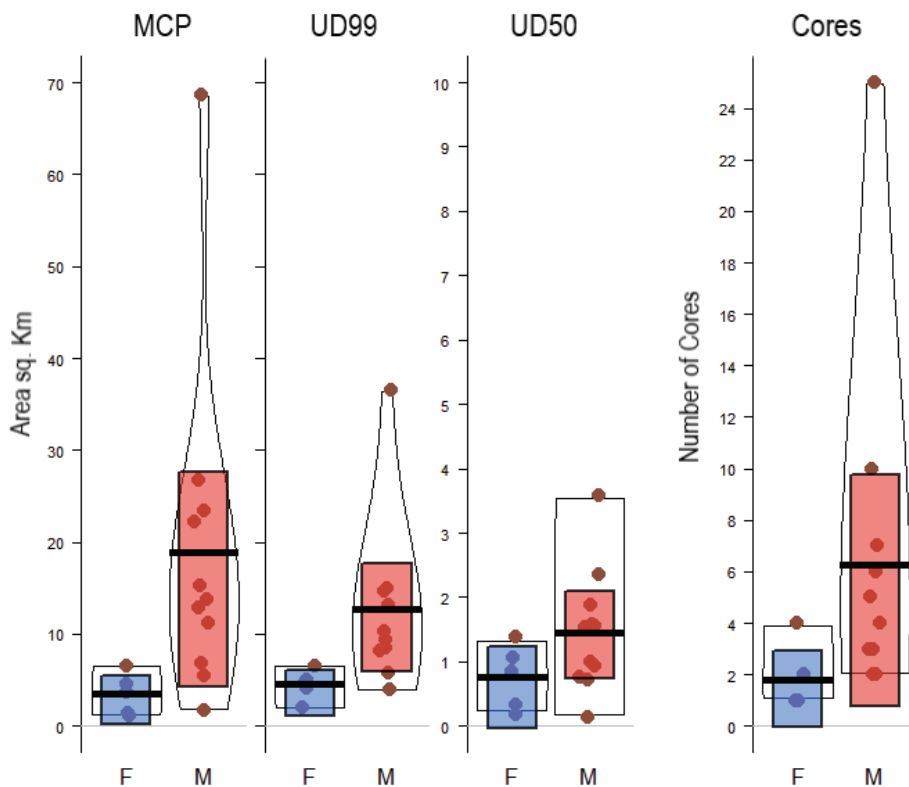


**Figure 3.** Violin graphs representing the available home range areas (discarding overlapping areas with the sea) of female (F) and male (M) feral cats tracked on Auckland Island using different home range estimators, including the minimum convex polygon (MCP), and 99% and 50% (core areas of activity) utilisation distributions using dynamic Brownian bridge models (dBBMM). The graph to the right represents the number of core areas of activity (UD50) per home range in each individual cat home range.

those of females (0.76 ±0.22 km$^2$ in an average of 1.80 ±0.58 cores) (Fig. 3). Mean MCP estimation (for comparison with previous research) was 18.94 ±4.49 km$^2$ (25.02 ±5.63 km$^2$ for males; 5.56 ±1.59 km$^2$ for females). The effective MCP was 14.08 ±4.16 km$^2$ (18.92 ±5.48 km$^2$ for males; 3.45 ±1.00 km$^2$ for females).

### Resource selection analyses

Multi-model inferences revealed the model including the predictors distance to shore decay, slope, aspect, cliffs, tracks and the dummy landscape variables was the most plausible model for the three cases studied, i.e. warm and cold seasons as well as all the seasons combined (Table 1). This model notably exceeded the performance of the following models

(AIC > 70 in all the models), which justified the use of these single models instead of a model averaging of the models tested in each multi-model inferences (Grueber et al. 2011).

Distance to shore decay showed a significant negative relationship with use by cats in the three cases, indicating cats tended to use areas near the shore more than inland locations (Table 2, Figs. 4 & 5). A significant negative coefficient and a positive quadratic term of the variable slope in the three cases indicated cats tended to use areas of low and high slope instead of mid-range values (Table 2, Fig. 4). Similarly, positive coefficient values for the variable cliffs revealed cats significantly selected sites near cliffs in the three cases (Table 2, Fig. 4). Cats also exhibited a positive association with aspect, although non-significant for the cold and overall

**Table 1.** Results on model ranking from multi-model inferences on feral cat resource selection in Auckland Island for cold (between March 21 to September 21), warm (rest of dates), and both seasons.

|  | All seasons | | | Warm season | | | Cold season | | |
| Rank | Models* | AIC | ΔAIC | Models* | AIC | ΔAIC | Models* | AIC | ΔAIC |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| 1st | 3 | 25 524 | 0 | 3 | 14 402 | 0 | 3 | 11 016 | 0 |
| 2nd | 1 | 25 694 | 170 | 1 | 14 483 | 81 | 1 | 11 088 | 72 |
| 3rd | 5 | 25 797 | 273 | 4 | 14 515 | 113 | 5 | 11 138 | 122 |
| 4th | 4 | 25 798 | 274 | 2 | 14 557 | 155 | 4 | 11 169 | 153 |
| 5th | 2 | 25 858 | 334 | 5 | 14 571 | 169 | 2 | 11 170 | 154 |
| 6th | 6 | 25 969 | 445 | 6 | 14 638 | 236 | 6 | 11 233 | 217 |
| 7th | 7 | 26 257 | 733 | 7 | 14 790 | 388 | 7 | 11 337 | 321 |
| 8th | 8 | 27 733 | 2209 | 8 | 15 528 | 1126 | 8 | 12 164 | 1148 |

* Model 1: elevation + elevation$^2$ + slope + slope$^2$ + aspect + aspect$^2$ + cliffs90 + tracks90 + landcover.var
Model 2: elevation + elevation$^2$ + roughness + roughness$^2$ + aspect + aspect$^2$ + cliffs90 + tracks90 + landcover.var
Model 3: dist. to shore decay + slope + slope$^2$ + aspect + aspect$^2$ + cliffs90 + tracks90 + landcover.var
Model 4: dist. to shore decay + roughness + roughness$^2$ + aspect + aspect$^2$ + cliffs90 + tracks90 + landcover.var
Model 5: elevation + elevation$^2$ + slope + slope$^2$ + aspect + aspect$^2$ + cliffs90 + tracks90
Model 6: elevation + elevation$^2$ + roughness + roughness$^2$ + aspect + aspect$^2$ + cliffs90 + tracks90
Model 7: elevation + elevation$^2$ + landcover.var
Model 8: null.model

**Table 2.** Results on coefficients included in the best models selected from multi-model inferences on feral cat resource selection in Auckland Island during the cold (between March 21 to September 21), warm (rest of dates), and both seasons. The best model for each season was the same model and included the variables shown in the table. p < 0.01 (*), p < 0.001 (**), p < 0.0001 (***).

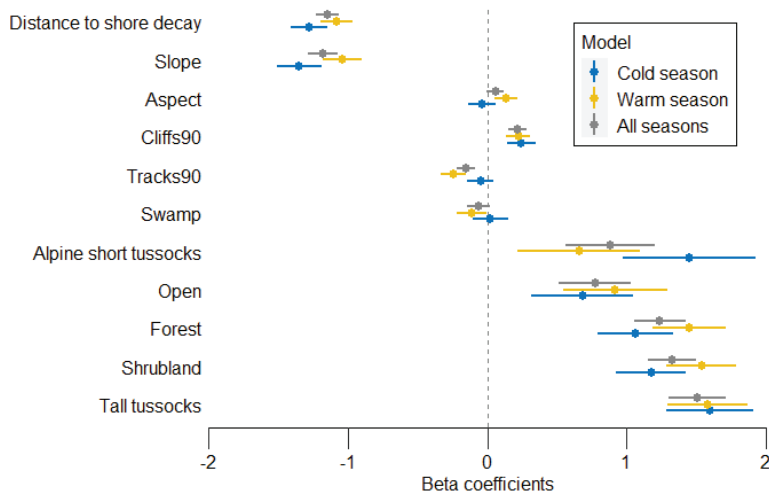|  | All seasons | | | Warm season | | | Cold season | | |
| Variables | β | SE | p | β | SE | p | β | SE | p |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Intercept | −2.25 | 0.12 | *** | −2.48 | 0.18 | *** | −2.18 | 0.16 | *** |
| distance to shore decay | −1.14 | 0.04 | *** | −1.08 | 0.05 | *** | −1.28 | 0.06 | *** |
| slope | −1.18 | 0.05 | *** | −1.04 | 0.07 | *** | −1.35 | 0.08 | *** |
| slope² | 0.50 | 0.03 | *** | 0.52 | 0.04 | *** | 0.46 | 0.05 | *** |
| aspect | 0.05 | 0.03 |  | 0.13 | 0.04 | * | −0.04 | 0.05 |  |
| aspect² | 0.53 | 0.07 | *** | 0.45 | 0.08 | *** | 0.63 | 0.10 | *** |
| cliffs90 | 0.21 | 0.03 | *** | 0.22 | 0.04 | *** | 0.24 | 0.05 | *** |
| tracks90 | −0.15 | 0.03 | *** | −0.24 | 0.05 | *** | −0.05 | 0.04 |  |
| swamp | −0.06 | 0.04 |  | −0.11 | 0.05 | * | 0.02 | 0.06 |  |
| alpine short tussocks | 0.88 | 0.16 | *** | 0.65 | 0.22 | ** | 1.44 | 0.24 | *** |
| open | 0.77 | 0.13 | *** | 0.91 | 0.19 | *** | 0.68 | 0.19 | *** |
| forest | 1.23 | 0.09 | *** | 1.44 | 0.13 | *** | 1.06 | 0.14 | *** |
| shrubs | 1.32 | 0.09 | *** | 1.53 | 0.12 | *** | 1.17 | 0.13 | *** |
| tall tussocks | 1.50 | 0.10 | *** | 1.57 | 0.14 | *** | 1.59 | 0.16 | *** |

**Figure 4.** Coefficients for the predictors included in the best model identified for each of the multi-model inference on feral cat resource selection applied to the warm, cold (between March 21 and September 21) and all seasons on Auckland Island. The resulting best model in each multi-model inference was the same and included the variables represented in the graph. The graph includes coefficients and 95% confidence intervals. Confidence intervals including zero are considered as non-significant.

cases. The quadratic term indicated this association was stronger for lower and higher values of aspect (i.e. closer to 0 or 360°) depicting a selection for northern faces (Table 2, Fig. 4). We found no association between human tracks and cat use in all cases (Table 2, Fig. 4). Coefficients on swamp areas indicated a significant negative association in the overall and warm season and positive but non-significant in the cold season (Table 2, Fig. 4).

Dummy variables on vegetation for each habitat type indicated, respectively for each seasonal model, the log-odds ratio of each variable being chosen relative to other habitat types. These log-odds for habitat type selection in the warm season indicated a higher selection of tall tussock areas, shrubland, forest, open habitat, and alpine short tussock in this order. This order of selection was also the same during the cold season except for alpine short tussocks that became the second habitat variable with higher odds of selection (Table 2, Fig. 4).

Attending to the Baldwin (2009) classification on model performance, the model validation using 5-fold cross-validations of the seasonal and overall models revealed very good performance in all the cases. The prediction capacity for the overall and cold season models ($|r| = 0.98$ for both) was slightly higher than the warm season model ($|r| = 0.96$ for both).

**Movement behaviour**

Feral cats moved a minimum of between 9 to 9443 m per day within individual home ranges during the sampling period, with an average of 2376 ±33 m (mean ± SE). Males moved an average of 2488 ±46 m (range: 9 to 9443 m), and females an average of 2227 ±45 m (range: 35 to 7977 m). During the warm season, males moved an average of 2493 ±70 m per day (range: 66 to 9443 m), and females 2320 ±70 m (range: 74 to 6220 m). During the cold season, males moved on average 2484 ±57 m per day (range: 9 to 8211 m) and females 2176 ±58 m (range: 35 to 7977 m).

## Discussion

This research represents one of the few studies of feral cats' spatial ecology on offshore islands of New Zealand (but see also Dowding 1998; Strang 2018). Our results provide valuable initial information on the home-range behaviour and resource selection of feral cats on Auckland Island to assist eradication efforts and enable further investigations on the space use and activities of the species. Using dBBMM rooted in animal movement properties, we identified males had larger home ranges and created more activity cores than females. Cats tended to use all the vegetation considered here, though most vegetation types used were those offering refuge and most likely food resources such as shrublands, forest, tall tussock areas, and alpine short tussocks during the cold season. Cats also concentrated their activities in areas near the coast where nesting birds and other food resources linked to the sea might provide additional food provisions.

Feral cat home ranges in New Zealand vary notably in different environments and conditions (Gillies & Fitzgerald 2005). The average home-range size of cats in this study (18.94 km² and 14.08 km² for full and available MCP, respectively) was notably larger than previous studies on substantially smaller offshore islands using VHF radio collars, such as the 0.47 km² of Motuihe Island (a highly invaded small island of only 1.79 km²) (Dowding 1998) and the 4.12 km² of Ponui Island (Strang 2018). Our estimated average size was also larger than previous estimations on mainland New Zealand using VHF radio collars (Gillies & Fitzgerald 2005) or GPS-collars (Recio & Seddon 2013), although closer to the 20.83 km² of Stewart Island (Harper 2007). Cat density was relatively low on Stewart Island and the main prey there, the rat (Harper 2010), could have explained larger cat ranges (Harper 2007). Similarly, a seasonal variation in prey distribution and abundance of mice (Sagar et al. 2022), increased patchiness and aggregation of other food resources (Norbury et al. 1998), and tolerance to conspecifics (Recio & Seddon 2013) could explain the relatively large average home range observed on Auckland Island.

Home-range size in feral cats is considered dependent on the availability of resources and the population density, and for males, also the density and distribution of females (Liberg et al. 2000; Say & Pontier 2004). Our results revealed larger home ranges and increased number of cores of activity for male cats, which together with their observed longer distances travelled per day during the warm season (i.e. mating period), suggests the abundance and distribution of females and resources could be determinants in males' movements. Uncollared cats identified by individual markings from trail camera footage were also cued into seasonal food sources,
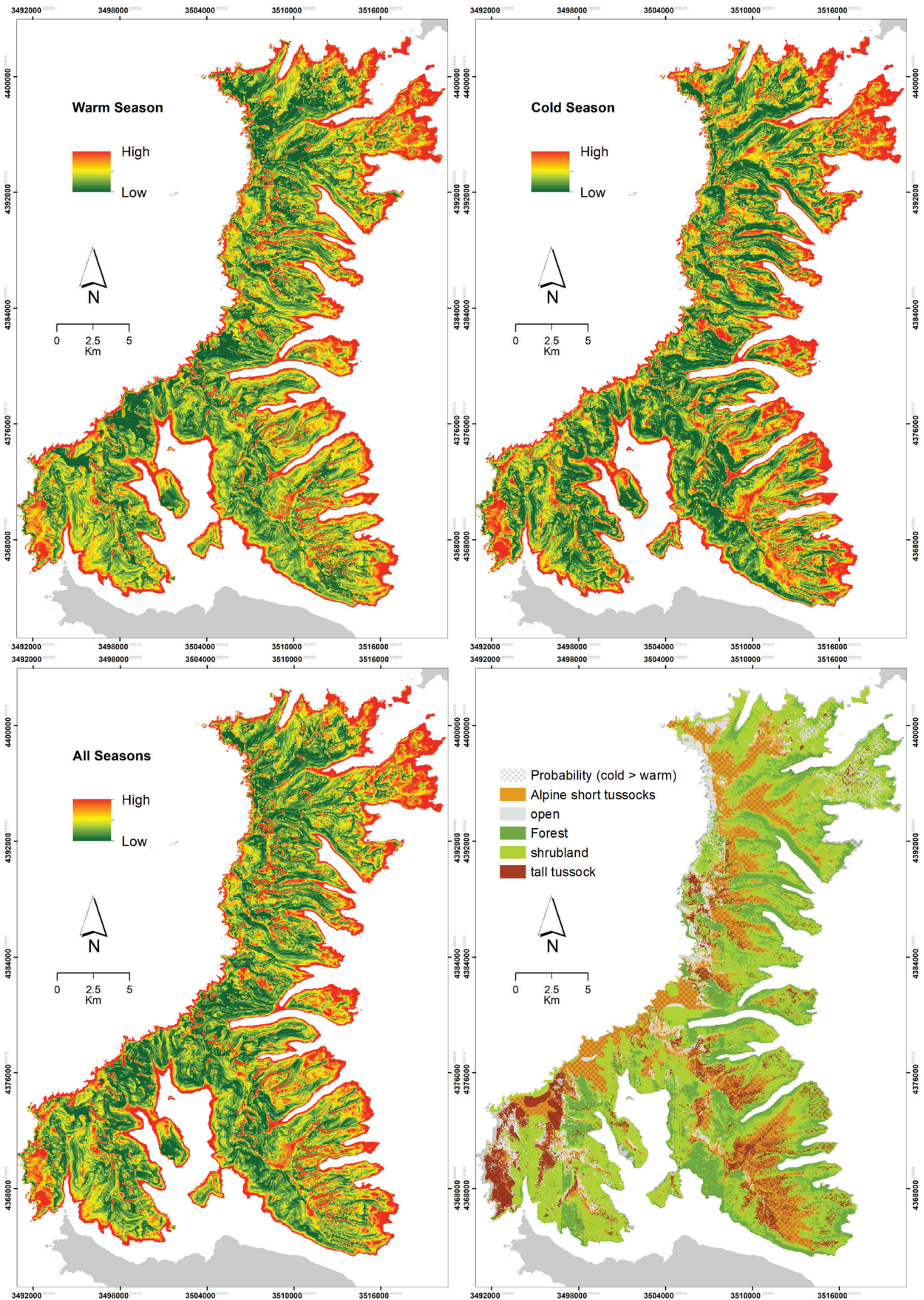
**Figure 5.** Above and left-below maps represent predictive maps on the probability of space use by feral cats on Auckland Island calculated by applying each of the best models identified in multi-model inferences for the warm (before March 21), cold (between March 21 and the end of the tracking campaign), and all seasons. Map to the right below represents the vegetation type and the areas with probability of use in the cold season higher than in warm season.

with one individual male cat traversing a minimum distance of 9 km of coastline in under 6 hours and swimming ~100 metres to access a small islet (Masked Island) where white-headed petrels (*Pterodroma lessonii*) were breeding in high density. At least four cats identified by individual markings were observed on this islet over a 19 day period, which suggests regular movements between the islet and Auckland Island (Cox et al. 2019). Conversely, the smaller female home ranges with fewer cores of activity suggest females might focus space use around a few specific sites with enough food resources and refuge for themselves and kittens (Liberg et al. 2000). One tracked female was known to be lactating during the warm season and two were pregnant during the end of the study period in the cold season. However, we acknowledge the number of females tracked was lower than males and only one male was tracked during the last 3 months of the cold season, requiring caution of interpretations. Further research accounting for home range overlapping, mice abundance and availability, and estimation of cat densities could assist to better understand the determinants of home-range behaviour of invasive feral cats on Auckland Island and similar islands (Recio & Seddon 2013).

Most tracked cats were caught close to the eastern coast, despite significant trapping effort in alpine tussock areas during summer 2018/19 where evidence of cats (fresh scats) was found. Cats might select coastal regions where resources are more reliable year-round, particularly around the eastern shores, where terrestrial birds, such as native bellbirds (*Anthornis melanura*), silvereyes (*Zosterops lateralis*) and tomtits (*Petroica macrocephala*), and exotic dunnocks (*Prunella modularis*) and blackbirds (*Turdus merula*), are found in the scrub and forest habitats. Shrubby areas also provide refuge and, together with rocky areas, are the most selected areas for feral cats' den sites on mainland New Zealand (Norbury et al. 1998). Relative bird abundance and diversity in alpine tussock is significantly lower, with only Auckland Island pipit (*Anthus novaeseelandiae aucklandicus*) and silvereyes recorded in this environment (RLS, unpubl. data). During October to April, burrowing seabirds concentrate in coastal areas that are less accessible to pigs (RLS, pers. obs). Adult seabirds landing on the surface are vulnerable to predation by cats, and numerous carcasses consistent with cat predation were found, suggesting seabirds are an important seasonal food source. For instance, a cat was observed feeding for several days on a fully grown white-capped albatross (*Thalassarche cauta steadi*) fledgling (c. 4 kg) in the South West Cape colony of the island during August 2019 (cold period) (Cox et al. 2019). Either preyed upon or scavenged, this observation suggests albatross may also become a resource to cats, which is also supported by reports of cats killing wandering albatross (*Diomedea exulans*) chicks on the Kerguelen Islands (Barbraud et al. 2021).

Alpine tussocks were most used in the cold season, which could explain the unsuccessful efforts to capture cats in this habitat during the warm season. Likely, cats selected alpine tussock habitat to traverse the tops to access cliffy areas, and to prey on mice. During the study period, mice population densities were elevated in all habitats, but particularly during the warm season in response to a large tussock mast seeding event (usually occurring every 5–10 years) (Sagar et al. 2022). Mice abundance was lower in all habitats during the cold period than during the preceding warm period, but mice were significantly more catchable and active (day and night), a likely legacy of the mast event (Sagar et al. 2022). Shrublands and forests were less used in the cold season, which might be due

to a reduction of bird activity and abundance in these habitats and the search for sites providing easier mouse hunting in the more open alpine tussocks. However, this increased use of alpine tussocks could be an exception caused by the large mast event and thus, shrublands, high tussocks and to a lesser extent forest, might be the most sheltered and common habitats for cats during winter outside of tussock mast events.

In terms of topography, cats tended to either select areas of flatter or steep areas near cliffs. Cliffs are relatively common in the central regions and the west coast of the island and might be associated with a surplus of food due to the likely presence of crevice or burrow-nesting seabirds like prions (*Pachyptila* spp.), species of storm petrels (family Oceanitidae), and other birds nesting in steep rocky areas predominately during the warm period. Cats may reach the most accessible nests or prey upon adults or fledglings on the ground outside of nests. Further research is required to confirm this point, as little information is available on the use of these habitats by birds in the Auckland Islands (Miskelly et al. 2020). Cats also selected low or high values of aspect depicting the less shady northern oriented slopes, where temperatures can be more bearable within the already cold and wet conditions of the island. The identified proximity to the coast suggests the sea can provide other food resources to cats such as stranded carcasses of marine mammals, shellfish in the tidal zone and other animals brought by the sea (e.g. squat lobsters *Munida gregaria*; PJ pers. obs.). Thus, the sea could become a source of extra food during periods of scarcity, particularly in the cold season (Cox et al. 2019).

Effective eradication strategies need to be site and population specific, and multiple methods or strategies may be required (Strang 2018). Ensuring at least one tool can target every individual is imperative. There must also be confidence in detecting remaining individuals to continue efforts or to call the programme successful with confidence. The use of aerial and ground-broadcast cat-specific vertebrate toxic agent (cat VTA) is planned on Auckland Island. Our results indicate that increasing the use of cat VTA baits around the coastline (relative to inland), including the western cliffs, is likely to maximise the likelihood of cats encountering and consuming baits year-round. Detection tools should account for all cats and habitats, and the spacing of these tools must consider our results on home range and the selected landscape resources to increase the probability of encounters with roaming cats (see Glen et al. 2022). The inaccessibility of cliffs to people must be considered to allow the deployment of baits and detection tools in this environment. Thus, the strategic use of 'food dumps' (large piles of attractive food sources such as sheep carcasses) could be used to concentrate cat presence in a certain area or draw animals out of difficult-to-access areas. Aggregated food increases tolerance and gregarious behaviour (Sunquist & Sunquist 2002) and this method could be particularly effective when natural food sources are limited. The application of eradication methods would need to be continually monitored and adjusted in response to information about the target species, especially as cat movements are likely to change with variation in population densities following the initial knockdown (Morales et al. 2010). Once the eradication attempt begins, intense pressure must be kept on the cat population to ensure it declines to zero rapidly.

National and international agendas to eradicate pest species from islands require ambitious planning that accounts for the target introduced species and their native preys' spatial ecology, demography, genetics, and optimal selective killing

methods. Connected scientific conclusions can inform decision-makers about suitable strategies to eradicate pest species and restore invaded ecosystems worldwide. Restoration projects worldwide regularly need to attempt control and eradication of invasive species as part of their objectives. Besides an initial step towards a better understanding of invasive feral cats' spatial ecology in the remote subantarctic environment of Auckland Island, our research provides a valuable study of initiatives, objectives and methods applicable to eradication projects elsewhere.

## Author contributions

## Acknowledgements

## References

Baldwin R 2009. Use of maximum entropy modeling in wildlife research. Entropy 11: 854–866.

Barbraud C, des Monstiers B, Chaigne A, Marteau C, Weimerskirch H, Delord K 2021. Predation by feral cats threatens great albatrosses. Biological Invasions 23: 2389–2405.

Bates D, Mächler M, Bolker B, Walker S 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67: 1–48.

Blackburn TM 2004. Avian extinction and mammalian introductions on oceanic islands. Science 305: 1955–1958.

Boyce MS, McDonald LL 1999. Relating populations to habitats using resource selection functions. Trends in Ecology & Evolution 14: 268–272.

Boyce MS, Vernier PR, Nielsen SE, Schmiegelow FKA 2002. Evaluating resource selection functions. Ecological Modelling 157: 281–300.

Clout MN, Russell JC 2006. The eradication of mammals from New Zealand islands. In: Koike F, Clout MN, Kawamichi M, De Poorter M, Iwatsuki K eds. Assessment and control of biological invasion risks. Gland, Switzerland, IUCN and Kyoto, Japan, Shoukadoh Book Sellers. Pp. 127–141.

Cochran WW 1969. Wildlife telemetry. In: Giles RH ed.

Wildlife management techniques. 3rd edn. Washington DC, The Wildlife Society. Pp. 507–520.

Courchamp F, Chapuis J-L, Pascal M 2003. Mammal invaders on islands: impact, control and control impact. Biological Reviews 78: 347–383.

Cox F, Jacques P, Kirby-Crowe M, Ware J 2019. Maukahuka Pest-free Auckland Island - 2019 winter trials operational report. Unpublished internal report. Wellington, Department of Conservation.

Cruz J, Woolmore C, Latham MC, Latham ADM, Pech RP, Anderson DP 2014. Seasonal and individual variation in selection by feral cats for areas with widespread primary prey and localised alternative prey. Wildlife Research 41: 650–661.

DeCesare NJ, Hebblewhite M, Schmiegelow F, Hervieux D, McDermid GJ, Neufeld L, Bradley M, Whittington J, Smith KG, Morgantini LE, Wheatley M, Musiani M 2012. Transcending scale dependence in identifying habitat with resource selection functions. Ecological Applications 22: 1068–1083.

Department of Conservation 2020. Towards a Predator Free New Zealand - Predator Free 2050 Strategy. Wellington, Department of Conservation. 43 p.

Derham T, Duncan RP, Johnson CN, Jones ME 2018. Hope and caution: rewilding to mitigate the impacts of biological invasions. Philosophical Transactions of the Royal Society B: Biological Sciences 373: 20180127.

Dowding JE 1998. A radio-tracking study of feral cats on Motuihe Island. Wellington, Department of Conservation.

Fernández N, Navarro LM, Pereira HM 2017. Rewilding: a call for boosting ecological complexity in conservation: a call for rewilding in conservation. Conservation Letters 10: 276–278.

Fisher P, Algar D, Murphy E, Johnston M, Eason C 2015. How does cat behaviour influence the development and implementation of monitoring techniques and lethal control methods for feral cats? Applied Animal Behaviour Science 173: 88–96.

Gillies C, Fitzgerald BM 2005. Feral cat. In: King CM ed. The handbook of New Zealand mammals. 2nd edn. Victoria, Australia, Oxford University Press. Pp. 308–326.

Gillies CS, Hebblewhite M, Nielsen SE, Krawchuk MA, Aldridge CL, Frair JL, Saher DJ, Stevens CE, Jerde CL 2006. Application of random effects to the study of resource selection by animals: random effects in resource selection. Journal of Animal Ecology 75: 887–898.

Glen AS, Sagar RL, Brav-Cubitt T, Jacques PM 2022. Monitoring and detection of feral cats on Auckland Island. New Zealand Journal of Ecology 46: 3494.

Grueber CE, Nakagawa S, Laws RJ, Jamieson IG 2011. Multimodel inference in ecology and evolution: challenges and solutions: multimodel inference. Journal of Evolutionary Biology 24: 699–711.

Gurarie E, Andrews RD, Laidre KL 2009. A novel method for identifying behavioural changes in animal movement data. Ecology Letters 12: 395–408.

Harper GA 2007. Habitat selection of feral cats (*Felis catus*) on a temperate, forested island. Austral Ecology 32: 305–314.

Harper GA 2010. Diet of feral cats on subantarctic Auckland Island. New Zealand Journal of Ecology 34: 259–261.

Hijmans RJ, van Etten J 2012. raster: Geographic analysis and modeling with raster data. http://CRAN.R-project.org/package=raster

Holmes ND, Spatz DR, Oppel S, Tershy B, Croll DA, Keitt

B, Genovesi P, Burfield IJ, Will DJ, Bond AL, Wegmann A, Aguiree-Muñoz A, Raine AF, Knapp CR, Hung CH, Wingate D, Hagen E, Méndez-Sánchez F, Rocamora G, Yuan HW, Fric J, Millett J, Russell JC, Liske-Clark J, Vidal E, Jourdan H, Campbell K, Springer K, Swinnerton K, Gibbons-Decherong L, Langrand O, de Brooke ML, McMinn M, Bunbury N, Oliveira N, Sposimo P, Geraldes P, McClelland P, Hodum P, Ryan PG, Borroto-Páez R, Pierce R, Griffiths R, Fisher RN, Wanless R, Pasachnik SA, Cranwell S, Micol T, Butchart SHM 2019. Globally important islands where eradicating invasive mammals will benefit highly threatened vertebrates. PLoS One 14: e0212128.

Horn S, Greene T, Elliott G 2019. Eradication of mice from Antipodes Island, New Zealand. In: Veitch CR, Clout MN, Martin AR, Russell JC, West CJ eds. Island invasives: scaling up to meet the challenge. Proceedings of the International Conference on Island Invasives 2017. Occasional Paper of the IUCN Species Survival Commission 62. Gland, Switzerland, IUCN. Pp. 131–137.

Horne JS, Garton EO, Krone SM, Lewis JS 2007. Analyzing animal movements using brownian bridges. Ecology 88: 2354–2363.

Hosmer DW, Lemeshow S 2000. Applied logistic regression. New York, Wiley.

Johnson DH 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61: 65–71.

Kernohan BJ, Gitzen RA, Millspaugh JJ 2001. Analysis of animal space use and movements. In: Millspaugh JJ, Marzluff JM eds. Radio tracking and animal populations. San Diego, Academic Press. Pp. 125–166.

Kranstauber B, Kays R, LaPoint SD, Wikelski M, Safi K 2012. A dynamic Brownian bridge movement model to estimate utilization distributions for heterogeneous animal movement: the dynamic Brownian bridge movement model. Journal of Animal Ecology 81: 738–746.

Liberg O, Sandell M, Pontier D, Natoli E 2000. Density, spatial organisation and reproductive tactics in the domestic cat and other felids. In: Turner DC, Bateson P eds. The domestic cat: the biology of its behaviour. Cambridge, Cambridge University Press. Pp. 119–147.

Lisle JF 1965. The climate of the Auckland Islands, Campbell Island and Macquarie Island. New Zealand Journal of Ecology 12: 37–44.

Lowe S, Browne M, Boudjelas S, De Poorter M 2004. 100 of the world's worst invasive alien species. A selection from the global invasive species database. The Invasive Species Specialist Group, IUCN.

Lyons AJ, Turner WC, Getz WM 2013. Home range plus: a space-time characterization of movement over real landscapes. Movement Ecology 1: 2.

Manly BFJ, McDonald LL, McDonald TL, Erickson WP 2004. Resource selection by animals. Statistical design and analysis for field studies. 2nd ed. Dordrecht, The Netherlands, Kluwer Academic Publishers.

McClelland P 2011. Campbell Island–pushing the boundaries of rat eradications. In: Veitch CR, Clout MN, Towns DR eds. Island invasives: eradication and management. Proceedings of the International Conference on Island Invasives. Occasional Paper of the IUCN Species Survival Commission 42. Gland, Switzerland, IUCN; and Auckland, New Zealand, Centre for Biodiversity and Biosecurity. Pp. 204–207.

McGlone MS 2006. Becoming New Zealanders: immigration and the formation of the biota. In: Allen RB, Lee WG eds. Biological invasions in New Zealand. Berlin Heidelberg, Springer-Verlag. Pp. 17–32.

Medina FM, Bonnaud E, Vidal E, Tershy BR, Zavaleta ES, Josh Donlan C, Keitt BS, Corre M, Horwath SV, Nogales M 2011. A global review of the impacts of invasive cats on island endangered vertebrates. Global Change Biology 17: 3503–3510.

Miskelly CM, Elliott GP, Parker GC, Rexer-Huber K, Russ RB, Taylor RH, Tennyson AJD, Walker KJ 2020. Birds of the Auckland Islands. Notornis 67: 59–151.

Morales JM, Moorcroft PR, Matthiopoulos J, Frair JL, Kie JG, Powell RA, Merrill EH, Haydon DT 2010. Building the bridge between animal movement and population dynamics. Philosophical Transactions of the Royal Society of London B: Biological Sciences 365: 2289–2301.

Navarro LM, Pereira HM 2015. Rewilding abandoned landscapes in Europe. In: Pereira HM, Navarro LM eds. Rewilding European landscapes. Cham Heidelberg New York, Springer Open. Pp. 3–23.

Nielsen SE, Cranston J, Stenhouse GB 2009. Identification of priority areas for grizzly bear conservation and recovery in Alberta, Canada. Journal of Conservation Planning 5: 38–60.

Norbury GL, Norbury DC, Heyward RP 1998. Space use and denning behaviour of wild ferrets (*Mustela furo*) and cats (*Felis catus*). New Zealand Journal of Ecology 22: 149–159.

Parkes J, Murphy E 2003. Management of introduced mammals in New Zealand. New Zealand Journal of Zoology 30: 335–359.

Pebesma E 2018. Simple features for R: standardized support for spatial vector data. The R Journal 10: 439–446.

Powell RA, Mitchell MS 2012. What is a home range? Journal of Mammology 93: 948–958.

R Core Team 2020. R: a language and environment for statistical computing. Vienna, Austria, R Foundation for Statistical Computing. http://www.R-project.org/

Recio MR, Seddon PJ 2013. Understanding determinants of home range behaviour of feral cats as introduced apex predators in insular ecosystems: a spatial approach. Behavioural Ecology and Sociobiology 67: 1971–1981.

Recio MR, Mathieu R, Maloney R, Seddon PJ 2010. First results of feral cats (*Felis catus*) monitored with GPS collars in New Zealand. New Zealand Journal of Ecology 34: 288– 296.

Recio MR, Mathieu R, Denys P, Sirguey P, Seddon PJ 2011. Lightweight GPS-tags, one giant leap for wildlife tracking? An assessment approach. PLoS ONE 6: e28225.

Recio MR, Mathieu R, Virgós E, Seddon PJ 2014. Quantifying fine-scale resource selection by introduced feral cats to complement management decision-making in ecologically sensitive areas. Biological Invasions 16: 1915–1927.

Recio MR, Maloney RF, Mathieu R, Virgós E, Moore AB, Seddon PJ 2017. Optimizing control programmes by integrating data from fine-scale space use by introduced predators. Biological Invasions 19: 209–221.

Recio MR, Seddon PJ, Moore AB 2015. Niche and movement models identify corridors of introduced feral cats infringing ecologically sensitive areas in New Zealand. Biological Conservation 192: 48–56.

Russell JC, Innes JG, Brown PH, Byrom AE 2015. Predator-Free New Zealand: conservation country. BioScience 65: 520–525.

Russell J, Horn S, Miskelly C, Sagar R, Taylor R 2020. Introduced land mammals and their impacts on the birds of the subantarctic Auckland Islands. Notornis 67: 247–268.

Sagar RL, Cox FS, Horn SR, Russell JC 2022. Population trends of house mice during tussock mast seeding on subantarctic Auckland Island. New Zealand Journal of Ecology 46: 3497.

Say L, Pontier D 2004. Spacing pattern in a social group of stray cats: effects on male reproductive success. Animal Behaviour 68: 175–180.

Signer J, Fieberg J, Avgar T 2019. Animal movement tools (amt): R package for managing tracking data and conducting habitat selection analyses. Ecology and Evolution 9: 880–890.

Strang KE 2018. The ecology of feral cats (*Felis catus*) on a New Zealand offshore island: considerations for management. Unpublished PhD thesis, Massey University, New Zealand.

Sunquist M, Sunquist F 2002. Wild cats of the world. Chicago, University of Chicago Press.

Torr N 2002. Eradication of rabbits and mice from subantarctic Enderby and Rose Islands. In: Veitch CR, Clout MN eds. Turning the tide: the eradication of invasive species. Proceedings of the international conference on eradication of island invasives. Occasional Paper of the IUCN Species Survival Commission 28. Gland, Switzerland, IUCN. Pp. 319–328.

Worton BJ 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70: 164–168.

Zuur AF, Ieno EN, Elphick CS 2010. A protocol for data exploration to avoid common statistical problems: data exploration. Methods in Ecology and Evolution 1: 3–14.